UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
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XILOFLORAS PERMIANAS DAS MARGENS NORDESTE E LESTE DA BACIA DO PARNAÍBA: TAXONOMIA, PALEOAMBIENTES E PALEOFITOGEOGRAFIA

Domingas Maria da Conceição

ORIENTADOR: Prof. Dr. Roberto Iannuzzi

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Domingas Maria da conceição

BANCA EXAMINADORA
Dra. Francine Kurzawe
Prof. Dra. Daiana Rockenbach Boardman— Universidade Federal do Rio Grande do Sul
Prof. Dra. Tânia Linder Dutra — Universidade do Vale do Rio dos Sinos, São Leopoldo, Rio Grande do Sul

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Universidade Federal do Rio Grande do Sul - Campus do Vale Av. Bento Gonçalves, 9500 - Porto Alegre - RS - Brasil
CEP: 91501-970 / Caixa Postal: 15001.
Fone: +55 51 3308-6329 Fax: +55 51 3308-6337
E-mail: bibgeo@ufrgs.br

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RESUMO

Nos últimos anos, muitas prospecções paleontológicas nos depósitos da Formação Pedra de Fogo têm sido realizadas, as quais têm revelado muitos afloramentos paleobotânicos inéditos para o Permiano da Bacia do Parnaíba. Esses afloramentos contêm muitos espécimes gimnospérmicos autóctones, parautóctones e alóctones. Assim, a presente tese teve como objetivo principal fazer as classificações taxonômicas dos lenhos encontrados nesses trabalhos. Os caules foram coletados em duas regiões distintas da bacia e distantes 400 km entre si (Nova Iorque e Duque Bacelar, Maranhão) em afloramentos estratigraficamente correlacionáveis. O nível excelente de preservação anatômica do material, bem como a variabilidade na composição da medula, permitiram identificar cinco novos gêneros e seis novas espécies para os depósitos da unidade Pedra de Fogo. Três desses gêneros e, consequentemente, três espécies são endêmicas (*Yvyrapitys novaiorquensis*, *Novaiorquepitys maranhensis* e *Ductolobatopitys mussae*); um quarto gênero (*Kaokoxylon Kräusel*, 1956), previamente registrado em várias áreas do Gondwana, incluindo a Bacia do Parnaíba, é registrado pela primeira vez na unidade Pedra de Fogo, com a nova espécie *Kaokoxylon brasiliensis*; e um quinto gênero (*Cordaixylon* Grand'Eury, 1877), o qual é reportado pela primeira vez na América do Sul, com dois morfotipos, *Cordaixylon* sp. 1 e *Cordaixylon* sp. 2). A presença de caules autóctones nos afloramentos foi crucial para a formulação de interpretações paleoambientais a partir dos dados estratigráficos e consequentemente, faciológicos, sugerindo que essas plantas viviam às margens de sistemas lacustres amplos, influenciados por sistemas fluviais efêmeros, sob um regime de sazonalidade regional. Tais plantas, por viverem em áreas úmidas adjacentes a esses lagos, foram parcialmente protegidas contra os efeitos dos períodos de seca e variações do nível de base local. Essa interpretação é suportada pela presença de certas características anatômicas na medula e no xilema secundário, bem como pela presença de outras plantas típicas de terrenos úmidos, identificadas nos mesmos afloramentos. Por fim, os dados taxonômicos deste estudo, que incluem três gêneros endêmicos, reforçam a hipótese de que a flora dessa bacia pode ser entendida como uma nova unidade paleofitogeográfica, conforme sugerido por Neregato e colaboradores. Além disso, a presença de um gênero típico do Hemisfério Norte em ambas as áreas estudadas nesta bacia, e representadas por um número significativo de espécimes, levanta outras questões sobre a verdadeira composição florística da Bacia do Parnaíba. O exame desse material pode, em um futuro próximo, revelar a presença de um número muito maior de táxons para os depósitos do Permiano desta bacia e, consequentemente, possibilitará construir um panorama paleofitogeográfico, a partir de mais dados taxonômicos.

PALAVRAS-CHAVE: lenhos petrificados, gimnospermas, taxonomia, ambiente lacustre, Bacia do Parnaíba, Formação Pedra de Fogo; Cisuraliano.

ABSTRACT

Several recent paleontological explorations of the deposits of the Pedra de Fogo Formation have revealed some new paleobotanical outcrops for the Permian of the Parnaíba Basin. These outcrops contain several autochthonous, parautochthonous and allochthonous petrified gymnosperm specimens. The main objective of this thesis was to taxonomically classify the stems found in these expeditions. The stems were collected in two different regions of the basin, 400 km apart (Nova Iorque and Duque Bacelar, Maranhão state), in stratigraphically correlated outcrops. The exceptional level of anatomical preservation of the material, as well as the variability in the composition of the pith allowed the identification of five new genera and six new species for the deposits of the Pedra de Fogo unit. Three of these genera and consequently three species are endemic (*Yvyrapitys novaiorquensis*, *Novaiorquepitys maranhensis* and *Ductolobatopitys mussae*); a fourth genus (*Kaokoxylon* Kräusel, 1956), previously recorded in several areas of Gondwana, including the Parnaíba Basin, is recorded for the first time in the Pedra de Fogo unit, with the new species *Kaokoxylon brasiliensis*; and a fifth genus (*Cordaixylon* Grand'Eury, 1877) is recorded for the first time in South America, with two morphotypes, *Cordaixylon* sp. 1 and *Cordaixylon* sp. 2. The presence of autochthonous stems in the outcrops was crucial for the formulation of paleoenvironmental interpretations from the stratigraphic and consequent faciological interpretations, which suggest that these plants lived on the shores of wide lake systems influenced by ephemeral river systems, under a regional semi-arid seasonality regime. These plants, because they lived in wetlands adjacent to these lakes, were partly protected against the effects of dry periods at the local base level. This interpretation is supported by the presence of certain anatomical features in the pith and in the secondary xylem, as well as the presence of other typical wetland plants in the same outcrops. Finally, the taxonomic data from this study, which include three endemic genera, reinforce the hypothesis that the flora of this basin can be understood as a new paleophytogeographic unit, as suggested by Neregato and collaborators. In addition, the presence of a typical Northern Hemisphere genus in both areas studied in this basin, and represented by a significant number of specimens, raises further questions regarding the true floral composition of the Parnaíba Basin. Examination of this abundant material may in the near future reveal the presence of a much larger number of taxa from the Permian deposits of this basin, and consequently, it will make it possible to construct a paleofitogeographic panorama, based on more taxonomic data.

KEYWORDS: petrified woods, gymnosperms, taxonomy, lacustrine environment, Parnaíba Basin, Pedra de Fogo Formation, Cisuralian.

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SOBRE A ESTRUTURA DESTA TESE:

A estruturação da presente tese foi desenvolvida com vistas a atender a regulamentação da Norma 118 do Programa de Pós-graduação em Geociências da Universidade Federal do Rio Grande do Sul (PPGGeo-UFRGS). Deste modo, a mesma foi elaborada em formato de artigos científicos submetidos em periódicos com corpo editorial permanente e revisores independentes, logo o corpo principal está composto por três artigos e encontra-se organizada nas seguintes partes principais:

a) **Parte I**: breve introdução sobre o tema da tese e os caminhos que possibilitaram alcançar o objeto de estudo. Aborda ainda, o estado da arte referente ao escopo principal da tese (*e.g.*, taxonomia de lenhos do Gondwana, aspectos geológicos e paleobotânicos da área de estudo e paleofitogeografia). Além disso, as informações referentes aos materiais e métodos estão sumarizadas nessa seção.

b) **Parte II**: essa parte compreende os resultados que compõem o corpo principal da tese, os quais se encontram detalhados em torno de três artigos, publicados, aceitos ou submetidos em periódicos internacionais da área de Geociências.

c) **Parte III**: compreende os anexos, a saber: resumos em anais de eventos na área de Paleobotânica, e certificados de trabalhos premiados em eventos científicos durante o desenvolvimento da tese; assim como documentos referentes à submissão dos artigos.

PARTE I

1. INTRODUÇÃO

O presente trabalho trata-se de uma contribuição à caracterização taxonômica da paleoxiloflora de gimnospermas petrificadas encontradas em afloramentos permianos assinalados à base da Formação Pedra de Fogo, Bacia do Parnaíba, e localizados em municípios do estado do Maranhão, Nordeste do Brasil.

Nos depósitos permianos da Bacia do Parnaíba há um dos mais significativos registros de florestas petrificadas do Paleozoico Superior no mundo, que está formado por associações xilofossilíferas permineralizadas de uma preservação excepcional, o que permite estudá-las sob aspectos anatômicos, morfológicos, ontogenéticos e tafonômicos (Dias-Brito *et al*., 2007). Até o momento, os afloramentos mais importantes estão localizados na porção sudoeste da bacia, norte do estado do Tocantins, e compõem a Floresta Petrificada do Tocantins Setentrional (FPTS). Por constituírem o mais completo registro de uma flora tropical-subtropical paleozoica do Hemisfério Sul, e por questões ligadas ao tráfico de fósseis, a área da FPTS foi transformada em unidade de Conservação de Proteção Integral: “Monumento Natural das Árvores Fossilizadas do Tocantins” — MNAFTO (Dias-Brito *et al*., 2007; figura 1). Nessa região, estão concentrados quase todos os estudos de cunho taxonômico dos caules permineralizados, tanto gimnospérmicos quanto de pteridófitas dessa bacia (‘veja’ seção 2).

Por outro lado, na margem nordeste e leste da bacia, as investigações a respeito das paleoxilofloras são incipientes. No entanto, nos últimos oito anos, muitos trabalhos de prospecções paleontológicas em áreas que afloram na Formação Pedra de Fogo têm sido desenvolvidos. As supracitadas prospecções foram feitas a partir de projetos financiados tanto por instituições internacionais (*i.e*. *Negaunee Foundation*), através do Dr. Ken Angielczyk (Museu de História Natural, Chicago), quanto instituições brasileiras (*e.g*. Conselho Nacional de Desenvolvimento Científico e Tecnológico-CNPq 401848.2010–8 456608/2014–1, PQ312747/2017–9), liderados por pesquisadores brasileiros *i.e*., Dr. Juan Carlos Cisneros e Dr. Roberto Iannuzzi (Universidade Federal do Piauí-UFPI e Universidade Federal do Rio Grande do Sul-UFRGS, respectivamente). Esses trabalhos possibilitaram georreferenciar cerca de oito afloramentos inéditos para os depósitos da Formação Pedra de Fogo (Cisuraliano), margem leste, nordeste e sudeste da bacia, os quais contêm uma quantidade significativa de lenhos gimnospérmicos, incluindo troncos em posição de vida. Tais trabalhos de prospecções e georreferenciamentos constituíram objeto de pesquisa da dissertação da autora da presente tese (‘veja’ Conceição *et al*., 2016 a, b).

Os trabalhos assinalados acima permitiram catalogar cerca de 200 caules gimnospérmicos petrificados, tanto autóctones a parautóctones, quanto alóctones. Além disso, registraram-se ainda espécimes de pteridófitas, por exemplo, membros das ordens Marattiales e Calamitales (Conceição *et al*., 2016 a, b). A partir disso, houve a coleta de um número amostral significativo de lenhos gimnospérmicos relativamente bem preservados, os quais compuseram o objeto de estudo desta tese, cujo principal objetivo foi a preparação, descrição e classificação taxonômica desses lenhos.

É importante destacar que as descrições geológicas, correlações estratigráficas e interpretações paleoambientais dos afloramentos foram realizadas com o apoio de estratígrafos da Universidade Federal do Pará (UFPA), cujos principais resultados estão sendo publicados a parte (Andrade *et al.*, submetida) e não faze parte do escopo principal dessa tese, mas compõem uma parte importante da Geologia e encontram-se parcialmente discutidos nas três publicações principais que constituem a tese.

2. ESTADO DA ARTE

2.1. O registro paleoxilológico do Permiano gondvânico

A flora gondvânica do Permiano está representada no registro fossilífero, sobretudo, por compressões/impressões de folhas e órgãos reprodutivos de elementos da “Flora *Glossopteris*”, a qual é frequentemente associada aos climas frios a temperados (Wnuk, 1996; Willis & McElwain, 2002). Não obstante, também há com relativa abundância caules petrificados de gimnospermas, “integralmente” (medula e xilema secundário) ou parcialmente preservados (apenas xilema secundário).

Kurzawe (2012) realizou um levantamento dos gêneros de caules e raízes anatomicamente preservados existentes para o Gondwana, o qual evidenciou a presença de 68 gêneros distribuídos nos cinco continentes modernos (*i.e*., Antártica, África, América do Sul, Índia e Austrália) que outrora formaram o antigo supercontinente do hemisfério Sul. Esse levantamento foi realizado conforme a distribuição em relação aos continentes que compunham o Gondwana, considerando também a forma como foram identificados *i.e*., a partir de lenhos com medula e xilema secundário ou apenas xilema secundário.

Na presente tese, o referido levantamento foi atualizado levando-se em consideração apenas as formas gimnospérmicas, dado o escopo da mesma. Observou-se que atualmente a Província Gondvânica possui aproximadamente 72 gêneros válidos de gimnospermas. Destes, 16 gêneros referem-se a espécimes identificados apenas a partir do xilema secundário, enquanto os demais foram identificados tanto a partir do xilema secundário quanto do primário, assim como da medula.

Na América do Sul, há uma ampla literatura envolvendo os estudos taxonômicos dos lenhos fósseis (= paleoxilologia) de gimnospermas do Permiano, o que de certo modo, encontra-se em um estágio avançado quando comparada a maioria dos demais terrenos do Gondwana (*e.g.,* Antártica, África e Austrália). Porém, esses estudos estão concentrados, especialmente, em depósitos sedimentares da Bacia do Paraná (Kräusel & Dolianiti, 1958; Mussa, 1958, 1974, 1978a, 1978b, 1978c, 1980, 1982, 1986a, 1986b; Guerra Sommer, 1976; 1977; Merlotti, 1989, 1998a, 1998b, 1999, 2000, 2002, 2009 Kurzawe & Merlotti, 2009; Kurzawe *et al*., 2012). Tais trabalhos, principalmente os da renomada Paleobotânica

Diana Mussa, configuram-se como importantes e pioneiras obras, as quais aportam informações sistemáticas valiosas e, notáveis considerações para o entendimento anatômico das gimnospermas arborescentes da Bacia do Paraná.

Em outras áreas da América do Sul, nos últimos anos o número de publicações também tem crescido de forma considerável, sobretudo em afloramentos da Formação Melo, no Uruguai (*e.g*., Crisafulli, 1995; 1998 a, b; 2001; 2002; 2003; Crisafulli & Lutz, 1995; 1997; 2000). É importante destacar que muitos gêneros oriundos dessas publicações são formas já registradas anteriormente no Permiano brasileiro, especialmente, na Formação Irati, ou em outras áreas do Gondwana (‘veja’ Mussa, 1982).

Por outro lado, ainda há uma lacuna nas investigações paleobotânicas no Permiano da Bacia do Parnaíba, notadamente sobre as formas gimnospérmicas. Até o presente, existem somente 10 gêneros descritos (Caldas *et al*., 1989; Coimbra & Mussa, 1984, Mussa & Coimbra, 1987; Kurzawe *et al*., 2013a, b) que foram caracterizados a partir de espécimes “integralmente preservados” (*e.g.*, corpos secundário e primário).

2.2. O *registro paleoxilológico permiano da Bacia do Parnaíba*

O primeiro fitofóssil do Brasil que mereceu uma descrição formal foi um caule petrificado de samambaia arborescente, oriundo das proximidades de Oeiras, no sul do Piauí, o qual foi denominado como *Psaronius brasiliensis* pelo renomado paleobotânico francês Adolph Brongniart, em 1827 (Santos & Carvalho, 2009). Em 1948, Dolianiti descreveu uma nova espécie de samambaia, *Psaronius arrojadoi*, a partir de espécimes encontrados na Chapada do Jaboti, sul do Maranhão.

Após um longo intervalo sem pesquisas voltadas à paleoflora permiana da Bacia do Parnaíba, Coimbra & Mussa (1984) descreveram três novas espécies de lenhos para depósitos sedimentares da Formação Pedra de Fogo (atualmente, considerados da Formação Motuca, em Iannuzzi *et al*., 2018), sudoeste da bacia, no Maranhão, *i.e*., *Arthropitys cacundensis* (Calamitaceae), *Carolinapitys maranhensis* (Cordaitales?) e *Amyelon bieloi* (raiz de Cordaitales). Três anos mais tarde, os mesmo autores (Mussa & Coimbra, 1987) apresentaram mais dois novos gêneros para esta mesma área e unidade, *i.e*. *Cyclomedulloxylon* e *Araguainorachis*, e três novas espécies: *Cyclomedulloxylon parnaibense*, *Cycadoxylon brasiliense* e *Araguainorachis simplissima*. Por outro lado, para a margem leste, em relação às gimnospermas, há uma única contribuição taxonômica relativa ao trabalho de Caldas *et al*. (1989, tabela 1), onde estudou-se uma associação de lenhos permineralizados encontrados em posição de vida, nas camadas da Formação Pedra de Fogo, às margens do Rio Poti, em Teresina, Piauí. Todavia, apenas uma amostra foi laminada para fins de estudos anatômico-taxonômicos, a qual foi nomeada como uma nova espécie, *i.e*. *Teresinoxylon eusebioi* Mussa (Caldas *et al*., 1989).

Dando sequência às contribuições acerca do registro paleobotânico da bacia, a partir da metade da década de 80, a compreensão a respeito da paleoxiloflora permiana aprofundou-se a partir de uma série de publicações sobre os estudos taxonômicos de caules permineralizados oriundos de depósitos situados à margem sudoeste da bacia, na área que corresponde atualmente à unidade de Conservação de Proteção Integral “Monumento Natural das Árvores Fossilizadas do Tocantins” — MNAFTO. Tais contribuições foram produzidas a partir de fitofósseis coletados em estratos atribuídos possivelmente à base da Formação Motuca, nos municípios de Araguaína e Filadélfia, no norte do Tocantins, e Carolina, no sudoeste do Maranhão. Foram analisadas, sobretudo formas de pteridófitas, a saber: Herbst (1986, 1992, 1999) descreveu duas novas espécies de caules de samambaias arborescentes relacionadas às Marattiales, *i.e*. *Tietea derbyi* e *Psaronius sinuosus*; Rößler & Galtier (2002a, 2002b, 2003) descreveram três novas samambaias, *i.e*. *Dernbachia brasiliensis*, *Grammatopteris freitasii* e *Botryopteris nollii*. Quanto às gimnospermas, dez anos após essas publicações relativas às samambaias, Kurzawe *et al*. (2013 a, b) descreveram quatro espécies vinculadas a três gêneros endêmicos, todos também da área de MNAFTO, em Filadélfia, *i.e*. *Parnaiboxylon* sp., *P. rohnae*, *Scleroabietoxylon chordas* e *Ductoabietoxylon solis* (Tabela 1), e seis novas espécies vinculadas a gêneros Gondvânicos, *i.e*. *Taeniopitys tocantinensis, Taeniopitys* sp., *Kaokoxylon punctatum*, *Damudoxylon buritiranaensis*, *D. humile, D. roesslerii* (Tabela 1).

Assim, é notável o quanto limitado e espaçado são os resultados obtidos dos estudos da paleoflora dessa bacia até o presente momento. Embora se tenha avançado consideravelmente na compreensão a esse respeito, como visto pelos trabalhos supracitados, percebe-se que dada à extensão da área aflorante das unidades Pedra de Fogo e Motuca, ainda há muito a ser compreendido sobre a flora permiana da Bacia do Parnaíba, e que a taxonomia é um passo primordial para tal compreensão. O bom potencial de preservação anatômica dessas materiais muito contribuirá em um futuro próximo para o enriquecimento do panorama florístico do Paleozoico do Hemisfério Sul.

Na Tabela 1 apresentada em seguida, todos os táxons de gimnospermas permianas citados acima são listados. Além disso, são apresentados os possíveis grupos aos quais estão vinculados e as unidades estratigráficas das quais provieram assim como, as distribuições geográficas dos gêneros (Uma vez que todas as espécies são endêmicas).

Tabela 1. Taxa gimnospérmicos registrados no Permiano da Bacia do Parnaíba e suas possíveis afinidades botânicas e distribuições estratigráficas e geográficas (modificado de Iannuzzi *et al*., 2018).

Táxon	**Afinidade Botânica**	**Autores**	**Formação**	**Outros registros do Gênero**
Amyelon bieloi	Cordaitales	Coimbra & Mussa, 1984	Motuca	Inglaterra, Estados Unidos, Escócia, China
Carolinapitys maranhensis	Cordaitales?	Coimbra &Mussa, 1984	Motuca	Endêmico
Cycadoxylon brasiliense	Pteridospermales Cycadales	Mussa & Coimbra, 1987	Motuca	França e Inglaterra
Cyclomedulloxylon parnaibense	Pteridospermales?	Mussa & Coimbra, 1987	Motuca	Endêmico
Teresinoxylon eusebioi	Pteridospermales	Caldas *et al*. 1989	Pedra de Fogo	Endêmico
Parnaiboxylon sp.	Gimnosperma	Kurzawe *et al*., 2013a	Motuca	Endêmico
Parnaiboxylon rohnae	Gimnosperma	Kurzawe *et al*., 2013a	Motuca	Endêmico
Scleroabietoxylon chordas	Gimnosperma	Kurzawe et al., 2013a	Motuca	Endêmico
Ductoabietoxylon solis	Gimnosperma	Kurzawe *et al*., 2013a	Motuca	Endêmico
Taeniopitys tocantinensis	Gimnosperma	Kurzawe *et al.* 2013b	Motuca	Antárctica
Taeniopitys sp.	Gimnosperma	Kurzawe *et al*. 2013b	Motuca	Antárctica
Kaokoxylon punctatum	Gimnosperma	Kurzawe *et al*., 2013b	Motuca	Índia, Austrália, South África, Argentina, Antártica
Damudoxylon buritiranaensis	Gimnosperma	Kurzawe *et al*. 2013b	Motuca	Índia, Austrália, Sul da África
Damudoxylon humile	Gimnosperma	Kurzawe *et al*., 2013b	Motuca	
Damudoxylon roesslerii	Gimnosperma	Kurzawe *et al*., 2013b	Motuca	
Novaiorquepitys maranhensis	Gimnosperma	Conceição *et al.* (2020)	Pedra de Fogo	Endêmico
Yvyrapitys novaiorquensis	Gimnosperma	Conceição *et al.* (2020)	Pedra de Fogo	Endêmico
Ductolobatopitys mussae	Gimnosperma	Conceição *et al.* (no prelo)	Pedra de Fogo	Endêmico
Kaokoxylon brasiliensis	Gimnosperma	Conceição *et al*. (no prelo)	Pedra de Fogo	Índia, Austrália, South África, Argentina, Antártica
Cordaixylon sp. 1	Cordaitales	Conceição *et al.*	Pedra de Fogo	França, Estados

		(submetido)		Unidos, Canadá, China e Europa
Cordaixylon sp. 2	Cordaitales	Conceição *et al.* (submetido)	Pedra de Fogo	

2.3. *Paleofitogeografia: ênfase nos elementos florísticos da Bacia do Parnaíba*

Para Chaloner & Lacey (1973) e Chaloner & Meyen (1973), as floras existentes na maior parte do Período Carbonífero apresentavam uma relativa uniformidade a nível global. Porém, posteriormente, esses mesmos autores reconheceram que havia uma diferenciação bem mais pronunciada nas floras continentais ao final desse período e início do Permiano. Diante de tais diferenças, estabeleceram-se quatro grandes unidades ou províncias paleofitogeográficas para esse intervalo estratigráfico, a saber: Euramericana, Cataísica, Angárica e Gondvânica (Figura 1).

Figura 1. O supercontinente Pangeia com destaque para a distribuição das quatro províncias paleoflorísticas do final do Paleozoico. A estrela marca a posição da Bacia Sedimentar do Parnaíba, nordeste do Brasil.

A Província Gondvânica (América do Sul, África do Sul, Madagascar, Arábia, Índia, sul do Tibete, Nova Guiné, Austrália e Antártica) encontrava-se em paleolatitudes médias a altas, no Hemisfério Sul, e sob influência de climas glacial/interglacial e pós-glacial durante o intervalo do Neocarbonífero – Eopermiano. Já a Província Angárica (leste dos Urais, Sibéria, Mongólia) ocupou áreas entre paleolatitudes médias a altas, sob regimes de climas frios a temperados no Hemisfério Norte, enquanto as províncias Cataísica (China, Japão, Coreia e

Indochina) e Euramérica (América do Norte, leste e oeste da Europa) estavam posicionadas em latitudes baixas, em regiões de climas equatoriais a tropicais (síntese em Wnuk, 1996). Porém, durante o Permiano, a Província Euro-americana passou a ser caracterizada por climas tropicais sazonais, com o predomínio de componentes florísticos que comumente são associados a climas sazonalmente secos, *i.e*. elementos gimnospérmicos (Scott, 1980).

No Pennsilvaniano – Cisuraliano, a Bacia do Parnaíba posicionava-se entre às duas principais províncias florísticas, a saber: Euramericana, no norte, e Gondvânica, no sul. Tal posicionamento permite interessantes discussões a respeito de seus elementos florísticos. Por exemplo, constata-se que metade dos morfogêneros com afinidades às pteridófitas *lato sensu* do Permiano dessa bacia (*e.g*., *Psaronius*, *Grammatopteris*, *Botryopteris*, *Cyclostigma*, *Arthropitys*) são elementos que ocorrem também na Província Euramericana enquanto que a outra metade é endêmica (*e.g*., *Tocantinorachis, Buritiranopteris, Dernbachia, Araguainorachis*). Dentro desse contexto, apenas três gêneros ocorrem em todas as províncias, *i.e*. *Arthropitys*, *Psaronius* e *Botryopteris*, e somente dois gêneros são compartilhados com a Bacia do Paraná, *i.e*. *Tietea* e *Psaronius*. Por outro lado, os espécimes de gimnospermas identificados para os mesmos depósitos dentro da bacia são gêneros compartilhados com outras áreas do Gondwana (*Dammudoxylon, Taeniopitys* e *Kaokoxylon*) ou com Euramérica (*Cycadoxylon, Amyelon*), ou endêmicos dessa bacia (*Ductoabietoxylon, Scleroabietoxylon*, *Cyclomedulloxylon*, *Parnaiboxylon*, *Carolinapitys, Teresinoxylon, Novaiorquepitys* e *Yvyrapitys*) (Tabela 1).

Ainda em relação a esse aspecto da vinculação fitogeográfica dos elementos da flora permiana da bacia, o último trabalho que discute essa questão, *e.g.* Neregato *et al*. (2017), faz considerações relevantes a esse respeito. Esses autores utilizaram métodos de análises de índices de similaridades muito comuns em Ecologia e na Biogeografia (*i.e*. análises de agrupamento e Índice Jaccard). Tais análises incluíram os gêneros das floras do final do Carbonífero e início do Permiano das províncias florísticas do Hemisfério Norte, e aqueles presentes nas bacias do Parnaíba e Paraná, para o Gondwana. A partir dos resultados obtidos, suportados por padrões paleoclimáticos, posição paleogeográfica da Bacia do Parnaíba, variabilidade de grupos taxonômicos, bem como questões relativas a aspectos sedimentológicos, os referidos autores consideraram essa bacia como uma região única ocupada por uma flora com características distintas. Assim, com base nesses resultados e apoiados nos critérios estabelecidos por Wnuk (1996), os autores propuseram uma nova unidade fitogeográfica para o Paleozoico, denominada *Região do Meio Norte do Brasil*. Contudo, vale salientar que as investigações paleobotânicas dessa bacia ainda são incipientes quando comparadas a outras bacias existentes nas demais unidades fitogeográficas, em especial as do Hemisfério Norte (*i.e*. Euramérica e Cataísia), e consequentemente, na medida em que os estudos se intensificam e novos espécimes forem identificados, tais inferências estarão sujeitas a novas análises e interpretações.

3. JUSTIFICATIVAS

Com as contínuas campanhas de campo nas sequências permianas da margem leste da Bacia do Parnaíba, alguns afloramentos contendo quantidades consideráveis de caules permineralizados têm sido revelados. Contudo, apesar de apresentarem um registro frequente, eles têm recebido pouca atenção dos especialistas em Paleobotânica, notadamente os caules oriundos das plantas com sementes (*i.e.*, lenhos gimnospérmicos) e da unidade Pedra de Fogo. Na realidade, para as margens nordeste, sudeste e leste da bacia, existem poucas contribuições apresentadas no âmbito da taxonomia dos caules permineralizados, apesar da abundância de afloramentos contendo esses fósseis (Caldas *et al*., 1989; Conceição *et al*., 2016 a, b; Iannuzzi *et al*., 2018). Os dados taxonômicos atualmente disponíveis para as áreas em questão são antigos e baseiam-se quase inteiramente no registro de samambaias arborescentes (*e.g*. Dolianiti, 1954; Oliveira, 1934; Brongniart, 1872; Pelourde, 1912). Até o momento, há apenas uma espécie de pteridófita (*i.e*. *Psaronius brasiliensis*) e uma de gimnosperma pteridospérmica (*i.e. Teresinoxylon eusebioi*) identificadas por Brongniart (1827) e Caldas *et al*. (1989), respectivamente. Por outro lado, os depósitos da margem sudoeste da bacia têm recebido expressiva atenção nas últimas décadas, com a proposição de vários *taxa* (gêneros e espécies) de pteridófitas (Herbst, 1985, 1992, 1999; Rößler & Galtier, 2002a, b, 2003, Tavares *et al*., 2014; Neregato *et al*., 2015, 2017) e gimnospermas (Coimbra & Mussa, 1984; Mussa & Coimbra, 1987; Kurzawe *et al*., 2013a, b). A origem estratigráfica desses materiais da borda sudoeste tem sido matéria de debate na literatura, sendo atribuídos tanto a Formação Pedra de Fogo quanto à Motuca (Iannuzzi *et al*., 2018). Nas margens nordeste, leste e sudeste, não há dúvida de que os caules permineralizados provêm da Formação Pedra de Fogo (Caldas *et al*., 1989; Conceição *et al*., 2016 a, b; Iannuzzi *et al*., 2018; Conceição et al., 2020).

Assim, justifica-se o presente estudo dada a abundância de caules permineralizados relativamente bem preservados e a lacuna no estudo dos mesmos, comprovadamente existentes para os depósitos das margens nordeste, leste e sudeste da Bacia do Parnaíba, como exposta acima. A determinação de uma composição taxonômica mais diversa e precisa da paleoflora destas áreas, tornará possível construir um panorama florístico para os depósitos da Formação Pedra de

Fogo e, consequentemente, realizar inferências mais seguras a respeito de aspectos paleoambientais, paleoclimáticos e mesmo bioestratigráficos para essa unidade. Além disso, dados taxonômicos mais completos irão contribuir para a compreensão de como se processou a relação desses elementos com as demais províncias florísticas do Paleozoico. O relativo endemismo florístico ou cosmopolitismo dos táxons já descritos nessa bacia pode refletir condições climáticas ou paleogeográficas específicas. Logo, quanto mais dados disponíveis para análise, mais robustos e confiáveis serão os resultados sobre (i) a extensão e delimitação das províncias florísticas permianas através do paleocinturão tropical/subtropical e (ii) a caracterização da nova unidade fitogeográfica *Região do Meio Norte do Brasil*, recentemente proposta com base no registro do Permiano na bacia (Neregato *et al*., 2017).

4. OBJETIVOS

4.1. Objetivo geral

A presente tese teve como objetivo geral *a descrição taxonômica da paleoxiloflora da Formação Pedra de Fogo, a partir dos aspectos anatômicos dos lenhos gimnospérmicos coletados na margem leste e nordeste da Bacia do Parnaíba*.

4.2. Objetivos específicos

(i) Prospectar novas áreas contendo lenhos fósseis permineralizados na faixa de afloramentos da unidade Pedra de Fogo, nas margens nordeste, sudeste e leste da Bacia do Parnaíba;

(ii) Caracterizar anatomicamente e classificar taxonômicamente os espécimes inéditos de lenhos de gimnospermas, tanto os que já estavam catalogados e depositados na Coleção de Paleobotânica da UFPI, quanto os que foram encontrados nas prospecções realizadas durante o desenvolvimento do doutorado, a fim de determinar a composição das paleofloras analisadas;

(iii) Interpretar os paleoambientes de vida daquelas plantas que compõe associações autóctones (preservadas em posição de vida) a hipo-autóctones, a fim de auxiliar no entendimento da paleoecologia desses vegetais;

(iv) Formular considerações relativas às correlações bioestratigráficas da unidade analisada, a partir dos dados taxonômicos e estratigráficos obtidos;

(v) Finalmente, colaborar nas atuais discussões paleogeográficas existentes para o registro paleoflorístico desta bacia, a partir das classificações taxonômicas desse trabalho e comparações com aqueles das maiores províncias florísticas permianas (*e.g.*, Euramérica e Gondwana).

5. MATERIAIS E MÉTODOS

Os manuscritos que compõem o corpo principal desta tese possuem uma seção em que são descritos os métodos utilizados na sua elaboração, bem como dados da geologia local das áreas de estudo (perfis estratigráficos). No entanto, a metodologia relativa aos procedimentos realizados na elaboração das lâminas será mais bem detalhada abaixo, por outro lado, as descrições dos afloramentos são mais bem detalhadas nos manuscritos.

5.1. Síntese da Geologia da área de estudo

5.1.1. Bacia do Parnaíba

A Bacia do Parnaíba, situada no nordeste do Brasil, ocupava a porção centro-norte do supercontinente Gondwana, durante o Permiano, e apresenta um preenchimento, sobretudo, Paleozoico. Essa bacia compreende uma ampla região sedimentar, abrangendo uma área de 300.000 km^2 e recobrindo maior parte dos estados do Maranhão, Piauí e Tocantins, e, em menor escala, os estados do Pará e Ceará (Santos & Carvalho, 2009; Góes & Feijó, 1994 – Figura 1).

Os poucos conhecimentos litoestratigráficos, paleoambientais e paleontológicos a respeito da Bacia do Parnaíba, são oriundos de uma série de trabalhos pioneiros feitos a partir da segunda metade do século XX, pelo Conselho Nacional de Petróleo (*e.g.,* Carozzi *et al*., 1975; Mesner & Wooldridge, 1964; Caputo, 1984; Góes *et al*., 1990), das publicações no âmbito do Departamento Nacional de Produção Mineral, agora Agência Nacional de Mineração (*e.g.,* Kegel, 1951, 1953; Cruz *et al*., 1973, Lima & Leite, 1978), bem como da Petrobras (síntese em Góes & Feijó, 1994; Vaz *et al*., 2007). No entanto, as informações acerca dessa bacia ainda são reduzidas quando comparadas as de outras bacias paleozoicas. Isto se deve principalmente às poucas contribuições de trabalhos prospectivos, tanto no âmbito geológico quanto no paleontológico, devido, em parte, à ausência de reservas significativas de carvão e aparentemente de petróleo e gás, por exemplo.

Desde os trabalhos de Small (1914), o arcabouço litoestratigráfico da Bacia do Parnaíba vem sendo modificado por muitos autores, sobretudo a partir da segunda metade do século XX. As cartas mais recentes propostas foram as de Góes e Feijó (1994) e de Vaz *et al*. (2007 – Figura 2), ambas publicadas em boletins da Petrobras. Góes e Feijó (1994) subdividiram a coluna sedimentar da bacia em cinco grupos, designadas como Grupo Serra Grande (Siluriano), Grupo Canindé (Devoniano), Grupo Balsas (Carbonífero-Triássico) e Grupo Mearim (Neojurássico-Eocretáceo), além das Formações Grajaú, Codó, Itapecuru, Urucuia e Areado, unidades associadas a um único ciclo deposicional. Essas unidades seriam correlacionáveis a ciclos tectônicos de caráter global.

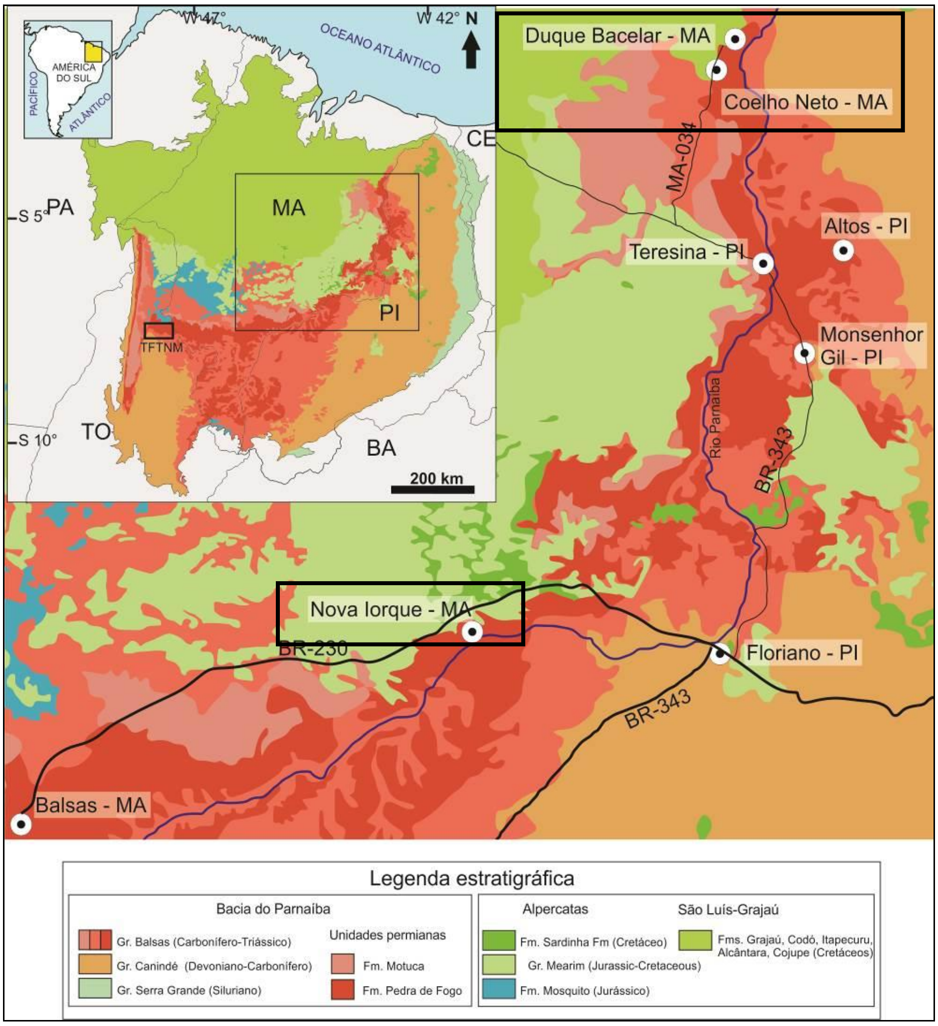

Figura 2. Distribuição das unidades litoestratigráficas da Bacia do Parnaíba, com destaque para a localização das áreas com florestas petrificadas permianas da bacia. Os retângulos indicam as áreas geográficas dos afloramentos estudados na presente tese. Modificado de Iannuzzi *et al*. (2018).

Em 1996, Góes e Coimbra subdividiram a área compreendida por essa bacia em quatro sub-bacias, com gêneses e idades distintas: Parnaíba (Siluriano-Triássico), Alpercatas (Jurássico-Eocretáceo), Grajaú (Cretáceo) e Espigão-Mestre (Cretáceo) (Figura 1). Góes & Rossetti (2001) e Silva *et al*. (2003), compartilhando da ideia de Góes & Coimbra (1996), sugeriram que o pacote sedimentar da Bacia do Parnaíba deveria ser representado apenas pelos grupos Serra Grande (Siluriano), Canindé (Devoniano) e Balsas (Carbonífero-Triássico), uma vez que esses grupos apresentaram seu desenvolvimento tectono-sedimentar associado à subsidência do substrato da bacia, enquanto que os sedimentos pós Grupo Balsas estariam associados ao processo de ruptura do Gondwana e, por isso, deveriam ser tratados e estudados à parte. Nesse contexto, os supracitados autores recomendaram ainda a denominação de Bacia São Luís-Grajaú, Bacia de Alpercatas e Bacia Espigão-Mestre, como bacias distintas aos depósitos paleozoicos da Bacia do Parnaíba, por essa razão, na presente tese a denominação de Bacia do Parnaíba refere-se apenas a Sequência Siluriano-Triássico.

O Grupo Balsas, termo utilizado por Góes & Feijó (1994), agrupa um conjunto de rochas clásticas e evaporíticas sobrepostas em discordância ao Grupo Canindé e sotoposto, também em discordância, às formações Mosquito (leste da bacia), Grajaú, Codó e Itapecuru (norte e noroeste), Urucuia (sul da bacia) e ao Grupo Mearim (na parte central).

De acordo com Góes *et al*. (1990), o Grupo Balsas marca o início da continentalização na Bacia do Parnaíba, com progressiva desertificação e deslocamento de seu depocentro para sua parte central. Conforme Barbosa *et al*. (2016), a sequência que marca o final do Carbonífero e início do Triássico começou com depósitos flúvio-eólicos, que mais tarde foram afogados por depósitos marinhos e costeiros e progressivamente substituídos por sistemas lacustres e desérticos.

O Grupo Balsas aflora principalmente nas regiões leste-nordeste da bacia. Compreende, ascendentemente, as formações Piauí, Pedra de Fogo, Motuca e Sambaíba, as quais compõem a Sequência Neocarbonífera-Eotriássica de Vaz *et al*. (2007 – Figura 2), cujas mudanças estruturais e ambientais registradas durante sua deposição são relativamente intensas e significativas (Góes & Feijó 1994). Nesse traalho será apresentada a seguir, em maiores detalhes, apenas a Formação Pedra de Fogo, uma vez que os sítios paleobotânicos de interesse direto nesse trabalho afloram nessa unidade.

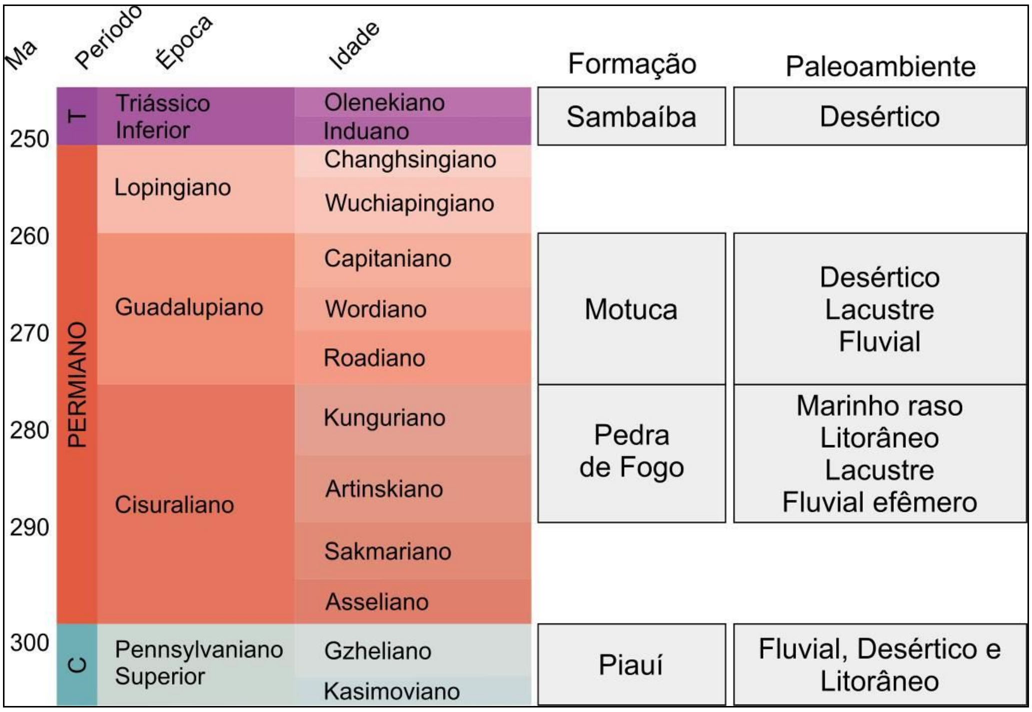

Figura 3. Parte da carta estratigráfica da Bacia do Parnaíba com destaque apenas para o Grupo Balsas que inclui as Formações Piauí, Pedra de Fogo e Motuca (Carbonífero-Permiano). Modificado: Vaz *et al*. (2007).

5.1.2. Formação Pedra de Fogo

Plummer (1948) propôs a denominação de Formação Pedra de Fogo para um conjunto de litotipos associados, sobretudo, a arenitos silicificados e expressivos níveis de sílex, calcários e com presença de fósseis vegetais do gênero *Psaronius.* Sua seção-tipo ocorre no leito do Riacho Pedra de Fogo, entre os municípios de Pastos Bons e Nova Iorque, sul do estado do Maranhão. Ainda, o autor supracitado considerou, de modo geral, esta unidade como uma das mais importantes e complexas, em termos de interpretação, quando comparada às demais unidades litológicas do norte do Brasil.

Dados bioestratigráficos indicam uma idade cisuraliana para a unidade Pedra de Fogo, a partir de correlações com depósitos do Hemisfério Norte, os quais possuem datações radiométricas (Röβler & Galtier, 2002a; b; Cisneros *et al*., 2015; Iannuzzi *et al*., 2018). Essa unidade apresenta abundante conteúdo fossilífero composto por caules petrificados de grande porte, especialmente gimnospérmicos, tanto autóctones a parautóctones quanto alóctones, e microbialitos (estromatólitos, pisoides e ooides, Caldas *et al*., 1989; Conceição *et al*., 2016a, b), além da ocorrência de uma importante fauna de vertebrados aquáticos e continentais

(Plummer, 1948; Price, 1948; Mesner & Wooldridge, 1964; Faria Júnior & Truckenbrodt, 1980; Cox & Hutchinson, 1991; Santos & Carvalho, 2009; Cisneros *et al*., 2015). Com áreas aflorantes, principalmente na borda leste da Bacia do Parnaíba, a Formação Pedra de Fogo forma uma faixa de exposições na direção Leste-Oeste com aproximadamente 600 km de extensão, sendo sucedida localmente pelas formações Motuca, também de idade permiana, e Sambaíba, de provável idade triássica (Faria Júnior, 1979, Faria Júnior; Truckenbrodt, 1980a – Figura 2).

Faria Júnior (1979) realizou um dos trabalhos estratigráficos mais completos e detalhados, até o momento, para a Formação Pedra de Fogo, no qual é inferido para a unidade cerca de 100 metros de espessura em superfície. Ele a subdividiu em três membros, da base para o topo, a saber: (i) Sílex Basal: bem distribuído na bacia, apresenta siltitos e folhelhos intercalados por bancos dolomíticos e concreções silicosas; (ii) Médio: consiste de arenitos e siltitos, às vezes carbonáticos, folhelhos com níveis de sílex, esteiras algálicas em bancos carbonáticos com gretas de contração, aflora sobretudo na parte central da bacia; (iii) Superior ou “Trisidela”: presente nas regiões leste e oeste da bacia e apresenta a parte inferior marcada por intercalações laminares de folhelhos, níveis de sílex e, por vezes, brechas intraformacionais, adicionalmente mostra bancos dolomíticos, intercalados por siltitos e folhelhos carbonáticos para o topo.

O ambiente deposicional da Formação Pedra de Fogo tem sido historicamente descrito como tendo uma influência marinha, variando de flúvio-deltaico a marinho raso (Aguiar 1964; Moore, 1964; Lima & Leite, 1978; Faria Júnior, 1979; Faria Júnior & Truckenbrodt 1980a, 1980b; Coimbra & Mussa, 1984; Caldas *et al*., 1989; Dino *et al*., 2002), com planícies de sabkha sob influências ocasionais de tempestades (Góes & Feijó, 1994). Recentemente, estudos bio- e litoestratigráficos sugeriram ambientes continentais restritivos (flúvio-lacustres), caracterizados por inundações episódicas resultantes de sazonalidades climáticas (Andrade *et al*., 2014; Araújo *et al*,. 2016; Abrantes Júnior *et al*., 2019). Adicionalmente, em recentes trabalhos nas margens nordeste e leste da Bacia do Parnaíba, utilizando-se tanto fósseis de vertebrados aquáticos (Cisneros *et al*., 2015) quanto análises faciológicas associadas a ocorrências fitofossilíferas autóctones a parautóctones (Conceição *et al*., 2016a), interpretaram os depósitos sedimentares da unidade Pedra de Fogo como sendo também resultantes de processos deposicionais flúvio-lacustres.

5.1.3. Afloramentos estudados

Os lenhos petrificados foram recuperados em afloramentos de duas regiões distantes 400 km entre si, nos municípios de Nova Iorque e Duque Bacelar, estado do Maranhão (Figura 1). Os depósitos sedimentares em que esses lenhos afloram correspondem a sucessões sedimentares atribuídas ao Grupo Balsas, especificamente em sedimentos da Formação Pedra de Fogo, e foram posicionados na base dessa unidade, ou seja, no Membro Sílex Basal (Conceição *et al*., 2016a, Andrade *et al*. Submetido para publicação; Conceição *et al*., 2020). Esses lenhos estão aflorando em sucessões com uma predominância de sedimentação siliciclástica de granulometria fina, intercalada com finas camadas tabulares a lenticular de arenito fino a médio, com microbialitos associados, as quais estão sendo interpretadas como parte de um sistema flúvio-lacustre em regime semi-árido, que periodicamente ou ocasionalmente estava sujeito a tempestade episódica e eventos de inundações (Andrade *et al*., Publicação submetida, Figura 4).

5.1.3.1. Duque Bacelar

Os afloramentos de Duque Bacelar, denominados: “Ladeira do Olho d’Água; Morro das Pedras Brancas; Fazendinha; Olho d’Água e Morro da Pandora” situam-se nos arredores das cidades de Duque Bacelar e Coelho Neto, leste do estado do Maranhão (MA), e estão todos inseridos dentro da Área de Preservação Ambiental dos Morros Garapenses (Maranhão, 2008). O acesso aos afloramentos é feito pela rodovia MA- 034, os quais, em sua maioria apresentam difícil acesso, pois estão localizados nas áreas mais elevadas dos morros testemunhos que compõem os denominados Morros Garapenses (Conceição *et al*., 2016a, Figura 5A).

Esses afloramentos correspondem à parte basal da Formação Pedra de Fogo e sobrepõe-se discordantemente aos arenitos eólicos e fluviais da Formação Piauí (Figura 4A). Troncos silicificados de gimnospermas estão expostos ao longo de toda a sucessão dos afloramentos (Figuras 5 e 6), tanto horizontalizados e imersos nas camadas de arenitos silicificados quanto ainda em posição de vida (Figuras 6A-C), sotopostos às camadas de arenitos com laminação truncada por ondas (Figura 4A), para informações detalhadas sobre esses afloramentos, consultar Conceição *et al.* (2016a).

5.1.3.2. Nova Iorque

Os afloramentos dessa região estão localizados nas margens do reservatório de Boa Esperança, sul do estado do Maranhão (Figura 7-B). Igualmente aos afloramentos Duque Bacelar, os de Nova Iorque também estão sobrepostos de forma discordante aos arenitos da Formação Piauí, Pennsilvaniano (Faria Júnior, 1979, Andrade *et al*.; submetidos para publicação; Conceição *et al*., 2020;– Figura 4B). Os mesmos apresentam uma espessura máxima de quatro metros e se estendem lateralmente por vários quilômetros. Os lenhos ocorrem horizontalizados e imersos nas camadas de siltitos silicificados, os quais estão sendo considerados como caules *in situ*, e estão associados às camadas de sílex maciço e nodular, bem como microbialitos. Mas, há também, com relativa abundância, caules dispersos sobre a superfície, tanto caules de gimnospermas (Figura 7C-D) quanto de pteridófitas arborescentes (samambaias e esfenófitas) que ocorrem em maior frequência.

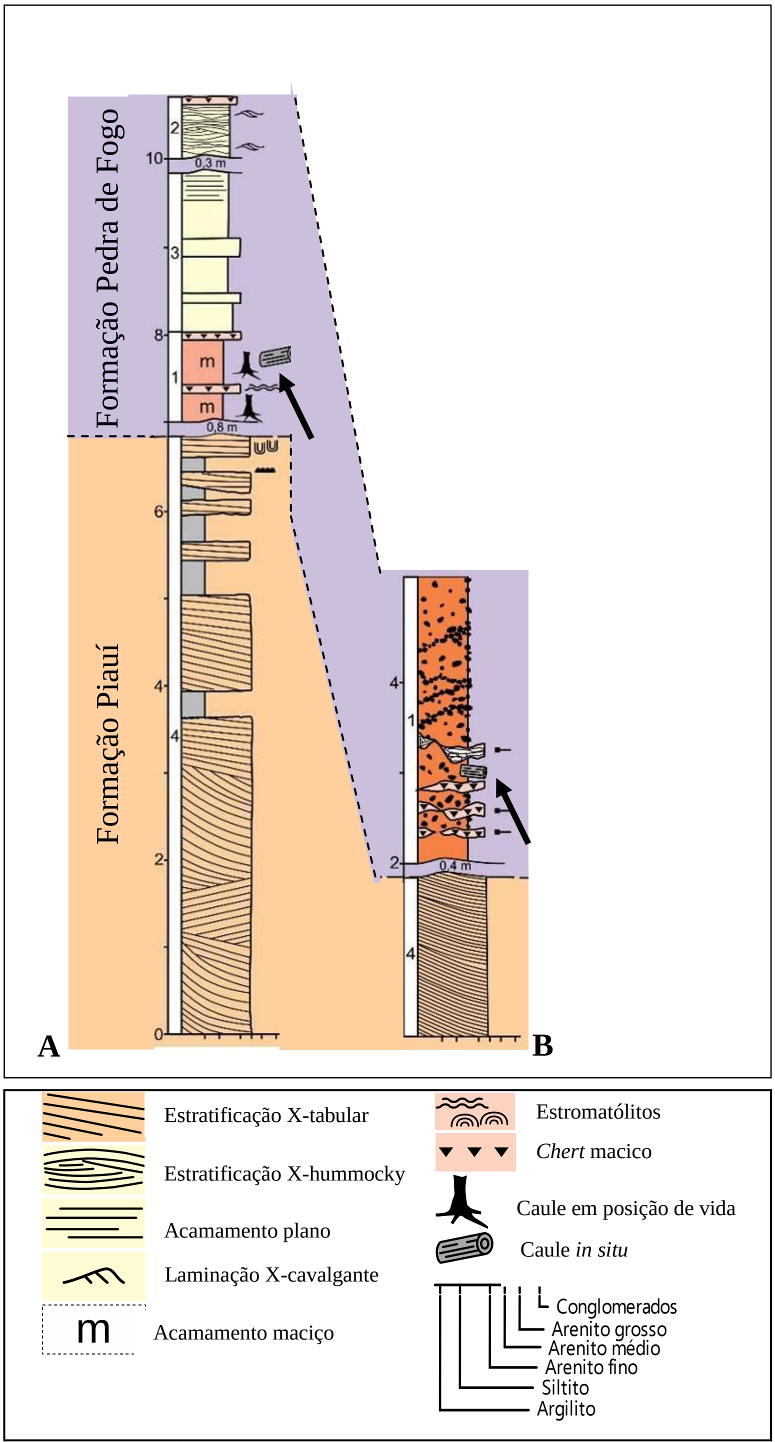

Figura 4. Perfis estratigráficos dos afloramentos paleobotânicos estudados. Duque Bacelar (A) e Nova Iorque (B), as setas indicam os níveis de ocorrência dos caules. Modificado de Conceição *et al*., 2016a; Conceição *et al*. (2020)

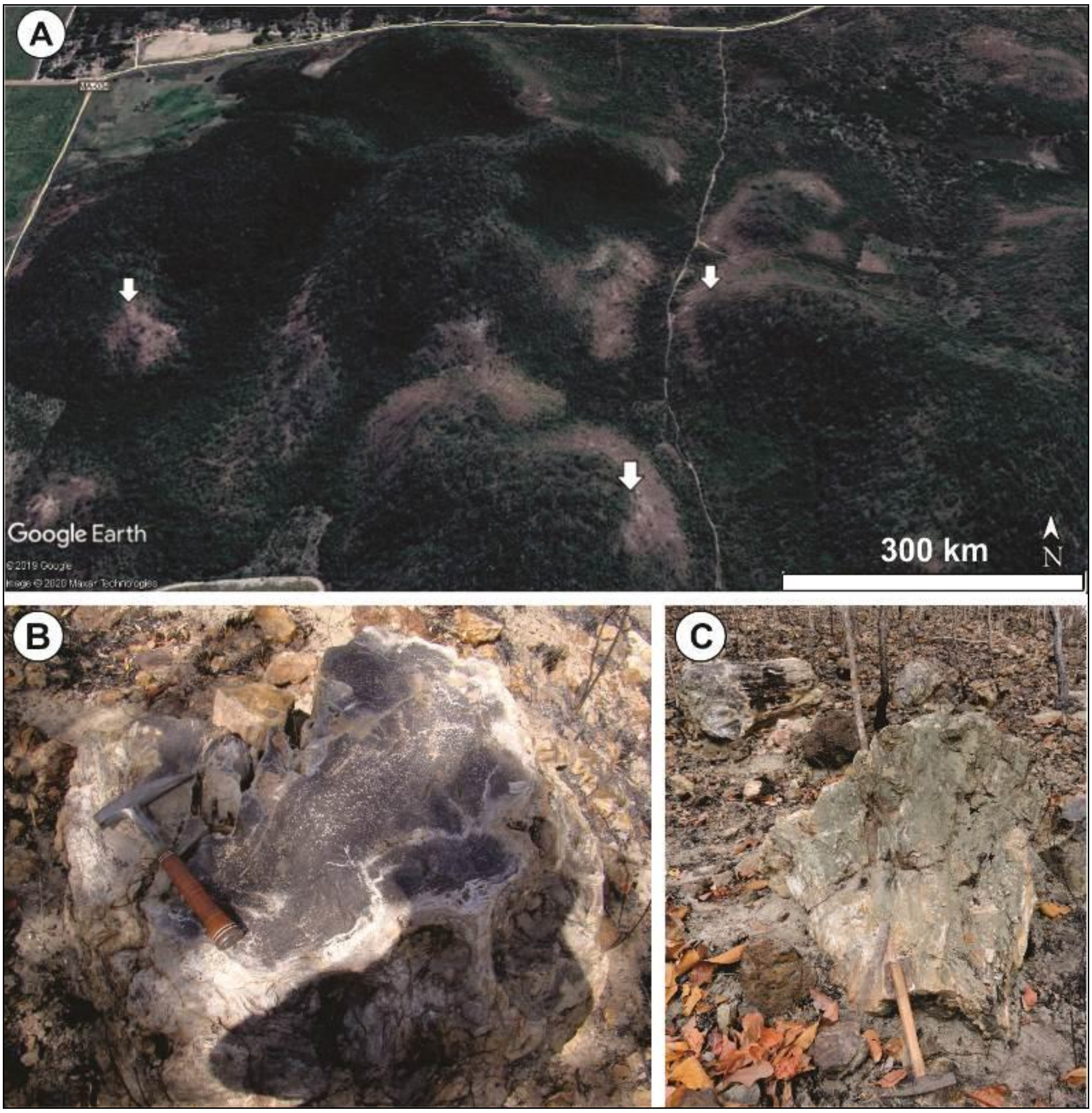

Figura 5. Imagem do Google Earth exemplificando a localização dos afloramentos nos topos dos morros testemunhos em Duque Bacelar, MA, e alguns exemplos dos caules petrificados que afloram na região **A**. setas estão indicando a posição dos afloramentos. **B-C**. caules gimnospérmicos de grande porte horizontalizados.

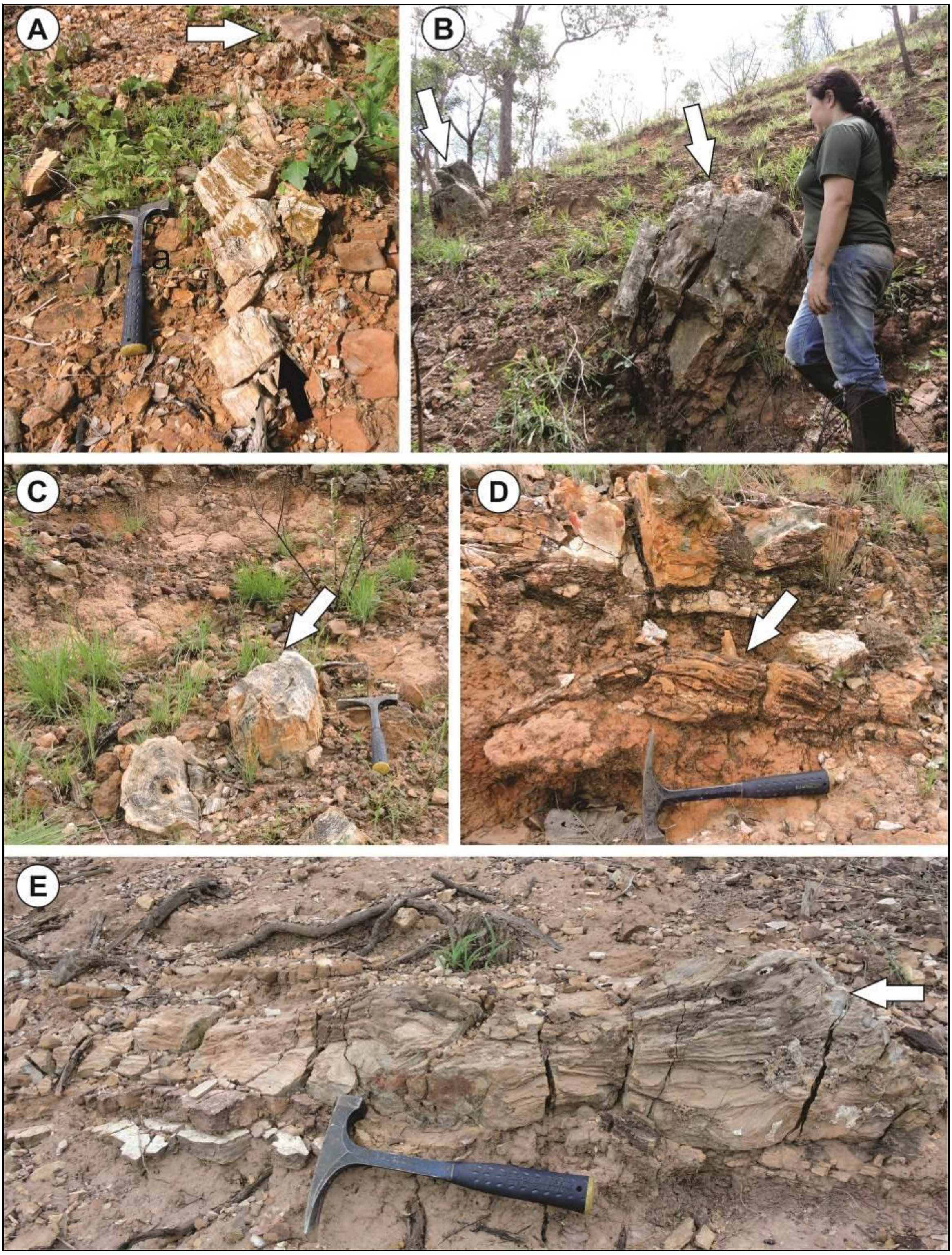

Figura 6. Exemplos em afloramento dos caules gimnospérmicos de Duque Bacelar. **A-C**. Caules em posição de vida (setas). A letra **A** mostra um exemplo de uma planta que possivelmente apenas tombou, a seta branca indica a base do caule ainda em posição de vida e a seta preta, o restante desta planta**. D-E**. Caules *in situ* (setas).

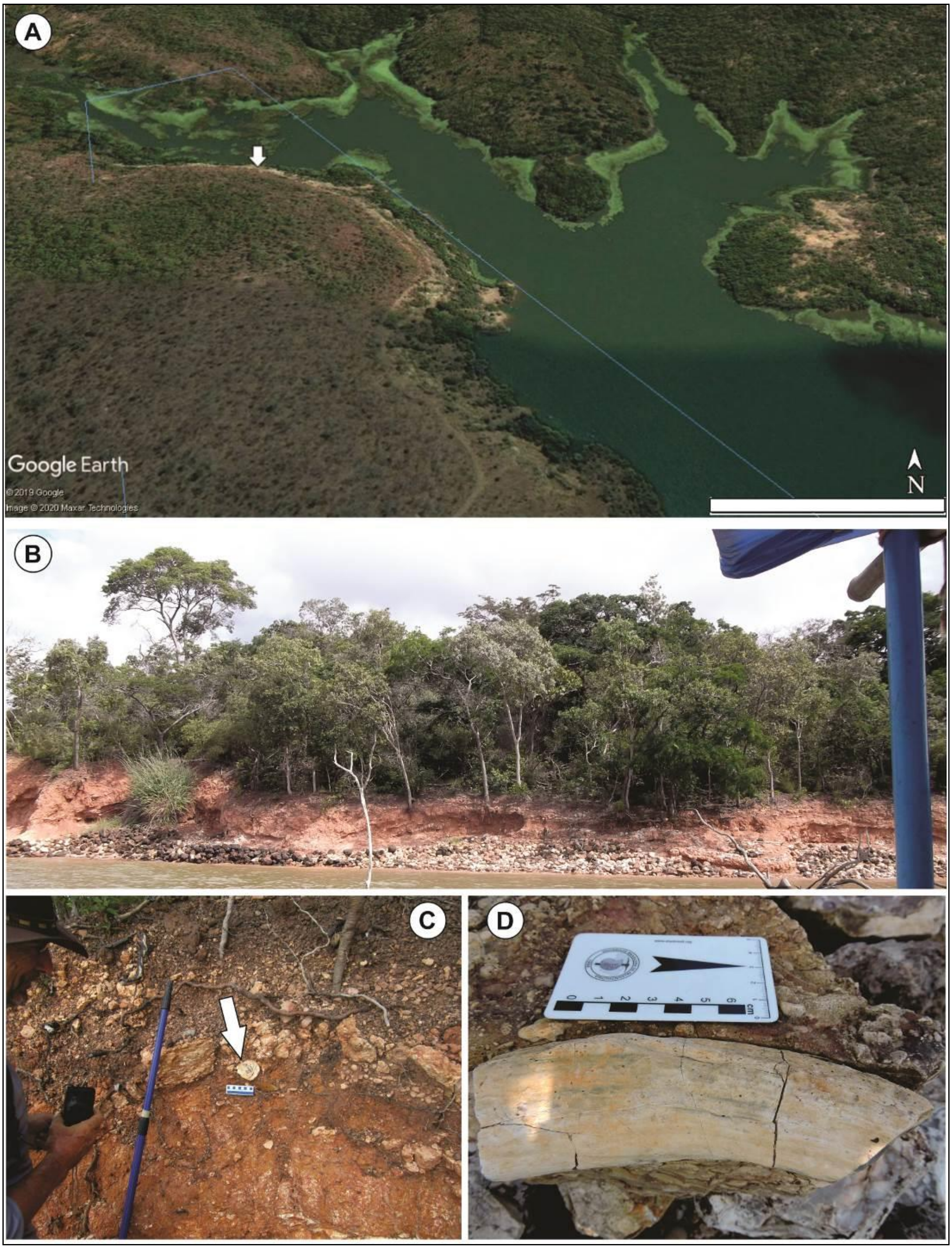

Figura 7. Imagem do Google Earth com a localização do afloramento nas margens do reservatório de Boa Esperança em Nova Iorque, MA, e exemplos de caules gimnospérmicos que afloram no local. **A**. seta indica um dos afloramentos em que foram coletadas as amostras. **B**. vista do afloramento. **C**. a seta indica caule de gimnosperma logo acima do chert. **D**. caule inserido em blocos com brecha.

5.2. Materiais

Os materiais correspondem tanto a lenhos coletados em trabalhos de campos efetuados em 2011 e 2012, quanto a novos espécimes coletados em expedições realizadas no período entre 2016 a 2018. Esses lenhos afloram em depósitos da Formação Pedra de Fogo nos municípios de Duque Bacelar e Nova Iorque, no estado do Maranhão (Figura 1). As figuras 6 e 7 (no item anterior) demonstram alguns exemplos de como esses materiais foram encontrados nos afloramentos.

O número aproximado de espécimes já levantados é de cerca de 200 caules permineralizados, maior parte deles de grande porte (Figura 6). Coletaram-se as amostras menores por questões relativas ao transporte e laminação, uma vez que as serras com discos diamantados disponíveis nos laboratórios consultados (CPRM-Teresina, UNISINOS, UFRGS, UNESP), por vezes, não possibilitam o corte de amostras maiores que cerca de 20 cm de diâmetro ou a dureza do material não permite. No entanto, é importante salientar que amostras dos caules de grande porte e em posição de vida também foram coletadas e laminadas para comparação anatômica do seu xilema secundário, pois em geral, esses caules não apresentam a preservação de suas cavidades medulares para análise – outro fator que limita o seu estudo.

As amostras laminadas consistem em 39 espécimes de gimnospermas, sendo nove oriundas de exposições em Nova Iorque e 30 em Duque Bacelar. As amostras de Nova Iorque variam de seis a 12 cm de comprimento e cinco a sete centímetros de diâmetro. Anatomicamente, esses caules apresentam um excelente nível de preservação, tanto de tecidos primários quanto dos secundários, o que permitiu a elaboração de dois artigos (‘veja’ **seção 6.1. Resultados**). Ainda, uma amostra dessa localidade foi incluída na terceira publicação (PAB 018.10). Em relação às amostras provenientes de Duque Bacelar, embora estejam todas laminadas, apenas seis (PAB 084, 137, 140, 142, 150, 151), cujas medidas variam de quatro a 10 cm de comprimento e 12 a 14 centímetros de diâmetro, foram descritas e classificadas, e compõem a terceira publicação desta tese. Os demais espécimes dessa localidade não puderam ser classificados em tempo hábil por questões relativas ao processo de preparação das lâminas e obtenção de cortes adequados ao estudo anatômico, o que demanda um tempo considerável, sobretudo, quando se tratam das seções radiais (‘**veja’ item 5.3.2. Síntese dos procedimentos relativos à preparação das**

lâminas). Porém, fez-se uma análise prévia da anatomia dos mesmos e, igualmente àqueles classificados, eles também apresentam um excelente estado de preservação anatômica e poderão ser objeto de publicações subsequentes. A Figura 7 mostra uma visão macroscópica de alguns desses exemplares provenientes dos dois municípios.

As amostras utilizadas nas publicações, tantos os caules quanto às lâminas, estão tombados com o prefixo PAB e pertencem à Coleção de Paleobotânica da Universidade Federal do Piauí (UFPI), com exceção de um exemplar que pertence à Universidade de São Paulo (USP-0135) e, por esta razão, está tombado com o prefixo USP. De qualquer modo, algumas lâminas feitas em duplicata deverão ser incorporadas à Coleção de Paleobotânica da Universidade Federal do Rio Grande do Sul (UFRGS), onde receberão o prefixo MP-Pb.

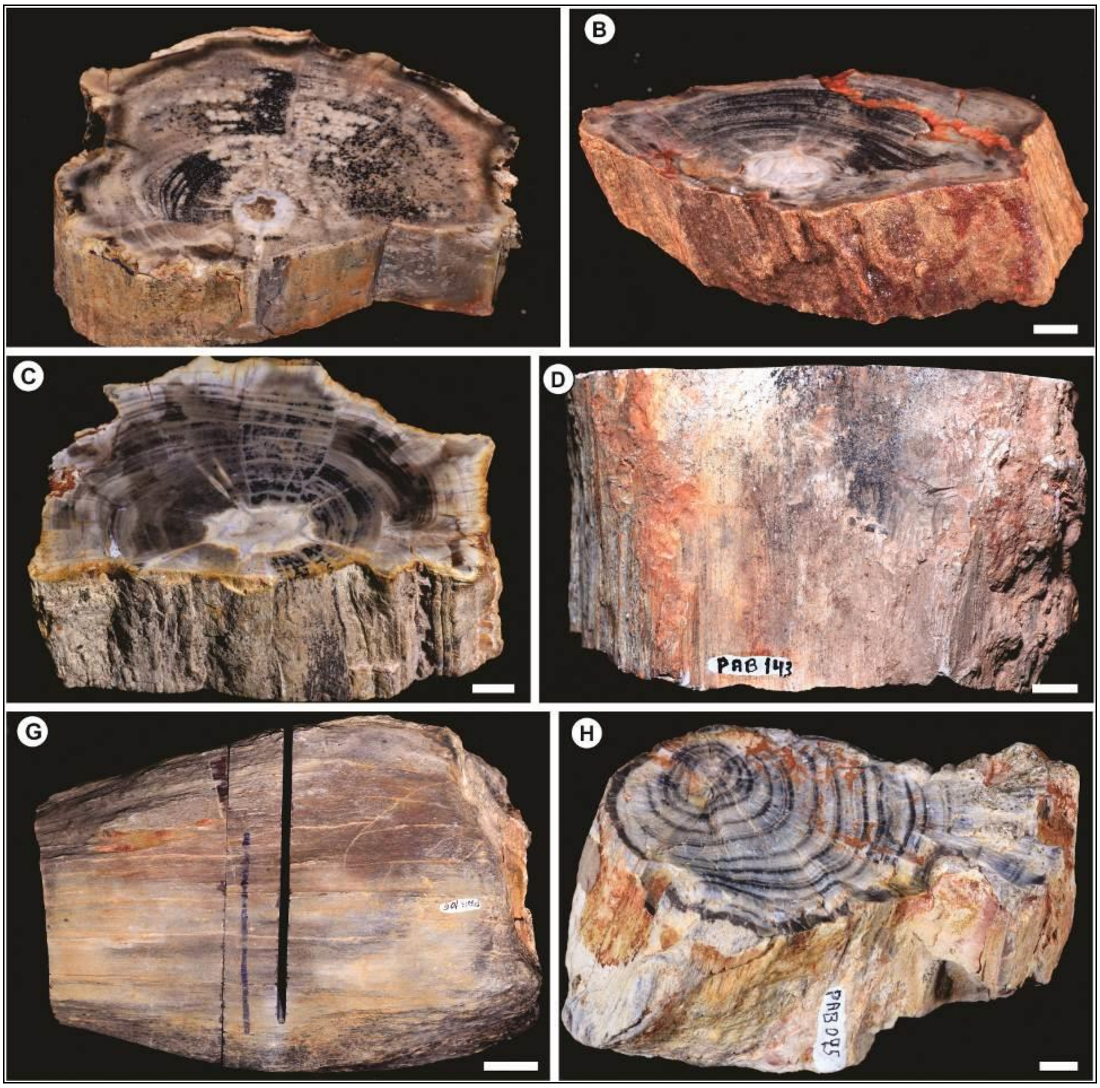

Figura 8. Exemplos de algumas amostras de lenhos coletados para elaboração de seções finas. **A**. Duque Bacelar. **G-H**. Nova Iorque. Escalas: 1 cm.

5.3. Métodos

5.3.1. Atividades de campo:

As atividades de campo foram constituídas por:

(i) análises de imagens de satélite da região, obtidas através do programa *Google Earth;*

(ii) prospecção e processamento dos fósseis: limpeza, atribuição de código de campo e identificação em nível macroscópico do material nas áreas aflorantes;

(ii) georreferenciamento dos troncos encontrados, com auxílio de *GPS* (*Global Positioning System*);

5.3.2. Síntese dos procedimentos relativos à preparação das lâminas:

Os procedimentos para a preparação das seções finas dos espécimes foram efetuados conforme a metodologia padrão, utilizada para taxonomia de lenhos fósseis e descritos em Merlotti & Rosa (2002). No entanto, antes de descrevê-los em detalhe abaixo, algumas considerações importantes, pertinentes aos tipos de cortes, serão brevemente descritas abaixo e podem ser visualizadas na Figura 9.

As análises anatômicas dos lenhos, em vista da presença dos sistemas axial e radial, exigem três planos distintos: TR — Transversal; LR — Longitudinal radial e LT — Longitudinal tangencial (Figura 9). O plano transversal, perpendicular ao eixo principal do tronco ou da raiz, permite observar o menor diâmetro dos elementos do sistema axial — tecidos primários e secundários — os anéis de crescimento e o comprimento dos raios (Figura 9A). O plano longitudinal tangencial, perpendicular aos raios, possibilita identificar a altura das células do sistema axial, o diâmetro e número de fileiras das células que compõem os raios xilemáticos (Figura 9B). Por fim, tem-se o plano longitudinal radial (Figura 9D) que permite observar as células do sistema radial como faixas horizontais.

Seções radiais devem ser utilizadas para determinar o arranjo das pontoações das paredes radiais das traqueídes, bem como os tipos de pontoações dos campos de cruzamentos, definidos como as áreas de contato entre parte da parede radial das células parenquimáticas dos raios lenhosos e parte da parede radial das traqueídes (Figura 9D – IAWA, 2004; Evert, 2013; Apezzato & Carmelo-Guerreiro, 2012). Cabe mencionar que nas gimnospermas, o arranjo das pontoações e os campos de cruzamentos, assim como na taxonomia atual (IAWA, 2004) são essenciais para taxonomia em lenhos fósseis gondvânicos (Merlotti, 2011).

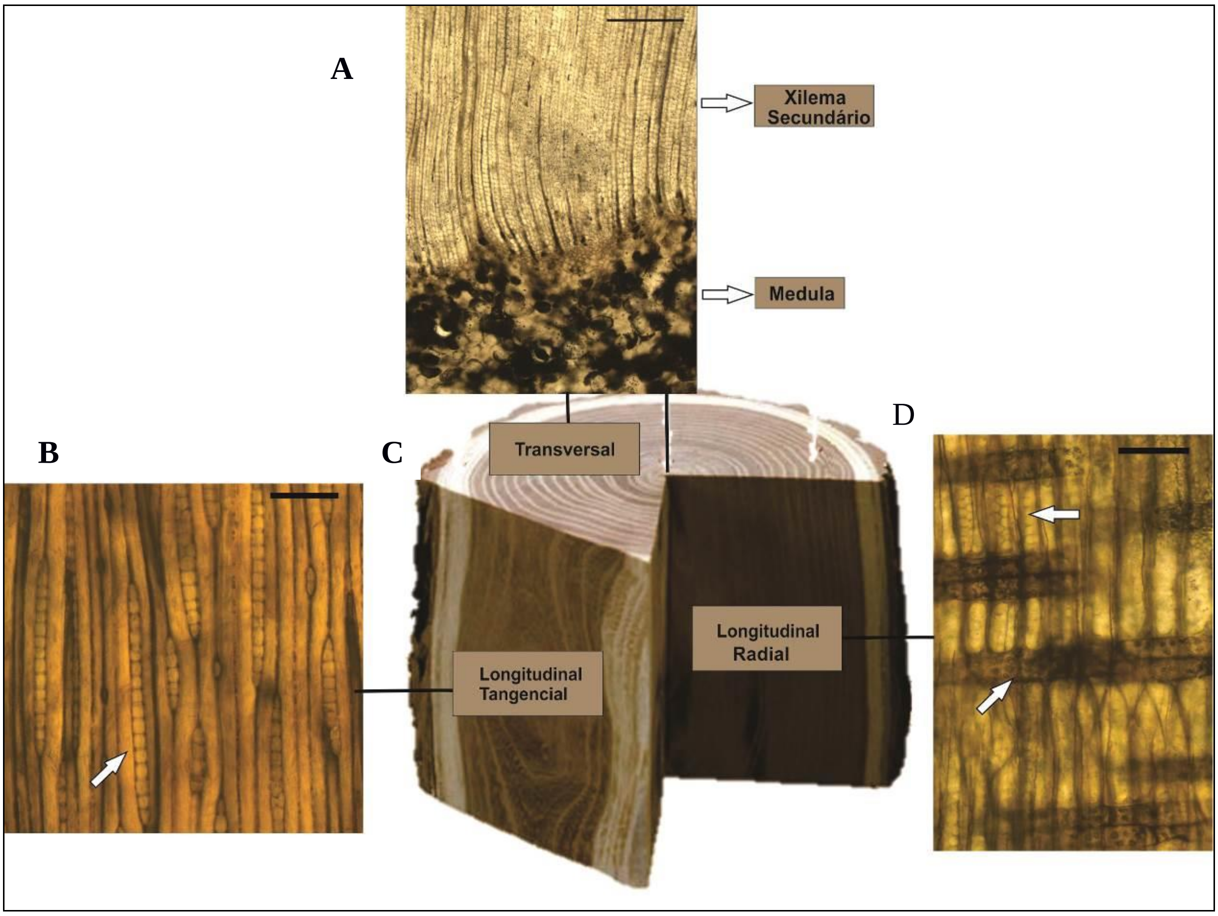

Figura 9. Exemplos dos cortes padrões feitos para os estudos de anatomia de lenhos fósseis. As fotos das lâminas são representativas de alguns fósseis estudados na presente tese. Imagem **C** disponível em: http://www.madeira.ufpr.br/disciplinasklock/quimicadamadeira Acessado em 13 de dez. 2020. Escalas: A, B e D: 200 µm.

Para confecção das lâminas petrográficas dos lenhos, as seguintes etapas foram efetuadas:

(i) escolha dos locais mais adequados nos espécimes para obtenção dos cortes nos distintos planos (*i.e.,* **TR, LR e LT**);

(ii) redução das amostras dos diferentes cortes em frações menores, as quais se assemelham a “tilojinhos”, utilizando-se para isso uma serra manual de disco diamantado;

(ii) polimento de uma das faces desses “tilojinhos” com carbureto de silício preto de granulações 400 e 600, aquecida em chapa térmica a 50°C por aproximadamente 20 minutos;

(iv) aplicação sobre essa face polida, ainda aquecida, de uma resina homogênea de dez gramas de Araldite (X6Y-1109) e um grama de endurecedor (HY-951), a qual é colada rapidamente em uma lâmina de vidro para evitar a formação de bolhas e inserida na estufa para secar (50°C) por duas horas aproximadamente;

(v) desbaste manual em politriz do bloco colado na lâmina, com carburetum de granulações 220, 400 e 600;

vi) acabamento e polimento da lâmina feito com carburetum de granulações 800 e 1200, em placas de vidro ou acrílico (0,5 x 25 x 30 cm) até que as estruturas celulares estejam visíveis para análises, o que é possível a partir de espessuras entre 30 e 70 µm, dependendo da amostra;

vii) inserção da lamínula sobre a lâmina e limpeza para armazenamento.

Neste trabalho, optou-se pela não inserção de lamínulas, pois isso torna mais difícil posteriormente o afinamento da mesma, caso seja necessário. Por exemplo, alguns problemas inerentes à espessura das lâminas ocorreram ao longo do trabalho e, em muitos casos, foi necessário o laminador deixar as lâminas com até 500 µm e a autora da tese efetuar o acabamento manualmente em placas de vidro ou acrílico (0,5 x 25 x 30 cm), utilizando carbeto de silício preto de granulações 600 e 800.

5.3.3. Análises anatômicas e taxonômicas

Fotos macroscópicas foram feitas com uma câmera Canon EOS T3i, com uma lente Macro DG 70 mm Sigma, no laboratório de fotografia do Departamento de Paleontologia e Estratigrafia da UFRGS. Tanto as análises microscópicas das lâminas quanto fotomicrografias foram feitas utilizando-se um microscópio Leica DM500, com uma câmera digital Leica MC170 acoplada. As medições das células foram realizadas por meio do software Image J.

A terminologia anatômica empregada nas descrições dos espécimes fósseis seguiu as recomendações da Associação Internacional de Anatomistas da Madeira (IAWA, 2004), bem como aquelas feitas por Mussa (1982), Falcon-Lang (2003), Philippe & Bamford (2008), e Merlotti (2011).

As discussões sistemáticas foram realizadas a partir de comparações com descrições prévias de táxons paleozoicos semelhantes, encontrados na literatura em diferentes regiões do globo, tanto do Hemisfério Sul (por exemplo, Crisafulli, 1998b;

Crisafulli & Lutz, 2000; Mussa, 1982; 1986a; b Coimbra & Mussa, 1987; Merlotti, 1998 a, b; Kurzawe e*t al*., 2013 a, b), quanto do Hemisfério Norte (por exemplo, Rothwell & Warner, 1984; Wang *et al*., 2003; Hilton *et al*., 2009; Falcon-Lang, 2007; Falcon-Lang *et al*., 2014), mais informações podem ser obtidas diretamente nos três artigos anexados na seção de resultados.

5.3.4. Descrição dos afloramentos e composição mineralógica

Para os levantamentos das seções estratigráficas e interpretações das associações de fácies, a fim de definir os sistemas deposicionais, foram empregados métodos similares aos utilizados por Allen (1981) e Miall (1985; 1988).

A determinação da composição mineralógica do sílex foi determinada por Difratometria de Raios-X, descrita em detalhes no artigo 1 a seguir.

6. ANÁLISE INTEGRATIVA DOS RESULTADOS

6.1. Resultados dos Artigos

O excelente nível de preservação anatômica dos caules encontrados nos afloramentos da Formação Pedra de Fogo permitiu, por enquanto, a obtenção de dados para elaboração de três artigos, a saber: **i) New petrified gymnosperms from the Permian of Maranhão (Pedra de Fogo Formation), Brazil. *Novaiorquepitys* and *Yvyrapitys*,** publicado na *Review of Paleobotany and Palinology,* **ii) New petrified gymnosperms from the Permian of Maranhão (Pedra de Fogo Formation), Brazil: *Ductolobatopitys* and *Kaokoxylon***, "aceito" na *Geobios*, **iii) First report of genus *Cordaixylon* Grand'Eury 1877 in Permian of South America, Parnaíba Basin, Brazil**, o qual se encontra submetido no *Journal of South American Earth Sciences*.

Os trabalhos de campo na região do município de Nova Iorque, sudeste do Maranhão, possibilitaram a coleta de um número pequeno (nove), no entanto, espécimes anatomicamente bem preservados, o que permitiu a elaboração de dois artigos (**Artigos 1** e **2**). Dada à variabilidade na composição anatômica da medula, os resultados foram divididos em duas publicações. Cabe notar que os lenhos dos afloramentos em Nova Iorque permitiram ainda a elaboração parcial do **Artigo 3**, referente às Cordaitales, cujo desenvolvimento se deu a partir de sete exemplares com medulas septadas, um de Nova Iorque (PAB 018.10), e seis coletados em Duque Bacelar, no leste do Maranhão (*i.e*., PAB 084, 137, 140, 142, 150, 151), uma vez que verificou que todos eles pertenciam ao mesmo gênero (*i.e*., *Cordaixylon*).

No **Artigo 1**, as análises anatômicas tornaram possível a descrição e classificação de dois novos gêneros e espécies endêmicas para a Bacia do Parnaíba, denominadas *Novaiorquepitys maranhensis* e *Yvyrapitys novaiorquensis*, respectivamente. De forma geral, esses dois táxons possuem medulas heterocellular, amplas (com até três centímetros de diâmetro) e não septadas. Adicionalmente, *Novaiorquepitys maranhensis* possui um sistema de lacunas bem organizado, disposto entre os feixes de xilema primário. Essas duas espécies compartilham xilemas primários endarcos, campos de cruzamentos cupressoides e xilemas secundários com interrupções de crescimento. Todavia, diferem em relação aos tipos celulares que compõem a medula e, de forma análoga, nas pontoaçõe radiais das traqueídes que são do tipo araucariano — *Novaiorquepitys maranhensis*

— e mistos — *Yvyrapitys novaiorquensis* e, ainda, na largura e altura dos raios xilemáticos que são variáveis entre os dois táxons. Em *Novaiorquepitys maranhensis*, os raios são parcialmente bisseriados e com até 52 células de altura, enquanto em *Yvyrapitys novaiorquensis* eles são predominantemente unisseriados e não ultrapassam 20 células de altura (Tabela 2).

Os resultados taxonômicos acima, interpretados de forma integrada com os dados sedimentológicos e, a presença na mesma área de plantas que vivem nas margens de corpos d'água ou em terrenos úmidos (por exemplo, fetos arbóreos e calamitáceas), indicam que essas plantas lenhosas viviam perto das margens de sistemas lacustres. Esses resultados taxonômico-anatômicos, juntamente com outros dados sedimentológicos e florísticos permitiram fazer relevantes interpretações paleoambientais e paleofitogeográficas, as quais estão discutidas em maiores detalhes no **Artigo 1,** bem como na seção de **discussão** abaixo.

No **Artigo 2,** igualmente ao **Artigo 1**, as análises anatômicas possibilitaram a descrição e classificação de mais duas formas oriundas de Nova Iorque, *i.e*. *Ductolobatopitys mussae* e *Kaokoxylon brasiliensis*, a primeira, um gênero e espécie novos, e a segunda, referente a um gênero já registrada na Bacia do Parnaíba (in Kurzawe *et al*., 2013b), porém representando uma espécie nova. Ambos os *taxa* possuem medula heterocellular, xilema primário endarco, pontoações radiais araucarianas e campos de cruzamentos cupressoides, e raios exclusivamente unisseriados e baixos (Tabela 2). Contudo, *Ductolobatopitys mussae* apresenta medula solenoide (com ductos secretores), uma feição anatômica notável para diferenciações intergenéricas em lenhos paleozoicos (maiores detalhes no **Artigo 2**). *Ductolobatopitys mussae*, possuí ainda, a medula lobada, característica observada tanto no holótipo quanto no parátipo, cujas seções finas foram feitas em dois níveis distintos de ambos os exemplares, visando maior confiabilidade taxonômica na utilização desse caractere anatômico. Considerando que esses táxons são oriundos dos mesmos afloramentos dos táxons do **Artigo 1**, as interpretações paleoambientais e, em parte, paleofitogeográficas são compartilhadas. Porém, uma das formas identificadas (*Ductolobatopitys mussae*) apresenta feições anatômicas relevantes em termos de interpretações paleoecológicos (ductos secretores), as quais são um suporte a mais para as interpretações paleoambientais (seção **6.1. Discussão** e **Artigo 2**).

No **Artigo 3**, foram descritos sete exemplares recuperados de afloramentos de ambas as áreas estudadas, *i.e*. Nova Iorque e Duque Bacelar, cuja anatomia configura-se como típica das Cordaitales encontradas no Hemisfério Norte (Euramérica e Cataísia) e, por essa razão, foram incluídas no gênero *Cordaixylon* Grand'Eury, 1877. Não obstante, a ausência de tecidos externos preservados nos exemplares, que são geralmente considerados nas classificações das espécies vinculadas a esse gênero, impossibilitou a classificação desses exemplares ao nível específico, tendo-se, portanto, optado apenas por uma identificação em nível genérico, sendo classificados em dois morfotipos, *i.e*. *Cordaixylon* sp. 1 e sp. 2 (Tabela 2).

Os exemplares apresentam medulas homogêneas (parenquimáticas), com septações regulares observadas com clareza ao longo das seções radiais dos caules. Os feixes de xilema primário são endarcos, relativamente discretos, apresentam ainda pontoações radiais araucarianas e campos de cruzamentos cupressoides. Além disso, mostram traços foliares que partem da medula como únicos e se dividem ao longo do xilema secundário, característica esta associada comumente às Cordaitales (Rothwell & Warner, 1984; Trivett, 1992). Os septos apresentam variações morfológicas significativas, por exemplo, no exemplar de Nova Iorque (PAB 018.10), os septos são mais largos, com terminações conectadas e tênues bifurcações, enquanto nos de Duque Bacelar (PAB 084, 137, 140, 142, 150, 151) são estreitos e com terminações divididas e bifurcações bem desenvolvidas. Essas diferenças podem estar relacionadas a um estágio ontogenético distinto, não obstante, para discutir tal hipótese, os caules precisariam ser mais completos, passíveis de observações através de cortes das porções basal, média e apical. Isso possibilitaria reconhecer as variações morfo-anatômicas da porção proximal à distal e, a partir disso, verificar as modificações ontogenéticas que ocorrem ao longo do crescimento da planta. Contudo, não foi possível obter espécimes mais completos e, logo, essas diferenças morfológicas nos septos foram consideradas diagnósticas, levando à classificação desses exemplares em *Cordaixylon* sp. 1 (amostras de Duque Bacelar) e *Cordaixylon* sp. 2 (amostra de Nova Iorque), o que eventualmente poderá mudar com o aumento do conhecimento sobre estas formas no futuro. A presença dessas plantas na Bacia do Parnaíba demonstra a existência de ambientes propícios ao crescimento vegetal, o qual requer níveis de umidades constantes. No entanto, isso contradiz os modelos climáticos clássicos para o oeste do Gondwana, que sugerem áreas predominantemente secas (Rees *et al*., 2002; Scotese *et al*., 2014).

Adicionalmente, a ocorrência do gênero *Cordaixylon* constitui um fato importante no sentido de contribuir nas discussões bioestratigráficas para a Formação Pedra de Fogo, uma vez que a ocorrência do mesmo no Hemisfério Norte está limitada a intervalos entre o Pennsilvaniano e o início do Permiano (Rothwell and Warner, 1984; Trivett, 1992; Falcon-; Wang *et al*., 2003; Hilton *et al*., 2009; Lang, 2007).

Tabela 2. Comparação anatômica entre os gêneros descritos neste trabalho.

Gênero	*Yvyrapitys.*	*Novaiorquepitys*	*Ductolobatopitys*	*Cordaixylon*	*Kaokoxylon*
Medula					
Forma	Circular	Circular	Lobulada	Circular	Circular
Tipo	Sólida e heterocellular	Sólida e heterocellular	Sólida, solenoide e heterocellular	Septada e homogênea	Sólida e heterocellular
Composição	Raras lacunas, bainha parenquimática e esclereídes	Esclerênquima e sistema de lacunas na periferia	Ductos e células esclerenquimáticas	Parenquima	Esclerênquima
Xilema primário					
Protoxilema	Endarco	Endarco	Endarco	Endarco	Endarco
Espessamentos do protoxilema e metaxilema	Anular, escalariforme e reticulado	Escalariforme a reticulado	Escalariforme	Escalariforme	Escalariforme
Xilema secundário					
Tipos de arranjos das pontoações radiais	Misto	Araucariano	Araucariano	Araucariano	Araucariano,
Seriação das pontoações	1-2	1-3	1-3	1-3	1-3
Campos de cruzamentos	Cupressoide, 1–6 pontoações	Cupressoide, 1–6 pontoações	Cupressoide, 1–4 pontoações	Cupressoide, 1–4 pontoações	Cupressoide, 3–4 pontoações
Tipos de raios	Homogêneos	Homogêneos	Homogêneos	Homogêneos	Homogêneos
Largura e altura dos raios	Unisseriados, raramente, bisseriados, 1–20 células de altura	Parcialmente biseriados, unisseriados, 1-9 e, bisseriados 4–57, células de altura	Unisseriados, 1-12 células	Unisseriados, 1-43 células, e, bisseriados 12-36 células de altura	Unisseriados, 1-8 células de altura
Anéis de crescimentos	Ausentes	Ausentes	Ausentes	Ausentes	Ausentes

6.1. Discussão

Maior parte dos táxons descritos nos três artigos que compõem a presente tese (*i.e*., **Artigo 1, 2** e **3**) apresentam caracteres anatômicos que eventualmente são úteis em interpretações paleoecológicas e paleoambientais, tais como: canais secretores ou ductos, lacunas, septos e xilemas secundários com interrupções de crescimentos (s*ensu* Falcon-Lang, 2003), ou seja, ausência de verdadeiros anéis de crescimentos. Entretanto, salienta-se que esses caracteres, quando interpretados isoladamente, ou seja, sem a fundamentação de outros dados do afloramento (*e.g*., composição florística e dados faciológicos) apresentam certas limitações, e devem ser utilizados com cautela para esse fim.

Nos afloramentos em questão, foram feitas algumas inferências paleoecológicas e paleoambientais, a partir da anatomia desses caules, as quais foram corroboradas com as informações provenientes da Geologia sedimentar e de outros grupos de plantas presentes nos mesmos depósitos. Os dados faciológicos de ambos os afloramentos estudados sugerem que as plantas dessas áreas viviam nas às margens de grandes lagos, que eram influenciados por um sistema fluvial composto por rios efêmeros (constituindo-se em um sistema flúvio-lacustre) e pela sazonalidade climática regional (‘veja’ discussão dos **Artigos 1**, **2 e 3**). Essas plantas conseguiam se proteger durante os períodos mais secos aproveitando-se da umidade existente nas margens desses lagos, mas também estavam sujeitas a todos os fatores relacionados à subida e descida do nível de base local. Situação que pode explicar, em parte, as sutis flutuações no crescimento do xilema secundário. De forma similar, a presença de feições como septações, lacunas, e ductos no tecido medular, são comumente interpretadas como adaptações anatômicas de vegetais que viviam em ambientes sujeitos a períodos de baixa oxigenação ou secas, pois elas serviriam para facilitar a aeração ou o armazenamento de água, e consequentemente, manteriam o funcionamento adequado de seu metabolismo nessas ocasiões (Mussa, 1980; 1982). Adicionalmente, afloram nesses depósitos, caules de samambaias Maratialles e Calamitales arborescentes (*e.g*., *Psaronius* spp. e *Artrhopitys* spp.), plantas cuja sobrevivência é limitada em ambientes com estresse hídrico prolongado (Iannuzzi & Vieira, 2005). Assim, as condições regionais podem certamente ter sido mais úmidas que o macroclima sugerido pelos modelos já propostos para o interior do Pangeia. Essas condições ambientais e climáticas poderiam assemelhar-se às regiões tropicais do Hemisfério Norte, em que as plantas cordaitaleanas são registradas em abundância. Nesse sentido, a presença de grandes lagos poderia explicar a existência da vegetação exuberante discutida por Iannuzzi et al. (2018). Esse sistema lacustre forneceria a umidade necessária para o crescimento da vegetação em uma região mais seca. Observa-se que os modelos de Rees et al. (2002) e

Scotese et al. (2014) são aplicáveis em escalas macroclimáticas e não levam em consideração a existência de variações microclimáticas em um contexto regional para local.

A importância dos resultados expostos nesse trabalho vai muito além da presença de caules autóctones, abundância ou ampla área de ocorrência destas gimnospermas, mas também adiciona importantes dados para as discussões sobre os elementos florísticos que compunham o oeste do Gondwana. Importância justificada pela posição paleogeográfica da Bacia do Parnaíba durante o Permiano, na qual se desenvolvia uma zona subtropical árida que se localizava entre as floras gondvânicas (ao sul) e euramericanas (ao norte).

O acréscimo de três novos gêneros endêmicos, *i.e*. *Novaiorquepitys*, *Yvyrapitys* e *Ductolobatopitys*, para os depósitos permianos da Bacia do Parnaíba, corroboram, em parte, a proposição de Neregato *et al*. (2017) a respeito da criação de uma nova unidade fitogeográfica para o Paleozoico, denominada de Região do Meio Norte do Brasil, por aumentar a quantidade de *taxa* endêmicos. Por outro lado, a presença do gênero *Cordaixylon* nos depósitos da Formação Pedra de Fogo de ambas as regiões — Duque Bacelar e Nova Iorque — com número considerável de exemplares, diminui o nível de endemismo da flora, uma vez que é um gênero reconhecidamente euramericano. Há possibilidade de essa região ter funcionado durante o Permiano como um corredor de dispersão florística (e faunística) entre as floras gondvânicas e euramericanas, como discutido em Iannuzzi *et al*. (2018) e, por essa razão constituir-se em uma flora tão particular. Nesse sentido, ressalta-se que para análises paleofitogeográficas futuras algumas observações importantes sobre os lenhos dos afloramentos dessa unidade, sobretudo de Duque Bacelar, devem ser consideradas, a saber:

(i) os espécimes utilizados para determinação de *Cordaixylon* são provenientes de afloramentos distantes entre si cerca de 400 km. Este fato indica que essas formas estavam distribuídas numa área geográfica ampla durante a deposição da unidade Pedra de Fogo, embora os afloramentos distribuídos dentro desse intervalo de 400 km ainda não tenham maioritariamente sido explorados, sobretudo visando à obtenção de dados paleobotânicos;

(ii) como discutido no Item **“5. Material e Métodos”,** a maior parte dos caules aflora nas adjacências de Duque Bacelar, tanto os autóctones quanto parautóctones, e, consequentemente, foi dessa área que se coletaram a maior parte dos caules laminados, embora apenas os de medulas septadas tenham sido utilizados nas publicações da presente tese (**Artigo 3**). Mas, as análises prévias da anatomia desses lenhos (20 espécimes), especialmente do xilema secundário (similarmente à anatomia de *Cordaixylon,* — Figura), sugerem fortemente afinidades às plantas cordaitaleanas, incluindo os caules em posição de vida.

A partir do exposto acima, ressalta-se que os estudos taxonômicos futuros dos caules da Formação Pedra de Fogo podem indicar um número maior que o esperado de táxons compartilhados com o Hemisfério Norte. Além disso, baseado no estudo feito por Neregato *et al*. (2017), sugere-se assim que para obtenção de informações paleofitogeográficas mais robustas a respeito da similaridade dos elementos florísticos da Bacia do Parnaíba, deve-se considerar, nas análises de similaridades, o maior número possível de táxons, especialmente das províncias florísticas do Gondwana e Euramérica, tanto estruturas reprodutivas quanto vegetativas. Entretanto, embora um crescente número de trabalhos taxonômicos tenha sido desenvolvido na Bacia do Parnaíba nos últimos anos, falar em dados quantitativos ainda parece ser um desafio nos estudos paleobotânicos dessa bacia, principalmente se tratando dos hiatos taxonômicos que ainda existem em relação às estruturas reprodutivas e formas lenhosas gimnospérmicas. Tal fato torna-se mais complexo ainda, devido ao número considerável de afloramentos reportados nos últimos anos na Formação Pedra de Fogo, os quais contêm muitos caules gimnospérmicos ainda sem classificações taxonômicas efetivadas.

7. CONSIDERAÇÕES FINAIS

Os afloramentos fitofossilíferos da Formação Pedra de Fogo georreferenciados por Conceição *et al*. (2016a), assim como aqueles descobertos em outras campanhas de campos, nas margens sudeste e leste da Bacia do Parnaíba, permitiram a obtenção de importantes dados geológicos (*e.g*., faciológicos e estratigráficos) e, consequentemente, interpretações estratigráficas e paleoambientais relevantes:

(1) Os lenhos gimnospérmicos desses afloramentos ocorrem na base da Formação Pedra de Fogo, ou seja, no Membro Sílex Basal, divergindo de posicionamentos estratigráficos anteriores, que os posicionavam no superior Membro Trisidela (“veja” discussão em Conceição *et al*., 2016 a);

(2) Essas plantas viviam em ambientes continentais dominados por um sistema flúvio-lacustre, periodicamente ou ocasionalmente sujeito a tempestades episódicas e consequentes eventos de inundações.

As análises taxonômicas, a partir dos dados anatômicos dos lenhos “integralmente preservados” (medulas, xilemas primário e secundário) provenientes desses afloramentos, possibilitaram a obtenção de importantes dados taxonômicos, igualmente, auxiliaram nas interpretações paleoambientais e paleoecológicas, bem como paleofitogeográficas, a saber:

(3) Identificação de seis novos táxons para os depósitos Permianos desta bacia, dos quais, três são gêneros endêmicos, *i.e*. *Novaiorquepitys*, *Yvyrapitys* e *Ductolobatopitys*, sendo os demais táxons bem conhecidos, um do Hemisfério Sul, *Kaokoxylon* Kräusel 1956, que ocorre em depósitos que se distribuem do Permiano ao Jurássico, representado aqui pela nova espécie *Kaokoxylon brasiliensis*, e o segundo com ocorrência limitada até agora às províncias da Euramérica e Cataísia, *i.e*. *Cordaixylon* Grand'Eury 1877, assinalado a partir de dois morfotipos denominados como *Cordaixylon* sp. 1 e *Cordaixylon* sp. 2, configurando-se assim no primeiro registro para o Gondwana;

(4) Feições anatômicas presentes nos tecidos medulares, como canais secretores, septações e lacunas, bem como ausência de anéis de crescimentos e a presença de fracas interrupções no crescimento do xilema secundário, são condizentes com as interpretações paleoambientais que sugerem que tais plantas viviam em ambientes flúvio-lacustres, temporariamente inundáveis, mas também passíveis de estresse hídrico; todavia, o estresse hídrico era provavelmente limitado, dado há abundância nos afloramentos de caules de *Psaronius* sp. e *Artrhopitys* sp., plantas arbóreas adaptadas a nichos úmidos e que por isso, precisam de suprimentos constantes de água ao longo do tempo para crescerem;

(5) Apesar de maior parte dos táxons aqui identificados constituírem formas endêmicas, também há gêneros típicos de outras províncias florísticas, como Euramérica e Cataísia, do Hemisfério Norte (*Cordaixylon*), ou do Gondwana (*Kaokoxylon*). De tal forma, a caracterização paleofitogeográfica da flora permiana dessa bacia ainda esbarra no volume pequeno de informações taxonômicas, assim, pesquisas sistemáticas com foco especialmente na taxonomia das gimnospermas serão cruciais para entender as relações com as floras permianas da Euramérica e do Gondwana;

(**6)** Finalmente, cabe mencionar que o registro do gênero *Cordaixylon* nos depósitos permianos dessa bacia, configura-se como mais um indicativo bioestratigráfico a corroborar com a idade cisuraliana sugerida para a Formação Pedra de Fogo, uma vez que a ocorrência desse gênero no Hemisfério Norte está limitada ao intervalo que se estende do Pennsilvaniano ao início do Permiano.

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PARTE II

Corpo principal da tese: manuscritos publicados, aceitos ou submetidos em formato de artigos científicos.

New petrified gymnosperms from the Permian of Maranhão (Pedra de Fogo Formation), Brazil: Novaiorquepitys and Yvyrapitys

Domingas Maria da Conceição, Alexandra Crisafulli, Roberto Iannuzzi, Rodrigo Neregato, Juan Carlos Cisneros, Luiz Saturnino de Andrade

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New petrified gymnosperms from the Permian of Maranhão (Pedra de Fogo Formation), Brazil: *Novaiorquepitys* and *Yvyrapitys*

Domingas Maria da Conceição [a*], Alexandra Crisafulli [b], Roberto Iannuzzi[a] Rodrigo Neregato[a], Juan Carlos Cisneros [c], Luiz Saturnino de Andrade [d]

[a] *Programa de Pós-Graduação em Geociências, Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul. Caixa Postal 15.001, CEP 91.509-900, Porto Alegre, Brazil*

[b] *Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste y CECOAL-CONICET Ruta 5, km 2,5 - 3400, Corrientes, Argentina*

[c] *Universidade Federal do Piauí, Museu de Arqueologia e Paleontologia, CEP 64.049-550, Teresina, PI, Brazil and Programa de Pós-graduação em Geociências, Universidade Federal do Pernambuco, Recife, Brazil*

[d] *Instituto de Geociências, UFPA, Rua Augusto Correa 1, 66075-110, Belém, Brazil*

*Corresponding author, e-mail: domingasmary@hotmail.com

ABSTRACT

Anatomically preserved gymnosperm stems are relatively abundant in the Permian outcrops of the Parnaíba Basin, but their anatomy has rarely been studied in detail. Here we describe two new fossil gymnosperm trunks from the Lower Permian (Cisuralian) strata of the Pedra de Fogo Formation in the municipality of Nova Iorque, southern Maranhão State, northeastern Brazil. Two new genera et species are described, *Novaiorquepitys maranhensis* and *Yvyrapitys novaiorquensis*. These taxa have a broad, non-septate pith containing sclerenchyma and secretory cells, a parenchyma sheath, and a system of lacunae. Pycnoxylic secondary xylem with growth interruptions and the radial bordered pits on the tracheid walls are araucarian and mixed types. The recognition of two endemic forms indicates both a high degree of endemism for the flora of the Pedra de Fogo Formation and a higher taxonomic diversity of gymnosperm woods than hitherto noted. In addition, the anatomical characters of these taxa, together with sedimentological data and the presence in the same area of plants that live on the banks of water bodies or in wetlands (e.g., tree ferns and tree-calamitaleans), indicate that these woody plants lived near the shores of large lakes. These findings show that studies of Paleozoic woods in this region are potentially valuable.

Keywords: Petrified gymnosperm, Taxonomy, Maranhão State, Parnaíba Basin, Permian

1. Introduction

Iannuzzi and collaborators (2018) recently published a synthesis of the Permian floras of the Parnaíba Basin, northeastern of Brazil, based on publications from more than 50 years of research in this basin. According to these authors, even though the Permian fossil plants from the Parnaíba Basin were first studied in the nineteenth century, e.g., by Brongniart (1872), in recent decades they have received insufficient attention, particularly the flora from the Pedra de Fogo Formation strata. There is still a significant gap in our knowledge of the fossil flora in this basin, especially regarding the petrified gymnosperm woods, compared with other areas of western Gondwana (e.g., the Paraná Basin and Argentinean and South African deposits). Since the early 2000s, however, studies of fossil plants from the Permian units of the Parnaíba Basin have increased significantly, especially concerning the fossils recovered from the Motuca Formation in the Tocantins Fossil Forest National Monument – MNAFTO, southwestern margin of the basin (Kurzawe et al., 2013a, b; Tavares et al., 2014; Neregato et al., 2015, 2017). Additionally, the silicified stems previously referred to the Pedra de Fogo Formation by Coimbra and Mussa (1984), Herbst (1986, 1992, 1999), Mussa and Coimbra (1987), Rößler and Noll (2002), and Rößler and Galtier (2002a, b; 2003) were transferred to the Motuca Formation beds by Kurzawe et al. (2013a, b), Tavares et al. (2014), Neregato et al. (2015, 2017), and Iannuzzi et al. (2018), since they have been recovered in or nearby the same outcropping area from which the material studied by these authors. This change in the positioning of those plant fossils is also supported on stratigraphic work carried out in the southwestern part of the basin, i.e., in the MNAFTO area, by other researchers (Pinto and Sad, 1986; Dias-Brito et al., 2009). Therefore, there was a considerably increased the numbers of taxa from Motuca Formation in relation to Pedra de Fogo Formation in the last decade.

The main objective of the present study was to analyze paleobotanical material from the Pedra de Fogo Formation, in order to increase our understanding of the Permian floras of the Parnaíba Basin, complementing previous studies that focused on material from the overlying Motuca Formation. In this contribution, we report two new genera et species of gymnosperm woods, which allows us to discuss briefly some paleophytogeographic, paleoecological and paleoenvironmental aspects of the Permian sedimentary deposits of the Parnaíba Basin.

Our results are part of a larger research project and the Ph.D. dissertation of the first author, for the purpose of describing the petrified gymnosperms recovered from new outcrops along the southern and eastern rims of the Parnaíba Basin, to be addressed in subsequent contributions (see part II of this work in Conceiçao et al., in press).

2. Paleobotanical overview

Regarding the petrified stems from the Pedra de Fogo Formation, only two species of tree ferns, *Psaronius brasiliensis* Brongniart, 1872 (in Brongniart, 1872) and *P. arrojadoi* Pelourde, 1914 (in Pelourde, 1914); and one “pteridosperm” wood, *Teresinoxylon eusebioi* Mussa, 1989 (in Caldas et al., 1989) have been erected. The other fossil plants described for the Pedra de Fogo Formation are based only on impressions – compressions, such as *Pecopteris* sp. and *Calamites* sp., which were merely mentioned by Barbosa and Gomes (1957); and the lycophyte *Cyclostigma brasiliensis*, erected by Dolianiti (1962), both from the southwestern part of this basin (Iannuzzi and Scherer, 2001, Iannuzzi et al., 2018). More recently, Iannuzzi and Langer (2014) and Iannuzzi et al. (2018) provided the first records of impressions of *Rhachiphyllum schenkii*-type pteridosperm and pecopterid fronds and leaflet whorls of *Sphenophyllum* sp. from the outcrops of Nova Iorque Municipality in southern Maranhão State, in the southeastern part of the basin.

In comparison, the overlying Motuca Formation has much greater taxonomic diversity, consisting of nine fern species (Herbst, 1992; 1986, 1999; Rößler and Noll, 2002; Rößler and Galtier, 2002a, b; 2003; Tavares et al., 2014), six sphenophyte species (Coimbra and Mussa, 1984; Neregato et al., 2015, 2017), and 13 gymnosperm species (Coimbra and Mussa, 1984; Mussa and Coimbra, 1987; Kurzawe et al., 2013a, b). All these were recovered only in a relatively small area in the southwestern part of the basin.

Finally, in the last few years, several prospecting expeditions have been carried out in the Pedra de Fogo Formation, focusing on mapping petrified stem-bearing localities along the eastern and southeastern parts of the basin (Fig. 1). These expeditions located important outcrops containing plant assemblages composed mainly of petrified gymnosperm woods, some of them still preserved in the life position (Conceição et al., 2016a, b). Therefore, it is expected that the diversity of the paleoflora ascribable to the Pedra de Fogo Formation will increase significantly in the near future.

3. Geological setting

The Parnaíba Sedimentary Basin, essentially Paleozoic, covers a wide area (approx. 600,000 km²), mostly in the states of Piauí, Maranhão and Tocantins in northeastern Brazil, with small areas in the states of Ceará and Pará (Fig. 1). This basin includes rocks with ages spanning from the Silurian to the Cretaceous (Góes and Feijó, 1994; Santos and Carvalho, 2009; Vaz et al., 2007, fig. 1). The Permian deposits of this basin are represented by two lithostratigraphic units, i.e., the Pedra de Fogo and Motuca formations (Góes and Feijó, 1994, fig.1). According to Santos and Carvalho (2009) these two formations are among the most fossiliferous exposed strata of the Brazilian Paleozoic cratonic basins. The Motuca Formation overlies the Pedra de Fogo Formation, principally in the central and southwestern areas of the basin (Maranhão and Tocantins states).

The Pedra de Fogo Formation has a wide distribution, especially in the central part of this basin, overlying deposits of the mid-Pennsylvanian Piauí Formation and forming the landscape relief, especially from the southern to northeastern rims of the basin (Fig. 1). Toward the western and central parts of the basin, the Pedra de Fogo Formation is frequently superposed by rocks of the overlying Permian Motuca Formation or even the Triassic Sambaíba Formation. The fossil woods studied here come from exposures referable to the Pedra de Fogo Formation, which in general are characterized by rocks with a predominance of silicified sandstones and siltstones, containing abundant layers of chert and limestone; and by fossils such as *Psaronius*-type ferns and petrified stems of large gymnosperms (Plummer, 1948; Caldas et al., 1989; Conceição et al., 2016 a, b), microbialites (ooids, pisoids, bacterial mats, and stromatolites) (Conceição et al., 2016a; Iannuzzi et al., 2018), and aquatic and terrestrial vertebrates (Plummer, 1948; Cox and Hutchinson, 1991; Cisneros et al., 2015). All typical features of this formation except vertebrate fossils are present in the outcrops analyzed here.

The section studied is located on the shores of the Boa Esperança Reservoir, Parnaíba River, Nova Iorque Municipality, southern Maranhão State in northeastern

Brazil (Fig. 1). The succession of these outcrops (Plate I, 1–2) has a maximum thickness of *ca.* 4 m and is laterally continuous for several kilometers. The stratigraphic column (Fig. 2) starts with coarse-grained quartz-rich sandstone, 1 to 2 m thick, colored cream to light orange (Plate I, 5). The sandstone has cross-bedding (Ttg) (trough and tangentially directed) at the base, gradually changing to subcritical climbing-ripple cross-lamination (Cr) at the top (Plate I, 2 (3, 5). The sets are 0.1 to 0.5 m thick, with normal grading. The coset has a fining upward tendency. The foresets of the cross-stratification are asymptotic. The paleocurrent sets have a mean orientation between SW/NW, with vectors that are mainly toward the SW, based principally on cross-bedding (Fig. 2). After a gap of *ca.* 0.4 m, due to the occurrence of *ex-situ* lateritic iron crust, the massive mudstone (Mm) prevails. This mudstone is up to *ca.* 2.5 m thick, mottled orange in color. Associated with the Mm are layers of a massive chert (Mc), nodular chert (Nc), and “Chert breccia” (Cb) (Plate I, 3–4). Microbialites occur locally (Plate I, 7) and silicified woods are abundant (Plate I, 8–9). These stems occur both horizontally, immersed in the massive mudstone, and randomly scattered on the present-day surfaces (Plate I, 8–9, respectively) resulting from recent erosive dynamics.

Regarding the lithostratigraphic units, the lower sandstone of the stratigraphic column corresponds to the uppermost Piauí Formation, while the upper silex-enriched mudstone represents the basal most part of the Pedra de Fogo Formation, i.e., Silex Basal Member (see Fig. 2), similar to those observed in other parts farther north toward the eastern margin of the Parnaíba basin by Conceição et al. (2016). In conclusion, the petrified material studied in this contribution comes from the lowermost part of the Pedra de Fogo Formation (Fig. 2).

4. Materials and methods

The gymnosperm fossil woods studied here were collected in outcrops situated on the shores of the Boa Esperança Reservoir in Nova Iorque Municipality, southeastern Maranhão State (Fig. 1). All the material studied consists of stems, which preserve the pith, the primary xylem, and the secondary xylem. They were found scattered on the surface, quite close to the above-mentioned rock exposures; however, some were recovered directly from the massive mudstone and are considered *in situ* material (Plate I, 8).

The thin sections were made in the laminating laboratory at the University of Vale do Rio dos Sinos (UNISINOS), São Leopoldo, Brazil. For each wood, thin sections were prepared in three different planes: transverse section (TS), tangential longitudinal section (TLS), and radial section (RS), following standard procedures (*sensu* Jones and Rowe, 1999; Merlotti and Rosa, 2002). Macroscopic photographs were taken with a Canon EOS T3i camera with a Sigma 70 mm DG Macro lens. The microscopic observations and digital images were taken with a Leica MC170 digital camera attached to a Leica DM500 microscope.

The descriptions and discussions of anatomical features of the fossil stems are according to the terminology of Mussa (1982), García Esteban et al. (2002), IAWA Committee (2004), Philippe and Bamford (2008), and Falcon-Lang (2003). A minimum of 25 measurements including diameters and lengths were taken for each of the anatomical characters analyzed (e.g., tracheids, rays, sclerotic cells, pith cells, cross-fields, pits and lacunae). In the descriptions, the sizes of the cells are provided next to the cell type, with the minimum and maximum sizes outside parentheses, respectively, and the means within parentheses.

The specimen with the prefix LPRP-USP, belonging to the University of São Paulo, is stored temporarily in the Paleobotanical Collection of the Federal University of Rio Grande do Sul (UFRGS), Porto Alegre, Brazil. The specimen with the prefix PAB belongs to the Paleobotanical Collection of the Federal University of Piauí (UFPI), Teresina, Brazil.

A detailed stratigraphic analysis of the sections documented five lithofacies, grouped into one facies association. These lithofacies were identified based on differences in grain size, sedimentary structures, paleocurrent measurements, bed thickness, shape, and continuity, as well as fossil content (silicified woods), following Walker (1992) and James and Dalrymple (2010). The lithofacies code follows the rule established by Miall (1977), in which the first, capital letter indicates the predominant granulometry, and the second, small letters refer to the main sedimentary structure.

The mineralogical composition was determined by Powder X-ray diffractometry, carried out with 160 g of a pulverized aliquot of each of the four representative bulk materials (randomly oriented samples), using a Panalytical Empyrean X-ray Diffractometer (DXR), Co anode, ceramic X-ray tubes ($K\alpha1 = 1.789010$ Å), long fine focus, Fe $K\beta$ filter, PIXCEL3D detector -Medpix3 1×1, in scanning mode, with 40 kV voltage, 35mA current, step size 0.0263 ° at 2θ, scan from 3 ° to 85 ° at 2θ, time/step 30.6 s, divergent slot: 1/4 ° and anti-scattering: 1/2 °, mask: 10 mm.

5. Systematics

Division: Gymnospermophyta Sternberg, 1820

Genus*:* ***Yvyrapitys*** Conceição et Crisafulli, gen. nov., Plates II–III.

Etymology: The generic name comes from the Guarani language, where *Yvyra* = wood.

Generic diagnosis*:* Pith large, non-septate and heterocellular, with sclerenchyma cells, and parenchyma sheath on medullary border. Primary xylem strands of endarch maturation. Secondary xylem homoxylic. Bordered pits arranged in mixed type on radial walls of tracheids, and cupressoid cross-field pits. Ray cells unpitted, parenchymatous and uniseriate (rarely biseriate).

Yvyrapitys novaiorquensis Conceição, Neregato et Iannuzzi, sp. nov., Plates II–III.

Holotype: LPRP-USP 0135.

Repository: University of São Paulo (USP), Ribeirão Preto, Brazil.

Type locality: Nova Iorque, southern Maranhão State, Brazil.

Stratigraphic horizon and age: Pedra de Fogo Formation, Cisuralian.

Etymology: The specific epithet refers to the municipality in which the fossil specimen was collected.

Specific diagnosis: Pith as in the genus. Tracheid walls of primary xylem with annular and scalariform/reticulate thickenings. Secondary xylem with pits arranged irregularly on radial walls, bordered pits, uniseriate to biseriate, spaced or contiguous, when biseriate they are sub-opposites and contiguous. Ray cells unpitted, parenchymatous and uniseriate (rarely biseriate), 1 to 20 (mean: 6.2) cells high. Cross-field pits cupressoid, with 1 to 6 (mean: 2.8) pits per cross-field.

Descriptions

General features

Species represented by 2 pieces, silicified, light brown, decorticated, 8 cm long and 9 cm in diameter. The pith in TS is circular, 1.2 cm in diameter, surrounded by pycnoxylic secondary xylem with growth interruptions and primary xylem strands (Plate II, 1–2).

Pith

In TS, the heterocellular pith is composed of parenchyma cells, a parenchyma sheath, some lacunae in the medullary border and sclerenchyma cells (Plate II, 3–6). The parenchyma cells are circular to oval, radial diameter 50 to 250 µm (mean: 80), tangential diameter 50 to 150 μm (mean: 82). The parenchyma sheath consists of rectangular cells, radial diameter 45 μm to 50 (mean: 45), tangential diameter 90 to 150 μm (mean: 110) (Plate II, 3 and 5). Visible circular to oval lacunae are present at the boundary of the primary xylem wedge; in TS, tangential and radial diameters reach up to 200–250 and 150–180 μm, respectively (Plate II, 4). The sclerenchyma cells (Plate II, 6) are polygonal, radial diameter 25 to 40 μm (mean: 31), tangential diameter 35 to 70 μm (mean: 43).

Primary Xylem

In TS, the primary xylem has endarch protoxylem maturation (Plate II, 6). The tracheid walls of the metaxylem are polygonal in TS, radial diameter 20 to 35 μm (mean: 26), tangential diameter 25 to 35 μm (mean: 29). In RLS, the walls of the proto - and metaxylem show helical, scalariform and reticulated thickenings (Plate II, 7).

Secondary Xylem

The secondary xylem of the stem is pycnoxylic with growth interruptions (Plate III, 1–2). Parenchyma rays are separated by 1–6 rows of tracheids. These tracheids in TS are polygonal to circular, radial diameter 32 to 60 μm (mean: 50), tangential diameter 30 to 50 μm (mean: 44).

In RS, the ends of the tracheids are commonly bent and overlap with each other (Plate III, 3); occasionally appearing rounded or tapered (Plate III, 4). The tracheid walls exhibit circular bordered pits, uniseriate to biseriate, spaced or contiguous (Plate III, 4–7). When biseriate they are sub-opposite and contiguous (Plate III, 5). The cross-field pitting is cupressoid, with 1 to 6 (mean: 2.8) pits per cross-field, arranged in pairs and sub-opposite (Plate III, 8). In TLS, the xylem rays are parenchymatous, unpitted and uniseriate, rarely biseriate, 1 to 20 (mean: 6.2) cells high, and 31 rays per mm^2 (Plate III, 9).

Comparison and discussion

The heterocellular piths with sclerenchyma and parenchyma cells are common to several Paleozoic genera (e.g., Kräusel, 1928, 1956; Mussa, 1978, 1986a; Prasad, 1982; Aassoumi and Vozenin-Serra, 1996; Crisafulli, 1995).

Nonetheless, few genera have similar piths to the specimen analyzed, that is, having sclerenchyma and parenchyma cells, besides a parenchyma sheath bounding the endarch primary xylem strands, and additionally lacunae in the periphery of the pith (Plate II). These characteristics, especially the parenchyma sheath, are comparable to only a few genera (Table 1). *Taeniopitys* Kräusel, 1962 (in Kräusel, 1962) displays secretory ducts and mesarch primary xylem, whereas the specimen in question has sclerenchyma cells dispersed throughout the medullary tissue and endarch primary xylem. *Lobatoxylon* Kräusel, 1956 (in Kräusel, 1956) has a pith with distinct lobes and secretory cells, yet differs from the present specimen, which has a circular pith without secretory cells. *Nandorioxylon* Biradar et Bonde, 1981 (in Biradar and Bonde, 1981), is also easily distinguished from our specimen by the homocellular lobulated pith, which markedly differs from the heterocellular circular pith in our material. Furthermore, *Nandorioxylon* has radial pitting of the araucarian type on tracheid walls and crassulae are present, two characters that are not present in our specimen (see Table 1). *Koleoxylon* Zhang et Zheng, 2006 (in Zhang et al., 2006) has secretory tissue elements. In addition, *Koleoxylon* has radial pitting of the araucarian type on tracheid walls, versus the mixed type on tracheid walls in the specimen under consideration.

Scleroabietoxylon Kurzawe et Merlotti, 2013 (in Kurzawe et al., 2013a) appears to be the genus with the most similarity to the present specimen, because it has a circular pith with a parenchyma sheath surrounding the wedge-shaped projections of the endarch primary xylem. It is distinguished by the presence of isolated sclerenchyma cells, which are constrained between the parenchyma sheath and the primary xylem. In the specimen described here, as mentioned above, sclerenchyma cells are scattered throughout the pith and between the parenchyma sheath and the primary xylem. In addition, *Scleroabietoxylon* has pitted parenchymatous rays, a character that has been rarely documented in fossil gymnosperms (Feng et al., 2010), while in our specimen the cell walls of the rays are unpitted.

Importantly, all the above-cited genera show radial pitting of the araucarian type on tracheid walls (see IAWA Committee, 2004 and Philippe and Bamford, 2008). Our wood shows radial pitting of the mixed type on tracheid walls (Philippe and Bamford, 2008). The combination of all these anatomical characters of the pith and secondary xylem justifies the recognition of a new genus et species from the specimen described herein named *Yvyrapitys novaiorquensis.*

Genus: *Novaiorquepitys* Conceição et Crisafulli, gen. nov., Plates IV–V.

Etymology: The generic name refers to the type locality, Nova Iorque Municipality.

Generic diagnosis: Gymnosperm stem with pith and primary and secondary vascular tissues preserved. Pith broad, non-septate, circular and heterocellular with peripheral lacunae; secretory and sclerenchyma cells scattered in pith and with thickened walls. Endarch primary xylem strands. Ray cells unpitted and parenchymatous, uniseriate to partly biseriate. Araucarian radial pitting on walls of tracheids, and cupressoid cross-field pits.

Novaiorquepitys maranhensis Conceição, Neregato et Iannuzzi, sp. nov., Plates IV–V.

Holotype: PAB 16.4.

Repository: Museum of Archeology and Paleontology, Federal University of Piauí (UFPI), Teresina, Brazil.

Type locality: Nova Iorque, southern Maranhão State, Brazil.

Stratigraphic horizon and age: Pedra de Fogo Formation, Cisuralian.

Etymology: The specific epithet refers to Maranhão State where the fossil was collected.

Specific diagnosis: Pith as in the genus. Tracheid walls of primary xylem with scalariform/reticulate thickenings. Tracheid radial pits 1–3 seriated, opposite to alternate and contiguous. Cross-field pits cupressoid with 1 to 6 (mean: 2.8) pits per cross-field. Ray cells parenchymatous, uniseriate to partly biseriate. Uniseriate rays of moderate height, 1 to 9 (mean: 4.3) cells high. Partly biseriate rays very high, 4 to 57 (mean: 30.9) cells high.

Descriptions

General features

The species is represented by 4 fragments of a single specimen, brown, up to 8.4 × 6 cm long and 10.4 cm in diameter (Plate IV, 1). The silicified wood is pycnoxylic, with no extraxylary tissues. The stem is composed of pith, primary xylem and secondary xylem preserved, and growth interruptions in the secondary xylem.

Pith

In TS, the pith is circular, up to 3 cm in diameter, and heterocellular with peripheral lacunae arranged between the primary xylem strands (Plate IV, 1–3). The well-preserved content of the pith is found most commonly on the medullary border. It is composed of parenchyma and sclerenchyma cells, and some secretory cells (Plate IV, 3–5) The lacunae (Plate IV, 2 and 3) are ovoid, with radial diameter 375 to 750 µm (mean: 628), tangential diameter 125 to 637 µm (mean: 422). The parenchyma cells are circular, radial diameter 60 to 125 µm (mean: 87), tangential diameter 60 to 90 µm (mean: 73). Sclerenchyma cells are polygonal, radial diameter 60 to 90 µm (mean: 73), tangential diameter 70 to 80 µm (mean: 73). Secretory cells occur in fewer numbers next to the parenchyma and sclerenchyma cells, and are circular, radial diameter 20 to 70 µm (mean: 40), tangential diameter 25 to 30 µm (mean: 23).

Primary Xylem

In TS, the primary xylem strands forms cuneiform projections with endarch protoxylem maturation; sometimes they are obliterated (Plate IV, 5). The tracheids of the metaxylem are polygonal in cross-section, radial diameter 15 to 37 µm (mean: 25), tangential diameter 15 to 30 µm (mean: 19). In RLS, relatively well-preserved scalariform to reticulated thickenings are present on the walls of the metaxylem cells (Plate IV, 6).

Secondary Xylem

The secondary xylem of the stem is pycnoxylic with growth interruptions (Plate V, 1–2). In TS, the tracheids are separated by 1 to 8 (mean: 4) parenchyma rays. These tracheids are quadrangular to oval, radial diameter 30 to 75 µm (mean: 46), tangential diameter 31 to 51 µm (mean: 49). In RLS, the tracheids are relatively variable in length, and the ends are usually rounded or tapered. Smaller tracheids with tapered ends range from 100 to 350 µm in length (Plate V, 5). The tracheid walls have bordered pits, 1–3 seriated, opposite to alternate and contiguous (Plate V, 3–5). Sometimes, the pits cover the entire width of the radial walls (Plate V, 3–5). The cross-field pitting is cupressoid, with 1 to 6 (mean: 2.8) circular pits per cross-field (Plate V, 5–7).

In TLS, the xylem rays are parenchymatous, unpitted, and uniseriate to partly biseriate (Plate V, 8). The uniseriate rays range in height from 1 to 9 (mean: 4.3) cells. The biseriate rays range in height from 4 to 57 (mean: 30.9) cells. The tangential section shows a frequency of 27 rays per mm^2.

Comparison and discussion

The features, mainly medullary, present in this specimen are relatively common in Paleozoic gymnosperm woods: a non-septate, circular and heterocellular pith, formed by elements of parenchyma, sclerenchyma, secretory cells, and lacunae (Plate IV). The primary xylem is endarch and the secondary xylem has araucarian radial pitting on the radial walls of the tracheids (Plate V, 3–5) and cupressoid cross-field pits (Plate V, 5–7). Additionally, the margin of the pith also contains a well-organized system of lacunae of various dimensions, which appear only between the primary xylem strands (Plate IV, 1–3). All these characteristics do not often occur together in the same taxon (See Table 2). Thus, the set of anatomical characters of the present specimen is comparable to those of only a few genera: *Idioxylon* Crisafulli, 1995 (in Crisafulli 1995), in the presence of secretory cells, sclerenchyma in the pith and cupressoid cross-field pits; and *Mesopityoxylon* Assoumi et Vozenin-Serra, 1996 (in Vozenin-Serra, 1996), also in the presence of sclerenchyma and secretory cells. However, the presence of secretory ducts in both genera distinguishes them from the specimen described here. In addition, *Idioxylon* has mesarch primary xylem and mixed pitting on the radial tracheid walls.

Shenoxylon Feng, Wang et Röβler (in Feng et al., 2011) shares with our specimen a heterocellular pith with sclerenchyma, endarch primary xylem, and cupressoid cross-field pits. However, *Shenoxylon* has a sclerified sheath in the pith and lacks secretory cells, while a sclerified sheath is absent in our wood and secretory cells are present. *Europoxylon* Vogellehner, 1965 (in Vogellehner, 1965), also similar to our specimen, has heterocellular pith with sclerenchyma, secretory cells, endarch primary xylem, and araucarian radial pitting on the radial walls. However, *Europoxylon* has ducts in the pith, which are absent in our specimen.

Among the Permian genera of the Parnaiba Basin, *Teresinoxylon* Mussa (in Caldas et al., 1989), *Scleroabietoxylon* Kurzawe et Merlotti, and *Ductoabietoxylon*

Kurzawe et Merlotti (in Kurzawe et al., 2013a) have some similarities to the present material. *Teresinoxylon,* similarly to the specimen described here, has circular pith with secretory cells, araucarian radial pitting on the radial walls, and secondary xylem with uniseriate to partly biseriate vascular rays. However, this genus lacks sclerenchyma cells in the pith and displays endarch to mesarch primary xylem, in addition to having a podocarpoid cross-field (see Caldas et al., 1989), which differs from the endarch primary xylem and cupressoid cross-field pits in our specimen.

Similarly to our specimen, *Scleroabietoxylon* has sclerenchyma in the pith, while *Ductoabietoxylon* has secretory cells, and both have endarch primary xylem strands. In addition to these medullary and primary xylem characters, the latter two genera partially share the secondary xylem with the specimen in question, due to the presence of araucarian radial pitting on the radial walls. However, *Scleroabietoxylon* and *Ductoabietoxylon* have pitted parenchymatous rays. Also, the latter genus has ducts in the pith (Kurzawe et al., 2013). Furthermore, both have araucarioid cross-field pits, contrasting with the cupressoid cross-field pits and unpitted parenchymatous rays in our material (Plate V and Table 2).

Finally, an additional character of this material that is not shared with all the above-mentioned woods is the presence of a well-organized system of lacunae of various dimensions, which appear between the primary xylem strands (Plates IV, 1–2). Feature, that have been considered as taxonomic by many authors in the Permian of the Gondwana province (e.g., Kräusel, 1956; Mussa, 1982, 1986a, b; Merlotti; 2002; Merlotti and Kurzawe, 2011).

Therefore, the specimen described here shows a very particular combination of anatomical features, which are not shared in their entirety with the above-mentioned genera. These differences justify the recognition of a new genus and species based on the present specimens.

6. Discussion

6.1. Paleoenvironmental interpretation

Two facies associations were recognized in the study section, and are interpreted as follows (Fig. 2).

Facies association 1: Fluvial channel

Interpretation. The internal arrangement of the lithofacies shows climbing and trough cross-bedded sets, which are indicative of a generally southwesterly migration of small-scale sinuous-crested dunes. These sand bodies accumulated on the bed of a stream channel (Allen, 1983; Reesink et al., 2015). This interpretation is similar to features described by Soltan and Mountney (2016) in North Yorkshire (UK) and by Bristow (1993) in Bangladesh, where this last author envisaged downstream-accreting bedforms that developed during the high-flow stage in the Brahmaputra River, and also to bedforms that occur in very shallow braided rivers (Bristow, 1988). Similarly, Ghinassi et al. (2009) attributed small-scale trough and planar cross-bedding (3D and 2D mesoforms, respectively) from fluvial sediments to shallow low-sinuosity channel deposits. Preserved set thicknesses of <0.2 m suggest that the original mean dune height was 0.4 to 0.7 m (Leclair, 2011), which implies limited sediment input into a relatively shallow channel, within which flow conditions resulted in dune migration and climb at (net) subcritical angles (Collinson et al., 2006). The normal grading and coset fining upward tendency suggest a reduction in channel/water depth, with alternative changes in discharge and sediment load (Allen, 1965). This facies association corresponds to a fluvial channel positioned in the upper part of the Piauí Formation.

Facies association 2: lacustrine wet plain

Interpretation. Deposition of this monotonous facies association with mudstones and chert beds, associated with microbialite shapes, most likely occurred in a lacustrine environment (Talbot and Allen, 1996; Gierlowski-Kordesch and Kelts, 2000). The fine grain size and wide lateral extent of this association suggest that it was deposited in a predominantly low-energy environment. The mottling indicates that it has been subjected to pedogenic processes (PiPujol and Buurman, 1997; Retallack, 2001). The massive and homogeneous texture of the Mm facies might be the result of bioturbation to pedoturbation (Boggs Jr., 2006). Microbialites probably formed in this shallow-water environment (Hofmann, 1973). Silicified woods are associated with a wet lacustrine muddy plain, similar to those described by Sigleo (1978, 1979) and Opluštil et al. (2013). The wide lateral continuity of succession indicates a lake that extended over several kilometers. X-ray diffractometry (Fig. 3) shows that the cherts are composed entirely of quartz with a high crystallinity index and well-ordered crystal structure, suggestive of a long crystallization time (Murata and Norman, 1976; Williams et al., 1985; Williams and Crerar, 1985). The presence of chert nodules and chert beds as well as silicified woods and organo-sedimentary structures (Iannuzzi et al., 2018) may imply cyclic precipitation, possibly seasonally controlled, either by the ratio of freshwater input to evaporation or by seasonal variations in bioproductivity in the lake itself (Eugster, 1969; Peterson and von der Borch, 1965; Krainer and Spotl, 1998). This facies matches the Pedra de Fogo Formation, according to the sediment descriptions by previous authors (Andrade et al., 2014; Conceição et al., 2016a).

6.2. Paleophytogeographic significance

The Permian plants of the Parnaíba Basin constitute an important record within the Paleozoic, because in addition to their good preservation, abundance, and wide area of occurrence, they represent a flora that was located between the two of the major

Paleozoic floral provinces, the Gondwanan in the south and the Euramerican in the north, in a particular paleogeographic position at the southernmost limit of the tropical belt (Mussa and Coimbra, 1987; Dias-Brito et al., 2009; Neregato et al., 2017; Iannuzzi et al., 2018). Since the studies of Dolianiti (1948) and Mussa and Coimbra (1987), questions have arisen about the possible origin of the Permian floral elements in this basin, whether Gondwanan or Euramerican. Dolianiti (1948) and Mussa and Coimbra (1987), considered that the Permian strata of the Parnaíba Basin could contain a mixed flora, i.e., composed of Gondwanan and Euramerican elements, due to its paleogeographic position.

In recent decades, paleobotanical research in this basin has made considerable progress (e.g., Coimbra and Mussa, 1984; Mussa and Coimbra, 1987; Herbst, 1986, 1999; Rößler and Noll, 2002; Rößler and Galtier, 2002a, b; Rößler and Galtier, 2003; Tavares et al., 2014; Neregato et al., 2015, 2017; Kurzawe et al., 2013a, b), and the new information encourages us to reflect on this issue in greater depth. All these studies discussed the similarity of this flora to the Gondwanan and Euramerican, but only Neregato et al. (2017) addressed this problem in greater detail, using similarity-coefficient analyses. These analyses demonstrated that although the flora of the Parnaíba Basin has a high percentage of genera shared with both the Gondwanan and Euramerican Provinces, and to a lesser extent with the Cathaysian, the endemic elements predominate. This led these authors to propose a new formal phytogeographic unit coined the ‘Mid-North Brazilian Region’, based on the criteria proposed by Wnuk (1996). According to Neregato et al. (2017), a set of abiotic features exclusive to this region of the South American continent, such as the paleogeographic position (ca. 30°S in north-central Gondwana), palaeoclimatic conditions (tropical wet summer), and sedimentary environments (braided fluvial systems and playa lakes associated with microbial mats, stromatolites, and evaporitic and gypsum deposits), supports this conclusion (see also Iannuzzi et al., 2018). As a result of this study, we have added herein two more endemic genera to the Pedra de Fogo Formation which reinforces the hypothesis of the existence of a distinct flora in this region (see also part II in Conceiçao et al., in press).

6.3. Paleoecological considerations

Data from fossil-wood anatomy comprise a significant source of information on paleoenvironments and paleoclimates, which is especially valuable when coupled with information from the sedimentological record of a region (Creber and Chaloner, 1984; Taylor et al., 2009). None of the woods described here has true growth rings, because the boundaries between the growth rings are abrupt by definition (IAWA, 2004). True growth rings are an alternation between tracheids of late wood with thick walls and tracheids of early wood with thin walls and large diameters (Creber and Chaloner, 1984) and they result from the complete cessation of cambial activity (Schweingruber, 1996, 2006). The material described here contains only growth interruptions, which according to Schweingruber (1992, 1996) consist of a symmetrical or weakly asymmetrical ring boundary, exhibiting a gradual decrease and subsequent gradual increase in tracheid diameter, and are produced by a temporary slowing of cambial activity.

The paleoenvironmental characteristics of the petrified gymnosperm-bearing rocks, which outcrop in the northeastern part of the Parnaíba Basin (Conceição et al., 2016b), as well as those of the exposures in question (this study), indicate that these woody plants lived near the shores of large lakes (Conceição et al., 2016a). According to Parrish and Falcon-Lang (2007), plants that grew in a locally saturated environment where they were protected from regional seasonality, for instance riparian or lakeshore settings, tend to exhibit such growth interruptions. These interpretations are also supported by the presence of certain anatomical structures present in the taxa analyzed, such as the peripheral lacunae arranged between the primary xylem strands, which could serve to facilitate aeration or water storage to support metabolism in periods of low water oxygenation or extended drought (Mussa, 1986a; Metcalfe and Chalk, 1950). These inferences are also supported by the presence of arborescent pteridophytes, i.e. calamitean trees and tree ferns, that are also found associated with gymnosperm stems in this area (Plate VI), which indicates a stable and weakly seasonal paleoprecipitation regime. This interpretation is generally in line with the suggestion of Iannuzzi et al. (2018) that relatively humid environmental conditions existed during the period of prosperity of these tree-dominated communities along the lake shores.

7. Conclusions

After a long period with no research conducted on the taxonomy of petrified gymnosperm woods in the Pedra de Fogo Formation, we describe herein two new endemic forms, which are very different in terms of morphology and structure of the pith. This allowed us to erect two genera et species, since the pith is the main diagnostic character used as a criterion for the identification and classification of Paleozoic gymnosperm woods (Pant and Singh, 1987; Lepekhina, 1972).

These results provide additional evidence of the occurrence of an endemic gymnosperm association from the Parnaíba Basin, increasing our understanding of the flora that dominated this part of the basin during the Permian, and reinforces the recent hypothesis of the existence of a distinct biogeographical province in the Parnaíba Basin.

The anatomical characters of these newly proposed gymnosperm taxa, associated with sedimentological data and the presence in the same area of tree ferns and tree- calamitaleans plants that live in wetlands, indicate that these woody plants lived near the shores of large lakes. Therefore, this study demonstrates the potential of the Pedra de Fogo Formation for future studies of Paleozoic gymnosperm woods.

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Captions

Fig. 1. General geological map of the Parnaíba Basin. The star indicates the location of the paleobotanical outcrops. Permian forests in life position occur in the municipalities of Duque Bacelar, Maranhão State and Teresina, Piauí State. TFTNM, Tocantins Fossil Trees Natural Monument. Modified from Iannuzzi et al., 2018.

Fig. 2. Sample sketch log of the fluvial/lacustrine succession attributed to the upper part of the Piauí Formation and lower part of the Pedra de Fogo Formation, with plant fossil. Lithofacies: Ttg = trough and tangential cross-bedding; Cr = subcritically climbing-ripple cross-lamination; Mc = massive chert; Nc = nodular chert; Cb = chert breccia.

Fig. 3. X-ray powder diffraction patterns of pure macroscopic quartz, showing narrow peaks. NI-SX1, NI-SX2, NI-SX3 and NI-SX4 correspond to the four layers of chert.

Plate I. Sedimentary succession of the outcrops in Nova Iorque Municipality, Maranhão State, northeastern of Brazil. **1–2**. Typical morphology of the study area, characterized by outcrops with irregular thickness on the banks of the Parnaíba River. The black vertical rectangle in **2** indicates the location of the log shown in Plate I (3–6). **3–4.** Detail of the upper part of the succession, with abundant nodular and irregular layers of chert in the massive mudstone. **5–6**. Detail of the lower part of the succession, formed by climbing-ripple cross-lamination and trough to tangential cross-bedding sandstone. **7.** Microbialites. **8.** Silicified gymnosperm wood recorded in the massive mudstone. **9**. Silicified gymnosperms wood scattered on the current surfaces.

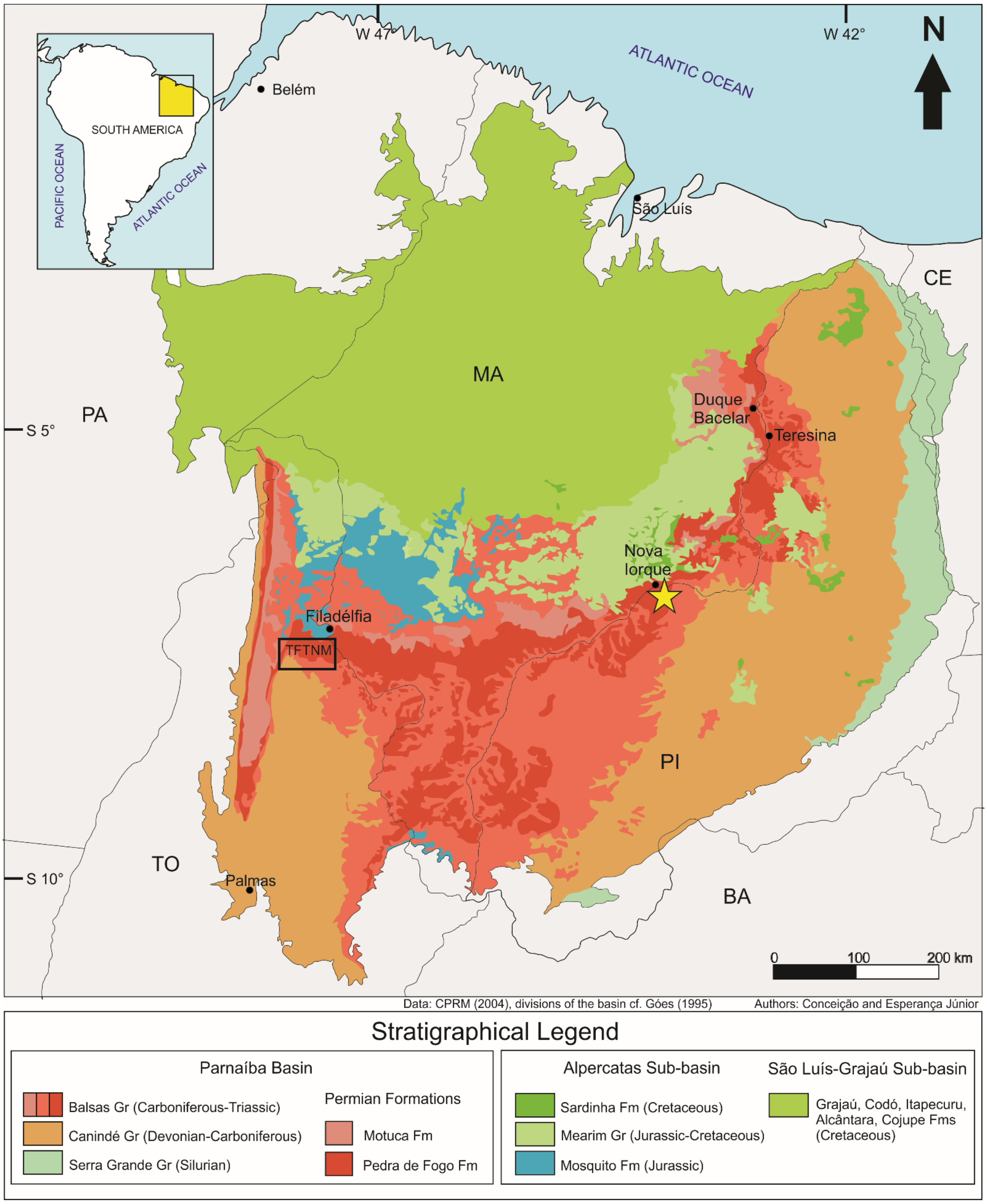
Plate II. *Yvyrapitys novaiorquensis* sp. nov., holotype (LPRP-USP 0135). Overview of the stem and the primary vascular tissues: **1**. TS, polished surface showing the pycnoxylic wood and pith. **2**. TS, detail of pith and secondary xylem. **3**. TS, general view showing parenchyma sheath (arrows). **4**. TS, showing details of the lacunae (arrows). **5**. Detail of parenchyma sheath cells and sclerenchyma cells (arrow). **6**. TS, strands of primary xylem endarch (arrowhead) and sclerenchyma cells (arrows). **7**. RLS, showing the pith (P); helical thickenings of the protoxylem (PX); scalariform/reticulate thickenings of the metaxylem (MX) and bordered pits on the tracheid walls in the secondary xylem (SX). Scale bars: **1 =** 1 cm; **2** = 1 mm; **3** = 400 µm; **4**, **5**, **6** and **7** = 100 µm

Plate III. *Yvyrapitys novaiorquensis* sp. nov., holotype (LPRP-USP 0135). Overview of the secondary xylem: **1**. TS, showing the pycnoxylic wood with growth interruptions (arrows). **2**. Detail of **1** showing the growth interruptions (arrows). **3**. RLS, showing the ends of tracheids, commonly bent and overlapping on each other (arrow). **4**. RLS, general view showing both, araucarian and abietinean uniseriate radial pitting. **5**. RLS, showing mostly biseriate sub-opposites araucarian pits. **6 and 7**: RLS, detail with both araucarian (black arrows) and abietinean uniseriate radial pitting (white arrows). **8**. RLS, cupressoid cross-fields pits (arrows). **9**. TLS, showing ray cells unpitted, parenchymatous and uniseriate with 1 to 20 (mean: 6.2) cells high. Scale bars: **1** = 500 µm; **2** = 200 µm; **3** and **4** =100 µm; **5, 6** and **7**= 50 µm; **8**= 25 **9**=100 µm.

Plate IV. *Novaiorquepitys maranhensis* sp. nov., holotype (PAB 16.4). General view of the stem and the primary vascular tissues: **1**. TS, polished surface showing the pycnoxylic wood with a broad pith. **2**. TS, view of part of stem with peripheral lacunae (arrowheads) arranged between the primary xylem strands. **3**. TS, detail of the lacunae (arrowheads) and pith with sclerenchyma cells (arrow). **4**. RLS, showing the pith (P), scalariform/reticulate thickenings of primary xylem (MX), and secondary xylem (SX). **5**. TS, strand of endarch primary xylem (arrowhead) and secretory cells (arrows). **6**. RLS, detail of **4** showing scalariform/reticulate thickenings of tracheids of the primary xylem (arrowheads). Scale bars: **1** = 10 mm; **2** = 5 mm; **3**, **4**, **5** and **6** = 200 µm.

Plate V. *Novaiorquepitys maranhensis* sp. nov., holotype (PAB 16.4). General aspect of the secondary xylem: **1**. TS, showing the pycnoxylic secondary xylem with growth interruptions (arrowheads). **2**. TS, detail of Fig. 1 showing growth interruptions (arrowhead). **3**. RLS, showing the triseriate araucarian pitting on the tracheid walls. **4**. RLS, showing the predominant alternating biseriate and contiguous bordered pits on the tracheid walls. **5**. RLS, showing the cupressoid cross-field pitting (arrow) and triseriate opposite bordered pits on the wall of a short tracheid (arrowhead). **6** and **7**. RLS, detail of **5** showing the cupressoid cross-field pitting .**8**. TLS, showing the uniseriate and biseriate parenchymatous rays. Scale bars: 1 = 500 µm; **2** and **3** = 200 µm; **4** = 50 µm; **5** = 100 µm; **6** and **7** = 25 µm; 8 = 250 µm.

Plate VI. Calamitalean and tree-fern stems from outcrops in Nova Iorque, Maranhão State.**1**. Calamitean tree (*Arthropitys* sp.). **2** and **3**. Tree-fern stems. **4.** Pecopterid fronds. Scale bars: **2** and **6**. 1 cm.



Data: CPRM (2004), divisions of the basin cf. Góes (1995)

Authors: Conceição and Esperança Júnior

Fig. 1

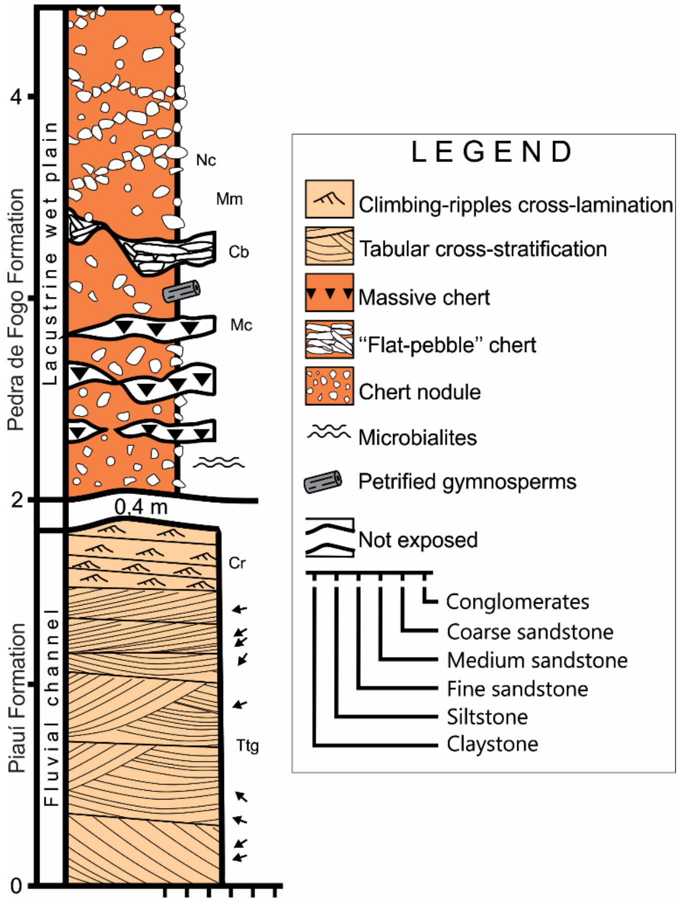

4
2
0
Pedra de Fogo Formation
Lacustrine wet plain
Piauí Formation
Fluvial channel
Nc
Mm
Cb
Mc
0,4 m
Cr
Ttg
LEGEND
Climbing-ripples cross-lamination
Tabular cross-stratification
Massive chert
"Flat-pebble" chert
Chert nodule
Microbialites
Petrified gymnosperms
Not exposed
Conglomerates
Coarse sandstone
Medium sandstone
Fine sandstone
Siltstone
Claystone

Fig. 2

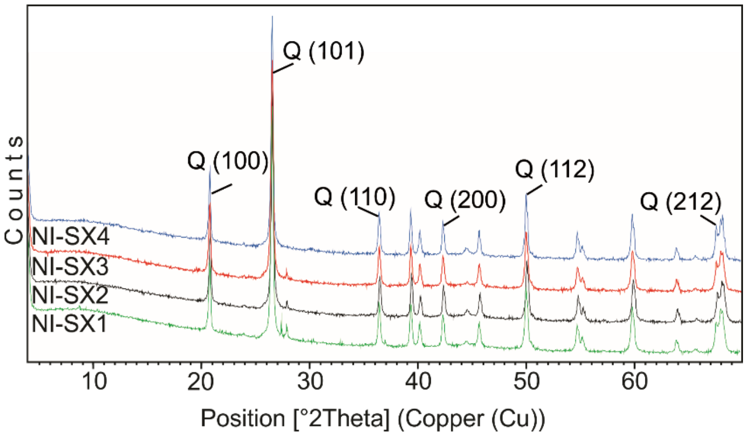
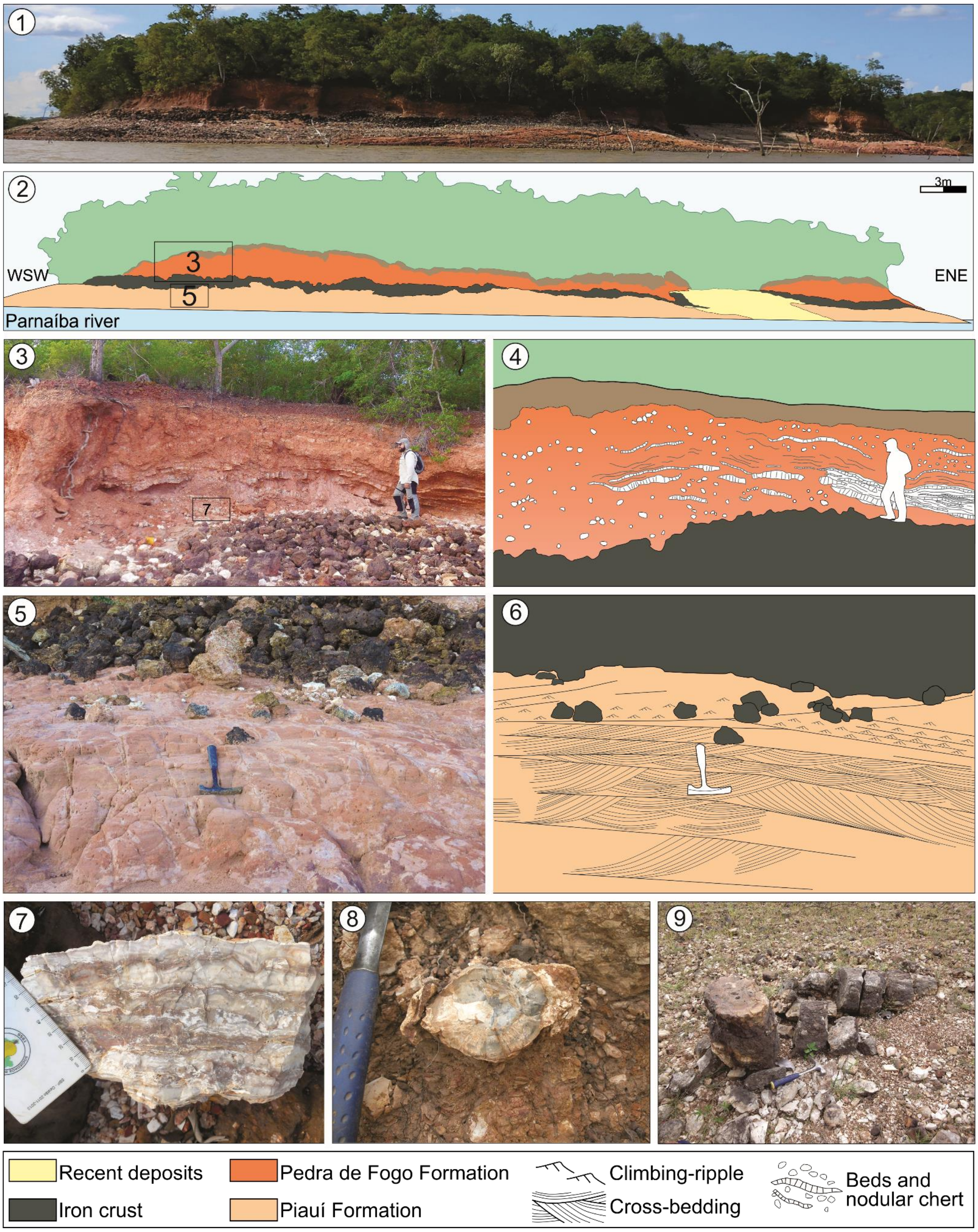

Counts
Q (101)
Q (100)
Q (110)
Q (200)
Q (112)
Q (212)
NI-SX4
NI-SX3
NI-SX2
NI-SX1
10
20
30
40
50
60
Position [°2Theta] (Copper (Cu))

Fig. 3


1
2
3m
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5
WSW
ENE
Parnaíba river
3
7
4
5
6
7
8
9
Recent deposits
Iron crust
Pedra de Fogo Formation
Piauí Formation
Climbing-ripple
Cross-bedding
Beds and nodular chert

Plate I

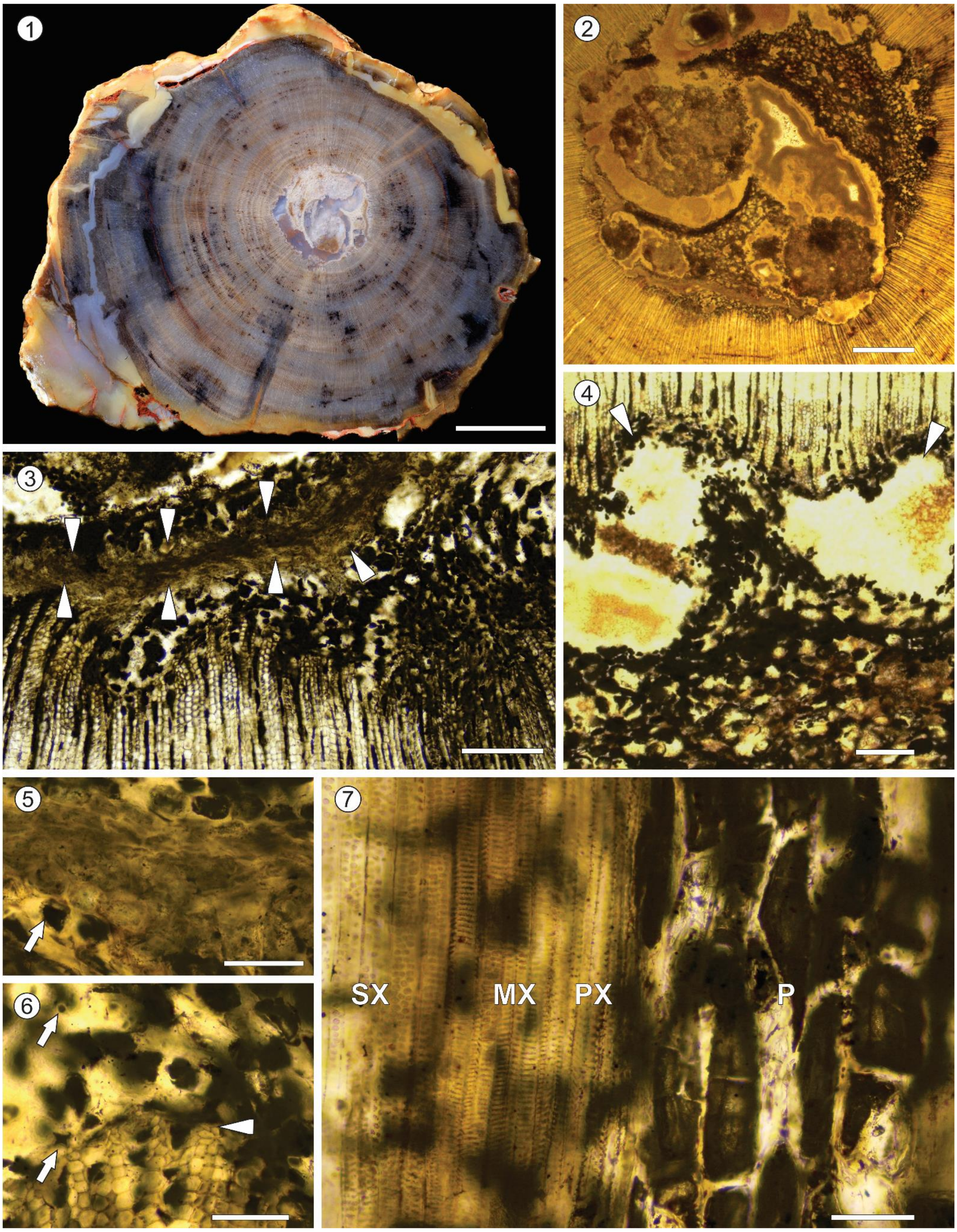

Plate II

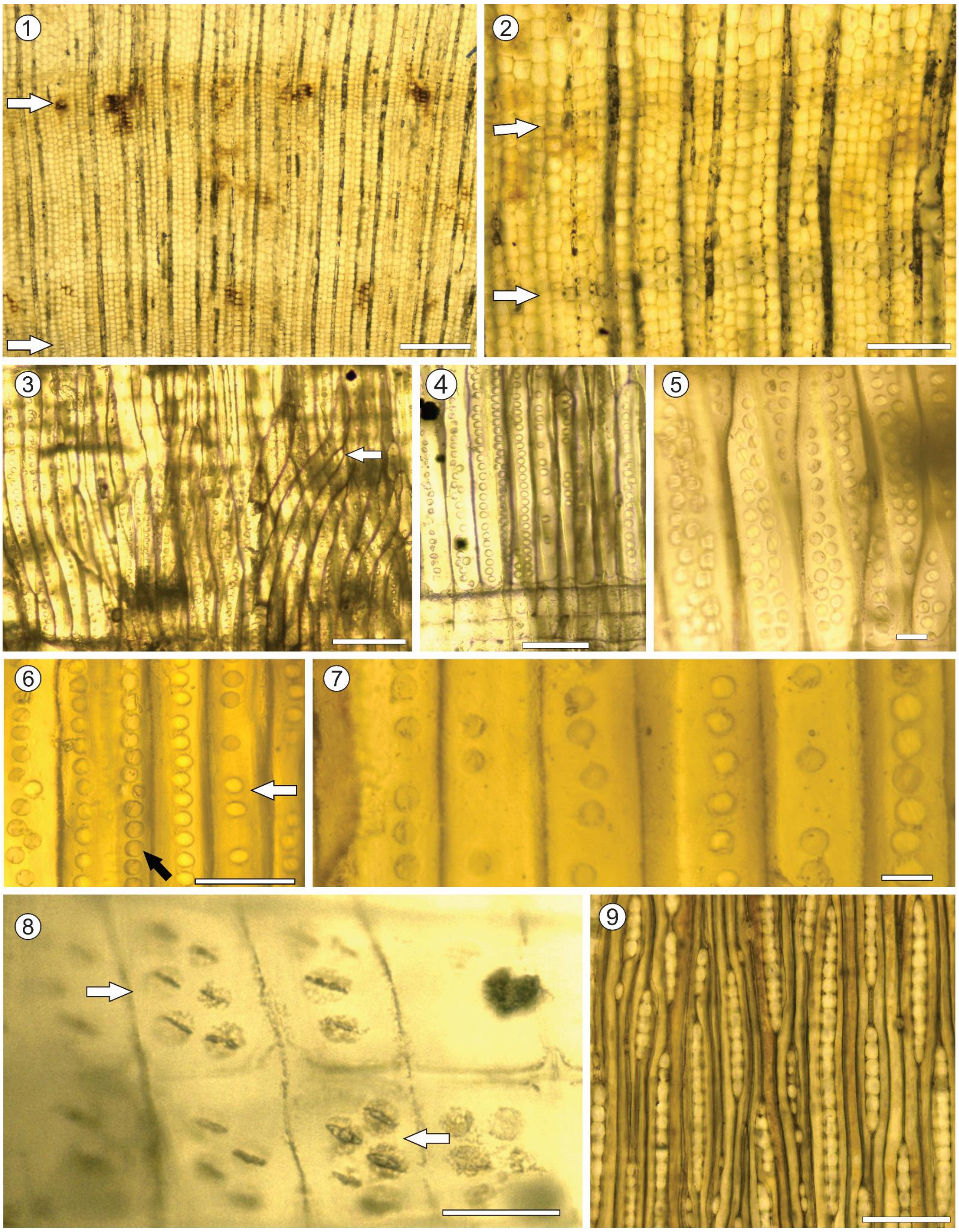

Plate III

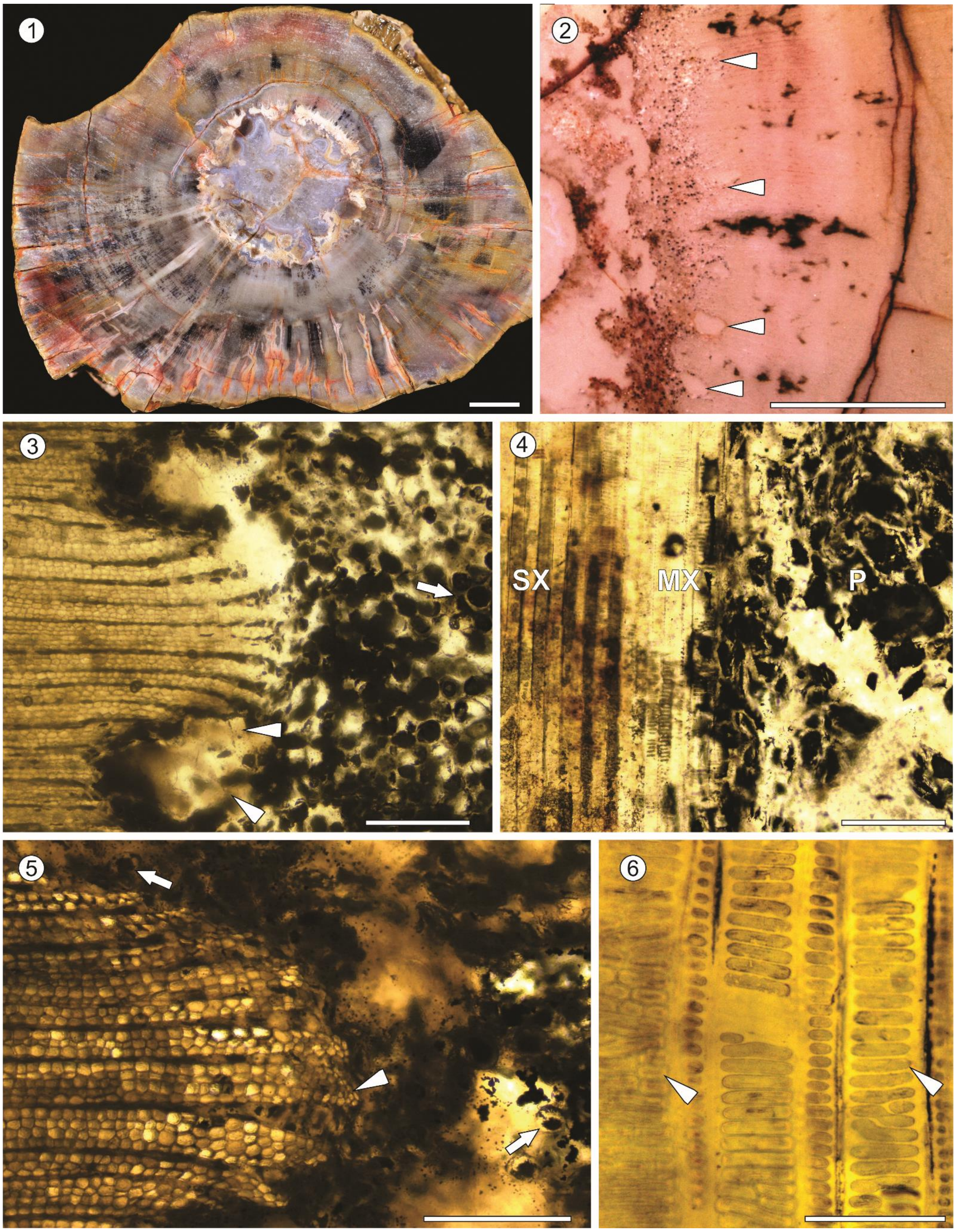

Plate IV

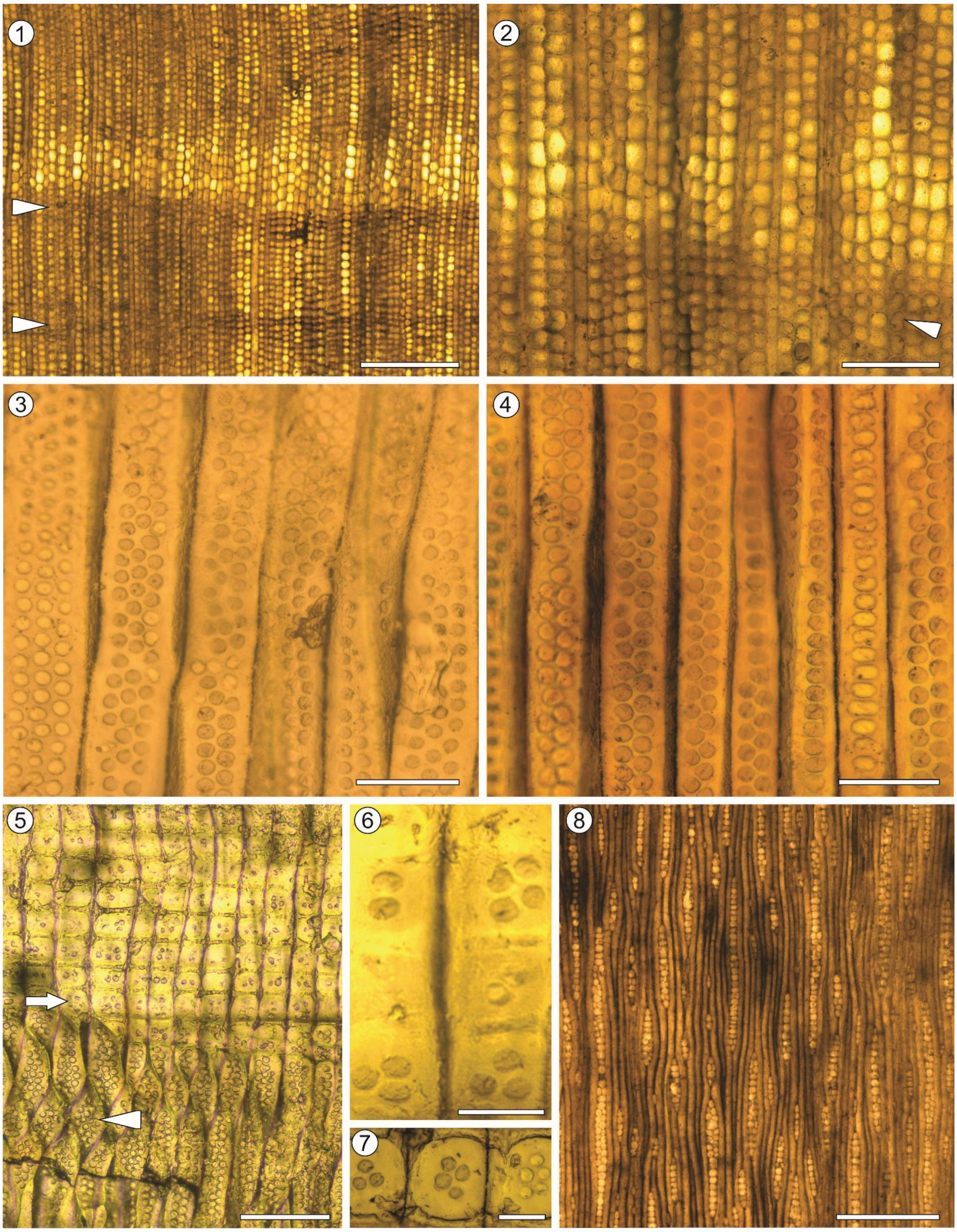

Plate V

Plate VI

Table 1: Genera with parenchyma sheath comparable with *Yvyrapitys*

Genus	Pith	Primary xylem	Secondary xylem			Type locality and age
			Pitting on radial walls	Cross-field pits	Xylem rays	
Lobatoxylon Kräusel, 1956	Solid, lobulated and heterocellular, with secretory cells and ducts	Endarch	Araucarian, uni to biseriat	Araucarioid, up to 3 pits	Uniseriate, up to 50 cells high	South African; Permian
Nandorioxylon Biradar et Bonde, 1981	Solid, lobulated and homocellular	Endarch	Araucarian, uni- to triseriate, crassulae is present	Cupressoid, up to 7 pits	Uniseriate, rarely biseriate, up to 36 cells high	Nandori Buzrug, India; Permian
Koleoxylon Zhang et Zheng 2006	Solid and heterocellular, with secretory tissue and sclerenchyma cells	Endarch	Araucarian	?	?	Taiyuan, China; Permian
Scleroabietoxylon Kurzawe et Merlotti, 2013a	Solid and heterocellular, with sclerenchyma	Endarch	Araucarian, uni- to biseriate, rarely triseriate	Araucarioid, up to 5 pits	Uniseriate, Uniseriate, locally biseriate, up to 28 cells high, and abietoid	Tocantins, Brazil; Permian
Taeniopitys Kräusel, 1962	solid and heterocellular, with secretory ducts	Mesarch	Araucarian, uniseriate to triseriate	Araucarioid, 4–6 pits	Uniseriate, rarely biseriate, up to 12 cells high	Allan Nunatak, Victoria Land; Permian? Triassic
Yvyrapitys Conceição et Crisafulli gen. nov	Solid and heterocellular, with sclerenchyma, parenchymal sheath and lacunae	Endarch	Mixed, uniseriate or biseriate	cupressoid with 1 to 6 pits	Uniseriate, rarely biseriate, up to 19 cells high	Maranhão, Brazil; Permian

Table 2: Genera with most similarities with *Novaiorquepitys*

Genus	Pith	Primary xylem	Secondary xylem			Type locality and age
			Pitting on radial walls	Cross-field pits	Xylem rays	
Ductoabietoxylon Kurzawe et Merlotti, 2013a	Solid and heterocellular, with secretory and sclerenchyma cells and ducts	Endarch	Araucarian, uni- to triseriate	Araucarioid, up to 5 pits	Uniseriate, locally biseriate, up to 37 cells high, and abietoid	Tocantins, Brazil; Permian
Europoxylon Vogellehner, 1965	Solid and heterocellular, with secretory cells and ducts	Endarch	Araucarian, uni- to biseriate	Up to 4 pits	Uniseriate, up to 11 cells high	Franconia, Germany; Middle to Upper Triassic
Idioxylon Crisafulli, 1995	Solid, solenoid and heterocellular, with secretory and sclerenchyma cells	Mesarch	Mixed, uni to biseriate	Cupressoid, 2–4 pits	Uniseriate, up to 38 cells high	Arroyo Seco, Uruguay; Permian
Mesopityoxylon Assoumi et Vozenin-Serra, 1996	Solid, solenoid and heterocellular, with resiniferous cells and sclerenchyma	Endarch	Araucarian, uniseriate	Cupressoid or taxodioid, up to 4 pits, or phyllocladoid, 1 pit	Uniseriate, locally biseriate, up to 30 cells high	Bou Rzem, Morocco; Permian
Scleroabietoxylon Kurzawe et Merlotti, 2013a	Solid and heterocellular, with sclerenchyma and parenchymal sheath	Endarch	Araucarian, uni- to biseriate, rarely triseriate	Araucarioid, up to 5 pits	Uniseriate, locally biseriate, up to 28 cells high, and abietoid	Tocantins, Brazil; Permian
Teresinoxylon Mussa, 1989	Solid, heterocellular, with secretory cells and transfusion tissue	Endarch	Araucarian, uni to biseriate	Podocarpoid one pit	uniseriate to partly biseriate, rarely triseriate	Piauí, Brazil, Permian
Shenoxylon Feng, Wang et Rößler, 2011	Solid and heterocellular with sclerenchyma and a sclerefied sheath	Endarch	Uni to biseriate	Cupressoid, up to 4 pits	Uniseriate, locally biseriate, up to 14 cells high	Shitanjing, China; Permian
Novaiorquepitys Conceição et Crisafulli, gen. nov.	Solid, and heterocellular, with secretory and sclerenchyma cells and peripheral lacunae	Endarch	Araucarian, uni- to triseriate	Cupressoid, 2–6 pits	Uniseriate to partly biseriate. Uniseriate 1 to 9 cells high and partly biseriate up to 56 cells high	Maranhão, Brazil; Permian

Geobios

New petrified gymnosperms from the Permian of Maranhão (Pedra de Fogo Formation), Brazil: Ductolobatopitys and Kaokoxylon

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Corresponding Author:	Domingas Maria da Conceição BRAZIL
First Author:	Domingas Maria da Conceição, Mrs.
Order of Authors:	Domingas Maria da Conceição, Mrs.
	Luiz Saturnino de Andrade, Dr.
	Rodrigo Neregato, Dr.
	Roberto Iannuzzi, Dr.
	Alexandra Crisafulli, Dra.
	Juan Carlos Cisneros, Dr.
Abstract:	Continuing the study of petrified gymnosperm trunks recovered from the Pedra de Fogo Formations, we identified two new taxa from the Permian deposits of the Parnaíba Basin, northeastern Brazil. One taxon is an endemic form named Ductolobatopitys mussae , characterized by solenoid, lobed and non-septate heterocellular pith, cauline bundles with endarch maturation, and secondary xylem with araucarian radial pitting on the tracheid walls. The other form is assigned to the genus Kaokoxylon , which has been recorded from most of Gondwana, including the Parnaíba Basin , but is recorded for the first time in Pedra de Fogo Formation, with a new species Kaokoxylon brasiliensis nov. sp. It is characterized by solid, non-septate heterocellular pith with sclerenchyma cells; endarch cauline bundles; and uni- to triseriate radial pitting on the walls of the tracheids. The sedimentological interpretations of the outcrops where the fossils were collected indicate that these plants lived on the shores of large continental lakes, with relatively high humidity but possibly periods of drought. These inferences are supported by the anatomical pith features, growth interruptions in the secondary xylem, the presence of calamitalean and tree-fern stems, and microbialites that crop in the same area. These new finds not only increase the known diversity of the flora in the Pedra de Fogo Formation, but also provide more accurate information for understanding the floristic elements that formed the subtropical flora during the Cisuralian in this basin in Western Gondwana.
Suggested Reviewers:	ANNE-LAURE DECOMBEIX, Dr. Research Associate, University of Missouri Kansas City anne-laure.decombeix@cirad.fr Paleobotanist working on the systematic and functional diversity of Paleozoic and early Mesozoic plants.
	Tatiane Tavares Marinho Vieira Tavares, Dr. Researcher, Universidade Federal do Tocantins, Brazil tatianetavares@uft.edu.br Expert in fossil plant anatomy, with extensive experience in the Parnaíba Basin.
	Zhuo Feng, Dr. researcher, Yunnan University jumperfeng@126.com Expert in wood anatomy of gymnosperm paleozoic.
Response to Reviewers:	

New petrified gymnosperms from the Permian of Maranhão (Pedra de Fogo Formation), Brazil: *Ductolobatopitys* and *Kaokoxylon*

Domingas Maria da Conceição [a,*], Luiz Saturnino de Andrade [b], Rodrigo Neregato [a]; Roberto Iannuzzi [a], Alexandra Crisafulli [c], Juan Carlos Cisneros [d]

[a] Programa de Pós-Graduação em Geociências, Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul. Caixa Postal 15.001, CEP 91.509–900, Porto Alegre, Brazil

[b] Instituto de Geociências, Universidade Federal do Pará, Rua Augusto Correa 1, 66075–110, Belém, Brazil

[c] Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste y CECOAL–CONICET Ruta 5, km 2,5 – 3400, Corrientes, Argentina

[d] Universidade Federal do Piauí, Museu de Arqueologia e Paleontologia, CEP 64.049–550, Teresina, PI, Brazil and Programa de Pós-graduação em Geociências, Universidade Federal do Pernambuco, Recife, Brazil

* Corresponding author: domingasmary@hotmail.com (D.M. da Conceição).

Abstract

Continuing the study of petrified gymnosperm trunks recovered from the Pedra de Fogo Formations, we identified two new taxa from the Permian deposits of the Parnaíba Basin, northeastern Brazil. One taxon is an endemic form named *Ductolobatopitys mussae*, characterized by solenoid, lobed and non-septate heterocellular pith, cauline bundles with endarch maturation, and secondary xylem with araucarian radial pitting on the tracheid walls. The other form is assigned to the genus *Kaokoxylon*, which has been recorded from most of Gondwana, including the Parnaíba Basin , but is recorded for the first time in Pedra de Fogo Formation, with a new species *Kaokoxylon brasiliensis* nov. sp. It is characterized by solid, non-septate heterocellular pith with sclerenchyma cells; endarch cauline bundles; and uni- to triseriate radial pitting on the walls of the tracheids. The sedimentological interpretations of the outcrops where the fossils were collected indicate that these plants lived on the shores of large continental lakes, with relatively high humidity but possibly periods of drought. These inferences are supported by the anatomical pith features, growth interruptions in the secondary xylem, the presence of calamitalean and tree-fern stems, and microbialites that crop in the same area. These new finds not only increase the known diversity of the flora in the Pedra de Fogo Formation, but also provide more accurate information for understanding the floristic elements that formed the subtropical flora during the Cisuralian in this basin in Western Gondwana.

Keywords: Gymnosperm woods; Pedra de Fogo Formation; lacustrine environment; Permian; Parnaíba Basin

1. Introduction

The paleobotanical record of the Permian in the Parnaíba Basin has been recognized since the late nineteenth century, with the classic work of Brongniart (1872). However, this record has received more attention only in the past 30 years, with numerous taxa described recently (e.g., Coimbra and Mussa, 1984; Mussa and Coimbra, 1987; Herbst, 1986, 1999; Rößler and Noll, 2002; Rößler and Galtier, 2002a, b; 2003; Kurzawe et al., 2013a, b; Tavares et al., 2014; Neregato et al., 2015, 2017). Most of these studies focused on outcrops of the Motuca Formation, whereas the exposures of the Pedra de Fogo Formation, especially the floristic components, are less thoroughly investigated. One of the most prominent features of the Pedra de Fogo Formation is the petrified stems of ferns and seed plants, as noted since the late nineteenth and early twentieth centuries (e.g., Brongniart, 1872; Pelourde, 1914; Oliveira, 1934; Plummer, 1948). The paleobotanical potential of the Pedra de Fogo Formation has been confirmed over the last few decades by the increase of published studies (Herbst, 1985; Caldas et al., 1989; Conceição et al., 2016a, b). Although paleobotanical research has intensified somewhat in recent years, much remains to be learned about this flora and its respective environments.

In this contribution, we report two new taxa based on silicified trunks from the Cisuralian lacustrine sedimentary deposits in the Pedra de Fogo Formation, Parnaíba Basin, northeastern Brazil. We discuss briefly the significance of these genera for the paleoecology and paleoenvironment in the deposits of this basin. These results are part of the first author's Ph.D. Thesis, whose first results are being presented in another contribution.

2. Geological setting

The fossil plants are found in deposits assigned to the Pedra de Fogo Formation (Plummer, 1948), which together with Motuca and Sambaíba formations form the Balsas Group (Carboniferous–Middle Triassic) of the intracratonic Parnaíba Basin (Góes and Feijó, 1994, fig. 1). This sedimentary basin fill dates from the Ordovician–Silurian to the Cretaceous, reflecting a multi-episodic sedimentation in an intracratonic basin (Vaz et al., 2007). Detailed recent information about the stratigraphy of Parnaíba Basin is obtainable in Góes and Feijó (1994), Santos and Carvalho (2009), and Vaz et al. (2007). The Pedra de Fogo Formation was defined by Plummer (1948) as strata-bearing chert containing tree ferns of the genus *Psaronius* that crop out between the municipalities of Pastos Bons and Nova Iorque, southern Maranhão State (Fig.1). Lithostratigraphically, the Pedra de Fogo Formation is characterized by abundant chert levels in oolitic/pisolitic limestones and fine- to medium-grained silicified sandstones (Faria and Truckenbrodt, 1980a; Vaz et al., 2007; Andrade et al., 2014).

The two new taxa of the silicified gymnosperm woods were found in the upper succession of deposits located on the shores of the Boa Esperança Reservoir, Parnaíba River, in Nova Iorque Municipality, southern Maranhão State in northeastern Brazil (Fig. 1– 2). The deposit is only ca. 4.5 m thick but extends laterally and continuously for several kilometers. The stratigraphic section was subdivided into the lower and upper successions, in which each succession is characterized by a set of architectural types (Fig. 2(A)). An outcrop scale paraconformity surface bounds the lower and upper architectural successions. This surface is partially covered by an *ex-situ* lateritic iron crust ca. 0.4 m thick.

The lower succession (Fig. 2(A, E)) is characterized by medium- to coarse-grained quartz-rich sandstone with normal grading and usually organized in fining upward sequences. Primary sedimentary structures are represented predominantly by small-scale cross-bedding sets (up to 0.5 m thick). The foresets of the cross bedding are asymptotic, with occasional trough cross bedding. The cross-bedding cosets are overlapped gradually by subcritical climbing-ripple cross-lamination with sets between 0.1 to 0.2 m thick. Trends from paleocurrent data indicate a mean orientation of paleoflow between SW/NW, with a general southwesterly trending azimuth.

The upper architectural succession consists of mottled and massive mudrocks up to 2.5 m thick (Fig. 2(A–D)). The geometry is tabular and laterally continuous. Frequent, irregular and discontinuous layers of massive chert and abundant, randomly dispersed nodular chert occur within the mudrock succession (Fig. 2(C, F)). Microbialites occur locally, and silicified gymnosperm woods (Fig 2(D)) are abundant both immersed in the mudrocks and dispersed on the actual surface. The massive cherts are cm-scale lenses and semi-continuous beds up to 0.2 m thick that conform to horizontal planes. Nodular chert, up to 0.05 m in diameter, occurs in a variety of oblate, spherical or irregular shapes.

3. Material and methods

The specimens were found in the eastern part of the Parnaíba Basin, in outcrops situated on the shore of the Boa Esperança Reservoir in Nova Iorque Municipality (Fig. 1). The material comprises stems with preserved pith, primary xylem, and secondary xylem. The silicified trunks reported here commonly occur as fragments, typically less than 7 cm in diameter, and were found on the surface or sometimes recovered directly from the massive mudrocks and considered still in horizons which were preserved. (Fig. 2(D)).

To investigate the morphological characteristics and internal anatomy of petrified specimens, petrographic thin sections were prepared in the laminating laboratory at the University of Vale do Rio dos Sinos (UNISINOS), São Leopoldo, Brazil. For each specimen, thin sections were prepared, oriented along three different planes: transverse section, tangential longitudinal section, and radial section, following standard procedures (*sensu* Jones and Rowe, 1999; Merlotti and Rosa, 2002). Morphological overviews were photographed with a Canon EOS T3i camera with a Sigma 70 mm DG Macro lens. The microscopic analysis and photomicrographs were made with a Leica MC170 digital camera attached to a Leica DM500 microscope.

The descriptions and discussions of anatomical features of the fossil stems follow the terminology of the Mussa (1982), IAWA Committee (2004), Philippe and Bamford (2008), and Falcon-Lang (2003a). A minimum of 30 measurements, including diameter and length, were taken for each of the anatomical characters analyzed (e.g., tracheids, rays, sclerenchyma and secretory cells, ducts, and cross-field pits). In the descriptions, the sizes of the cells are provided next to the cell type, with the minimum and maximum sizes outside parentheses and the means within parentheses.

The trunks and thin sections are deposited in the Paleobotanical Collection of the Museum of Archeology and Paleontology, Federal University of Piauí (UFPI), Teresina, Brazil.

4. Systematic paleobotany

Division Gymnospermophyta Sternberg, 1820

Genus ***Ductolobatopitys*** Conceição et Crisafulli, gen. nov.

Derivation of the name: The generic name derives from the presence of ducts only in the lobe of the pith.

Diagnosis: Pith heterocellular, lobed, solenoid, solid, with sclerenchyma cells commonly grouped through the entire pith. Secretory ducts concentrated only in the lobed part of the pith. Endarch primary xylem. Parenchymatous rays with smooth cell walls, exclusively uniseriate. Araucarian radial pitting on the tracheid walls and cupressoid cross-field pits.

Ductolobatopitys mussae Conceição, Neregato et Iannuzzi, nov. gen., nov. sp. Figs. 3–5

Derivation of the name: The specific epithet is dedicated to the Brazilian paleobotanist Diana Mussa, for her pioneering research on the petrified woods from the Parnaíba Basin.

Holotype: PAB 109.2.

Paratype: PAB 077.

Repository: Museum of Archeology and Paleontology, Federal University of Piauí (UFPI), Teresina, northeastern Brazil.

Type locality: Nova Iorque, southern Maranhão State, northeastern Brazil.

Stratigraphic horizon and age: Pedra de Fogo Formation, Cisuralian.

Diagnosis: Pith as in the genus. Tracheid pits 1–3 seriated and contiguous. When triseriate, radial pits are mostly alternately arranged. Cross-field pits cupressoid, 1–4 (mean: 2.8) circular cupressoid pits per field. Uniseriate rays very low, 1–12 (mean: 2.8) cells high.

Description:

General features. Species described from 2 specimens and 3 fragments, yellow to gray, ranging from 6 to 12 cm long and 5 to 7 cm in diameter (Fig. 3(A)). Cortex and periderm not preserved. The specimens are characterized by small-lobed and eccentric pith (ø 7–10 mm) surrounded by primary xylem bundles and pycnoxylic secondary xylem with growth interruptions (Figs. 3(B), 5(A)).

Pith. The pith is solid (non-septate), small, heterocellular and lobed (Fig. 3(B)); it is characterized by grouped and isolated secretory ducts (Fig. 3(C–E)), parenchyma and sclerenchyma cells (Fig. 4(A–E)). Secretory ducts present only in the lobed area (Fig. 3(B–E)). The sclerenchyma cells form nests and are dispersed through the entire pith (Fig. 4(A–D)). In transverse section, the parenchyma cells are circular to rectangular, of variable size, larger in the center and smaller in the perimedullary region. The larger cells are 80–140 µm (mean: 96) in radial diameter and 60–130 µm (mean: 93) in tangential diameter; the smaller cells are 30–50 µm (mean: 36) in radial diameter and 10–50 µm (mean: 29) in tangential diameter. The secretory ducts are 200–250 μm (mean: 225) in radial diameter and 150–250 μm (mean: 210) in tangential diameter.

Primary xylem. The primary xylem strands show endarch maturation. In transverse section, tracheids of the metaxylem are circular to polygonal, 10–16 μm (mean: 14) in radial diameter and 12–16 μm (mean: 115) in tangential diameter. In radial section, the metaxylem cell walls bear spiral and scalariform thickenings (Fig. 4(E)).

Secondary xylem. The secondary xylem is pycnoxylic, composed of tracheids and parenchyma rays (Fig 5(A)). In transverse section, the tracheids are rectangular to polygonal and arranged in radial rows with a mean of 4 rows between rays. The tracheids are 16–70 μm (mean: 77) in radial diameter and 15–65 μm (mean: 46) in tangential diameter.

In radial section, the tracheids are short, 100–400 μm (mean: 220) in length, with tapered to rounded ends, sometimes superimposed on each other (Fig. 5(B–D), respectively)). Tracheid pits are 1–3-seriate and contiguous (Fig. 5(B–D)); if triseriate, radial pits are mostly arranged alternately (Fig. 5(B)). The cross-fields are cupressoid, with 1 to 4 (mean: 2.8) circular cupressoid pits per field (Fig. 5(D–E)). In tangential section, the parenchyma rays are homogeneous, with smooth cell walls, exclusively uniseriate and very low, 1–12 (mean: 2.8) cells high, with a density of 30 rays per mm^2 (Fig. 5(F)).

Remarks: Solenoid-type steles with solid pith are well represented in the Upper Paleozoic gymnosperms, especially in Gondwana (Kräusel, 1956; Kräusel and Dolianiti, 1958; Surange and Maithy, 1962; Mussa, 1986; Crisafulli, 1995; Merlotti, 2002; Kurzawe et al., 2013a); whereas in the Northern Hemisphere (Euramerica and Cathaysia) this type of stele is less frequent (Vogellehner, 1965; Aassoumi and Vozenin-Serra, 1996; Wan et al., 2017).

Among genera included in the solenoid group and solid pith, we can compare our samples with the following Permian taxa: *Lobatoxylon* Kräusel, 1956; *Solenopitys* Kräusel et Dolianiti, 1958; *Barakaroxylon* (Surange et Maithy) emend. Kulkarni Maithy et Surange, 1971; *Megaporoxylon* (Kräusel) emend. Maheshwari, 1972; *Catarinapitys* Mussa, 1986; *Idioxylon* Crisafulli, 1995; *Ductosolenoxylon* Merlotti, 2002; *Ductoabietoxylon* Kurzawe et Merlotti, 2013 (in Kurzawe et al., 2013a); *Parnaiboxylon* Kurzawe et Merlotti, 2013 (in Kurzawe et al., 2013a); and *Ductoagathoxylon* Wan, Yang, Liu et Wang, 2017 (Table 1).

The genera *Solenopity*s, *Ductosolenoxylon* and *Barakaroxylon*, from the Permian of Gondwana (Kräusel and Dolianiti, 1958; Kulkarni et al., 1971; Merlotti, 2002), possess central and peripheral canals in the pith, which is not lobulate. *Solenopitys* and *Barakaroxylon* have a mixed arrangement of the pits on the tracheid radial walls, while our specimens have araucarian pits. Furthermore, the three above-mentioned taxa have araucarioid cross-field pits, contrasting with the cupressoid cross-field pits in the present specimens.

Catarinapitys, from the Paraná Basin, has lobed pith with peripheral ducts and central canal, taxoid secondary xylem (Kräusel and Dolianiti, 1958), and araucarioid cross-field pits (see Mussa, 1986). In contrast, the present specimens have lobed pith with the ducts concentrated only in the lobed part of the pith.

In *Ductoagathoxylon*, from Angara (Wan et al., 2017), and *Ductoabietoxylon*, from the Parnaíba Basin (Kurzawe et al., 2013a), the secretory ducts are distributed over the entire circular pith and the secondary xylem is *Agathoxylon*-type (Philippe and Bamford, 2008), differing from our specimens.

Idioxylon, from Uruguay (Crisafulli, 1995), and *Parnaiboxylon*, from the Parnaíba Basin (Kurzawe et al., 2013a), have only peripheral canals in the pith and endarch to mesarch primary xylem. In addition, *Parnaiboxylon* has *Agathoxylon*-type secondary xylem and *Idioxylon* has mixed pits on the tracheid radial walls, differing from the present specimens (Table 1).

Megaporoxylon, initially described from Namibia (Maheshwari, 1972), shares the endarch primary xylem and the araucarian pits on the tracheid radial walls with the specimens described here. However, *Megaporoxylon* can be distinguished by the absence of sclereids in the pith and the presence of phyllocladoid cross-field pits (see Maheshwari, 1972). The genus with the most similar pith compared to our sample is *Lobatoxylon*, from South Africa (Kräusel, 1956), which has lobed pith with secretory ducts and endarch primary xylem (Table 1). Nevertheless, it has a special parenchyma sheath on the medullary border and three lobes, besides the absence of sclereids in the pith. Additionally, it has *Agathoxylon*-type secondary xylem (see Kräusel, 1956), differing significantly from the study specimens. Because all the above-mentioned taxa have a different set of anatomical characters that contrast with our samples (Table 1), we propose a new taxon, *Ductolobatopitys mussae* nov. gen., nov. sp.

The lobed" aspect observed in the pith of *Ductolobatopitys mussae*, seem to correspond to zones with departing leaves or branch traces. In this sense it is worth mentioning that we are aware into account the possible variability of characters within a same species or genus and their limitations in taxonomic terms, especially when some characters are determined just from on sections at one level in a specimen. However, in our material thin sections were made in both specimens and at different levels, and in all levels sectioned the lobed aspect are visible. Because of this, we are considering this lobed feature as taxonomically diagnostic.

Class Coniferopsida

Genus *Kaokoxylon* Kräusel 1956

Type-species: *Kaokoxylon sclerosum* (Walton) Kräusel 1956

Kaokoxylon brasiliensis Conceição, Neregato et Iannuzzi., nov.sp. Figs. 6, 7

Derivation of the name: The specific epithet indicates that the fossil stem was collected in Brazil.

Holotype: PAB 92.1.

Repository: Museum of Archeology and Paleontology, Federal University of Piauí (UFPI), Teresina, northeastern Brazil.

Type locality: Nova Iorque, southern Maranhão State, Brazil.

Stratigraphic horizon and age: Pedra de Fogo Formation, Cisuralian.

Diagnosis: Small circular pith, non-septate and heterocellular, with long and isolated sclerenchyma cells resembling astrosclereids. Endarch primary xylem. Tracheid radial pits 1–3-seriate, alternate and contiguous. Cupressoid cross-field pits, with 3–4 pits per field. Rays predominantly uniseriate and low, 1–8 cells high (mean: 3 cells high).

Description:

General features. The species is based on two fragments of silicified wood from the same specimen, yellow to gray, 15 cm long and 7 cm in diameter (Fig. 6(A)). It is characterized by small, cylindrical and non-septate pith (ø 2.5 mm, fig. 6(B, E)), primary xylem and pycnoxylic secondary xylem with growth interruptions (Figs. 6(B), 7(D)).

Pith. Pith non-septate, heterocellular, formed by parenchyma and sclerenchyma cells. In transverse section, the parenchyma cells vary from circular to polygonal, radial diameter 49–115 µm (mean: 64), tangential diameter 48–115 µm (mean: 77). The sclerenchyma cells, in transverse section, are rectangular, radial diameter 49–114 µm (mean: 75) and tangential diameter 46–98 µm (mean: 72). These cells occur dispersed in the center and in the perimedullary region of the pith (Fig. 6(C–D)), running vertically in radial section as irregular columns through the pith, resembling astrosclereids with lobes or arms diverging from the central body (Figs. 6(E), 7(A)).

Primary Xylem. Cauline bundles with endarch maturation, with the cells almost indistinguishable from the innermost cells of the secondary xylem (Fig. 6(C)). The tracheids of the metaxylem are circular to polygonal in transverse section, radial diameter 7–25 µm (mean: 16), tangential diameter 6–30 µm (mean: 19). In radial section, the primary xylem possesses scalariform thickenings (Fig. 7(B–C)).

Secondary Xylem. The secondary xylem is pycnoxylic, comprising tracheids and parenchymatous cells (Fig. 7(D)). Tracheids are circular to polygonal, radial diameter 60–125 µm (mean: 87) and tangential diameter 27–47 µm (mean: 35). In transverse section, the secondary xylem consists of 1–8 rows of tracheids separated by uniseriate parenchymatous rays (Fig. 7(D)).

In radial section, the tracheids are short, ranging from 100–400 µm in height. The ends of these tracheids are rounded or tapered, frequently overlapping (Fig. 7(F)). Tracheid radial pits 1–3-seriate, alternate and contiguous (Fig. 7(E–F)). The cross-field pitting is cupressoid, with 3–4 pits per field (Fig. 7(G)). In tangential section, the parenchyma rays are homogeneous with smooth cell walls, predominantly uniseriate and low, 1–8 cells high (mean: 3 cells high), with a density of 34 rays per mm^2 (Fig. 7(H)).

Remarks: Solid and heterocellular pith with sclerenchyma cells has been used in combination with other characters (e.g., primary and secondary xylem) as the basis for taxonomic decisions at the generic or supra-generic level in the Permian of the Gondwana, Cathaysia and Euramerica (e.g., Kräusel, 1956; Mussa, 1980; Pant and Singh, 1987; Feng et al., 2012; Kurzawe et al., 2013a, b; Falcon-Lang et al., 2014, 2016). The specimen analyzed here has solid and heterocellular pith with only parenchyma and sclerenchyma cells, endarch cauline bundles, araucarian pits on the tracheid radial walls, and cupressoid cross-field pitting.

The specimen described here shares several features with *Scleromedulloxylon* Doubinger et Margerier, 1975 (in Doubinger and Margerier, 1975), and *Austroscleromedulloxylon* Mussa, 1980 (in Mussa, 1980) and *Macdonaldodendron* Falcon-Lang, Kurzawe et Lucas, 2014 (in Falcon-Lang et al., 2014) such as pith solid and heterocellular (parenchyma and sclerenchyma cells), cauline bundles with endarch maturation, araucarian pits on the tracheid radial walls, and cupressoid cross-field pitting (see Doubinger and Margerier, 1975; Mussa, 1980; Falcon-Lang et al., 2014, table 2).

However, *Scleromedulloxylon* and *Austroscleromedulloxylon* have pith with irregular septations, differing from our specimen by the non-septate pith. Additionally, *Scleromedulloxylon* has resiniferous cells in the medullary tissue that are not seen in our specimen (Table 2). Finally, *Macdonaldodendron* has triangular leaf bases and whorled plagiotropic branches, which were considered as diagnostic features for this genus (Falcon-Lang et al., 2014) and both are absent in our material. Our specimen most resembles the genus *Kaokoxylon* Kräusel, 1956 *(*in Kräusel, 1956*)*, initially described from Namibia, Africa (in Kräusel, 1956)). This genus is characterized by the presence of a small, compact and heterocellular pith with sclerenchyma elements of variable forms and order, in groups or isolated, distributed in the center of the pith and perimedullary region, cauline bundles with endarch maturation and araucarian pits on the tracheid radial walls.. Therefore, this set of anatomical characters, which also characterize our specimen, justifies its inclusion in the genus *Kaokoxylon* Kräusel, 1956.

Kaokoxylon, is now known to have a wide stratigraphic distribution in the Southern Hemisphere, from the Permian to the Jurassic, and comprises nine fossil species (Table 3). It is worth mentioning, that some of the newly described stems from the Permian Motuca Formation, in Parnaíba Basin, have also been placed in the genus by Kurzawe et al. (2013b).

Our specimen has long and isolated sclerenchyma cells resembling astrosclereids in the pith (Fig. 7(A)), rays 1–8 cells high (Fig. 7(H), tracheids with uniseriate to triseriate radial pits and cupressoid cross-field pitting (Fig. 7(E–G)). These anatomical differences found in our material support the erection of a new species for the material under consideration, here named *Kaokoxylon brasiliensis* nov. sp.

6. Discussion

6.1. Paleoenvironmental and paleoecological considerations

Field observations, such as the stratigraphic relationship and architectural form, allowed us to associate the deposits studied with the Piauí Fomation (lower succession, Fig. 2(A, E)) overlain by the Pedra de Fogo Formation (upper succession, Fig. 2(A–D)). The lower succession, i.e., the Piauí Formation, represents the internal dynamic of a low-sinuosity braided system with migration of small-scale 3D-dunes, indicated by the occurrence of small-scale cross-bedding sets overlapped by subcritical climbing-ripple cross-lamination (Allen, 1983; Miall, 1992; Miall, 2010). The regular thickness and the lateral continuity of the upper mudrock succession, as well as the occurrence of microbialites, gymnosperm trunks (Fig. 2(D)), and abundant chert (Fig. 2(A–C)) are typical characteristics of lacustrine environments from the Pedra de Fogo Formation (Plummer, 1948; Carvalho, 2009; Andrade et al., 2014; Abrantes et al., 2019).. The gymnosperm woods and microbialite communities colonized, respectively, sub-environments on the lakeshore plains and nearshores of the lacustrine Pedra de Fogo environment, in which the predominance of oxidized mudrocks suggests permanent shallow lacustrine conditions.

The occurrence of gymnosperm woods associated with lacustrine environments and the presence of rare tree calamitaleans and abundant tree ferns (= *Psaronius* spp.) indicate periods of high humidity. On the other hand, the absence of coal-bearing beds and the microbialite occurrences suggest probable dry conditions (Ziegler et al., 1987; Cecil, 1990; Franks and Stoz, 2009), indicating that during the deposition of the Pedra de Fogo Formation a seasonal climate prevailed. In general, the floristic response to increased aridity (seasonality) is marked by contraction of wetland habitats in basin lowlands (DiMichele and Aronson, 1992; DiMichele et al., 2005). This interpretation is concordant with the paleoclimate conditions in tropical Pangea during the transition from the Late Pennsylvanian to Cisuralian, in which the climate oscillated between wet sub-humid and dry sub-humid to possibly semi-arid (Crowley et al., 1989; DiMichele et al., 2001; Wang et al., 2014). In this particular, the Parnaíba basin was located at the southernmost limit of the tropical belt (ca. 30 °S in north-central Gondwana), which supports a seasonally dry climate for this region based on the climate modeling (Rees et al., 2002).

The good preservation of fossil plants and microbialites indicates that silicification occurred penecontemporaneously to deposition and prior to the neomorphic recrystallization of mineral phases that physically destroy the organic structures (Stein, 1982; Knoll, 1985; Bartley, 1996; Sugitani et al., 2015). Although the silica sources may vary widely between depositional environments, the absence of trace siliceous microfossils, as well as the lack of volcanic or hydrothermal evidence in the Pedra de Fogo deposits studied here, suggests that the main source of silica may have been related to fluctuations of the water table, triggered by a seasonal climate that prevailed for long periods (Knoll, 1985; Hesse, 1989; Matysová et al., 2010).

Additionally, the material from Nova Iorque lacks tree rings, showing a gradual decline in tracheid cell diameters instead of continuous concentric rings through the stem, which is considered here to be merely growth interruptions of the secondary xylem (*sensu* Schweingruber, 1992). These growth interruptions indicate a temporary slowing of cambial activity, suggesting sufficient water in the environment of these plants, occasionally with periods of water stress, but not enough to halt the vascular cambial activity (see Schweingruber, 1992; Falcon-Lang, 2003a).

These sedimentological interpretations of the outcrops indicate that these plants lived close to the shores of large lakes, which may have protected them from regional climate seasonality (Parrish and Falcon-Lang, 2007). On the other hand, they were also subject to fluctuations of the lake water levels, causing water stress, which is consistent with the presence of stems with solenoid pith in the outcrops. This kind of anatomical feature could function to store water to resist dry conditions (Mussa, 1986), which would be extremely useful in this climate seasonality scenario.

7. Conclusions

The gymnosperms described here display different anatomical features from the stems previously studied in the Pedra de Fogo Formation. This material contained a new endemic form, named *Ductolobatopitys mussae*, and the genus *Kaokoxylon*, recognized from most of Gondwana, including the Parnaíba Basin, nevertheless is recorded for the first time in Pedra de Fogo Formation, as the new species *Kaokoxylon brasiliensis*.

The geological interpretations suggest that the gymnosperms colonized the lakeshore plains during the deposition of the Pedra de Fogo Formation. The presence of gymnosperms associated with lacustrine environments and the occurrence of tree calamitaleans and tree ferns in the same outcrops indicate wet periods. On the other hand, the microbialites suggest dry conditions, although for short periods, which are consistent with solenoid piths (a probable adaptive trait for water storage) and discrete growth interruptions in the secondary xylem.

Future studies of fossil plants in the Pedra de Fogo Formation will provide valuable information in the ongoing search for more accurate evidence of the subtropical gymnosperm flora in the Western Gondwana during the Early Permian, as well as the relationships between this flora and other Paleozoic provinces.

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Table captions

Table 1. Genera with solenoid and solid piths comparable to *Ductolobatopitys*

Table 2. Genera that have both secondary xylem and pith anatomy most similar to our specimen.

Table 3. Species of *Kaokoxylon* Kräusel 1956.

Figure captions

Fig. 1. General geological map of the Parnaíba Basin. The rectangles indicate the location of the outcrop where the fossils were found. Permian forests in life position occur in the municipalities of Duque Bacelar (Maranhão State) and Teresina (Piauí State). TFTNM: Tocantins Fossil Trees Natural Monument. Modified from Iannuzzi et al. (2018).

Fig. 2. Stratigraphic column of the successions. **A**. On left side, is a sketch of the main sedimentological aspect of the lower and upper successions. **B.** Upper succession (Pedra de Fogo Formation) with irregular layers of chert and abundant nodular chert in the mottled and massive mudrocks. **C**. Detail of the upper part with frequent, irregular and discontinuous layers of massive chert (white arrows). **D**. Silicified trunk immersed in mudrock (arrow). **E.** Lower succession (Piauí Formation), characterized by medium- to coarse-grained quartz-rich sandstone with normal grading, usually organized in fining-upward sequences. **F**: Detail of nodular chert.

Fig. 3. *Ductolobatopitys mussae* nov. gen., nov. sp. PAB 109.1 (holotype). **A**. General morphology. **B.** Transverse section showing the lobed pith (arrows) and pycnoxylic wood. **C**. Transverse section of lobulate pith showing isolated secretory ducts (arrows). **D**. Transverse section showing detail of grouped secretory ducts (arrows) and parenchyma cells (PA). **E**.

Radial section showing secretory ducts (white arrow) and sclerenchyma cells (black arrow). Scale bars: 10 mm (A), 1 mm (B), 500 µm (C), 200 µm (D), 100 µm (E).

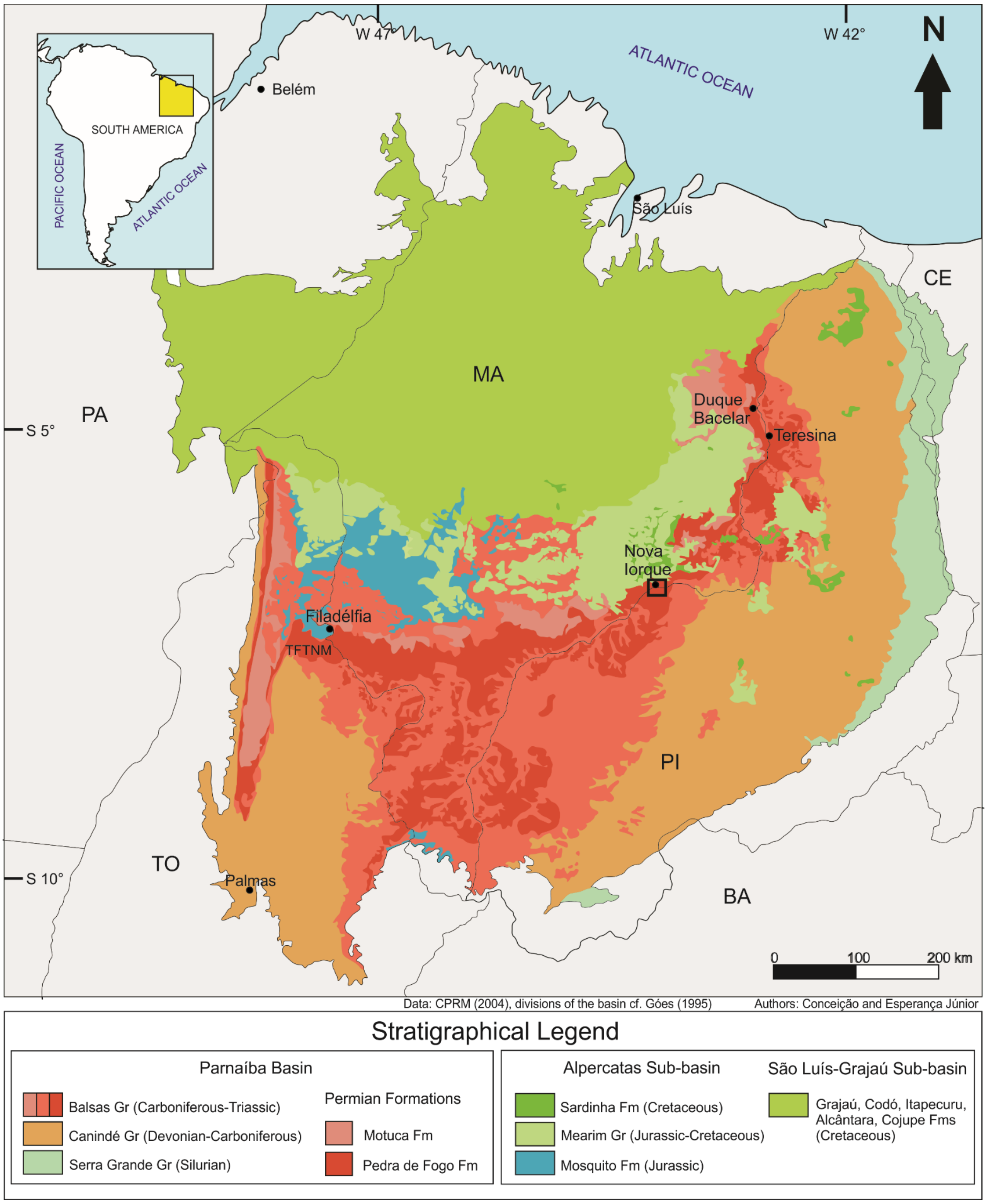
Fig. 4. *Ductolobatopitys mussae* nov. gen., nov. sp. PAB 109.1 (holotype). .**A**. Transverse section of the pith showing sclerenchyma cells with thicker walls (white arrow). **B.** Radial section of the pith showing sclerenchyma cells with thicker walls (white arrow) and parenchyma cells (black arrow). **C.** Radial section of the pith showing long sclerenchyma cells with thicker walls (white arrow) **D.** Transverse section showing endarch primary xylem (black arrows) and grouped sclerenchyma cells (white arrow). **E**. Radial section showing details of parenchyma cells (PA) and scalariform/reticulate thickenings of the metaxylem (MX). Scale bars: 200 µm (A–D), 50 µm (E).

Fig. 5. *Ductolobatopitys mussae* nov. gen., nov. sp. PAB 109.1 (holotype). **A**. Transverse section showing pycnoxylic wood and growth interruptions (arrow). **B**. Radial section showing ends of tracheids superimposed on each other (white arrow) and triseriate contiguous pits on the tracheid walls (black arrow). **C**. Radial section showing araucarian radial pitting on the tracheid walls, predominantly uniseriate and contiguous. **D**. Radial section showing cupressoid cross-field pitting (arrow) and uniseriate contiguous pits on the tracheid walls. **E**. Radial section showing cupressoid cross-field pitting with 3 to 4 pits per field. **F**: Tangential longitudinal section showing rays predominantly uniseriate and low. Scale bars: 250 µm (A), 100 µm (B), 80 µm (C, D), 25 µm (E), 100 µm (F).

Fig. 6. *Kaokoxylon brasiliensis* nov. sp. PAB.092.1 (holotype). PAB.092.1 (holotype). **A**. External morphology of the stem showing the second xylem and pith. **B**. Transverse section showing the stem with small pith (P) and secondary xylem (SX). **C**: Transverse section

showing cauline bundles of primary xylem with endarch maturation (ellipse) and secondary xylem (SX). **D**: Transverse section showing detail of the pith region, with some sclerenchyma cells (white arrow) and parenchyma cells (black arrow). **E**: Radial section showing pith (P) and secondary xylem (SX). Scale bars: 10 mm (A), 2 mm (B) 100 µm (C–D), 1 mm (E).

Fig. 7. *Kaokoxylon brasiliensis* nov. sp. PAB.092.1 (holotype). **A**: Radial section showing pith (P), with sclerenchyma cells running vertically as irregular columns through the pith, resembling astrosclereids (arrows). **B**: Radial section showing scalariform/reticulate thickenings of the metaxylem (MX). **C**: Detail of B, showing scalariform/reticulate thickenings of the metaxylem (MX). **D**: Transverse section showing the secondary xylem with weak growth interruptions (arrow) and uniseriate rays. **E**. Radial section showing uniseriate (black arrow) and biseriate (white arrow) pitting on the tracheid walls. **F**. Radial section showing triseriate pitting on the tracheid walls, alternately arranged (white arrow), and cross-field pitting (black arrow). **G**. Detail of G, showing cupressoid cross-field pitting (arrow). **H**. Tangential longitudinal section showing rays predominantly uniseriate and low. Scale bars: 250 µm (A), 100 µm (B), 25 µm (C), 200 µm (D), 100 µm (E, F), 10 µm (G), 100 µm (H).



Data: CPRM (2004), divisions of the basin cf. Góes (1995)

Authors: Conceição and Esperança Júnior

Fig. 1

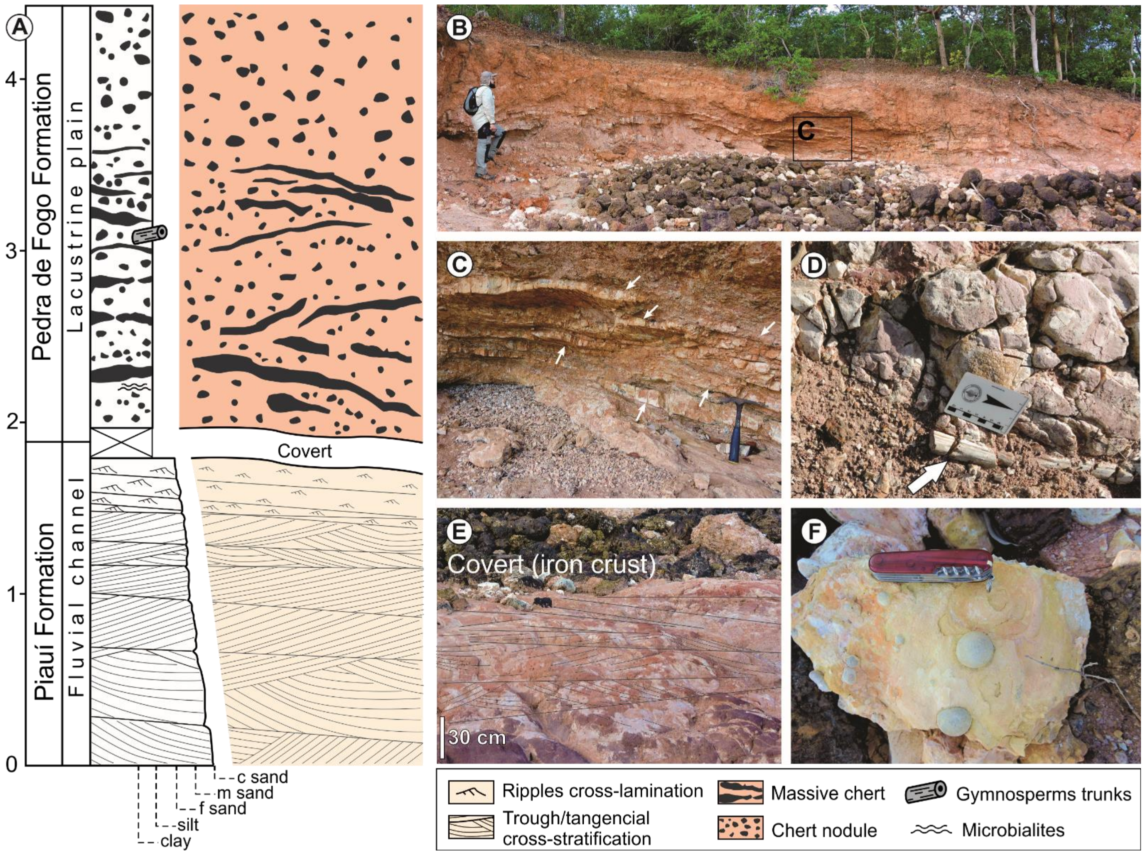

A
B
C
D
E
F
Pedra de Fogo Formation
Lacustrine plain
Piauí Formation
Fluvial channel
4
3
2
1
0
Covert
c sand
m sand
f sand
silt
clay
C
Covert (iron crust)
30 cm
Ripples cross-lamination
Trough/tangencial cross-stratification
Massive chert
Chert nodule
Gymnosperms trunks
Microbialites

Fig. 2

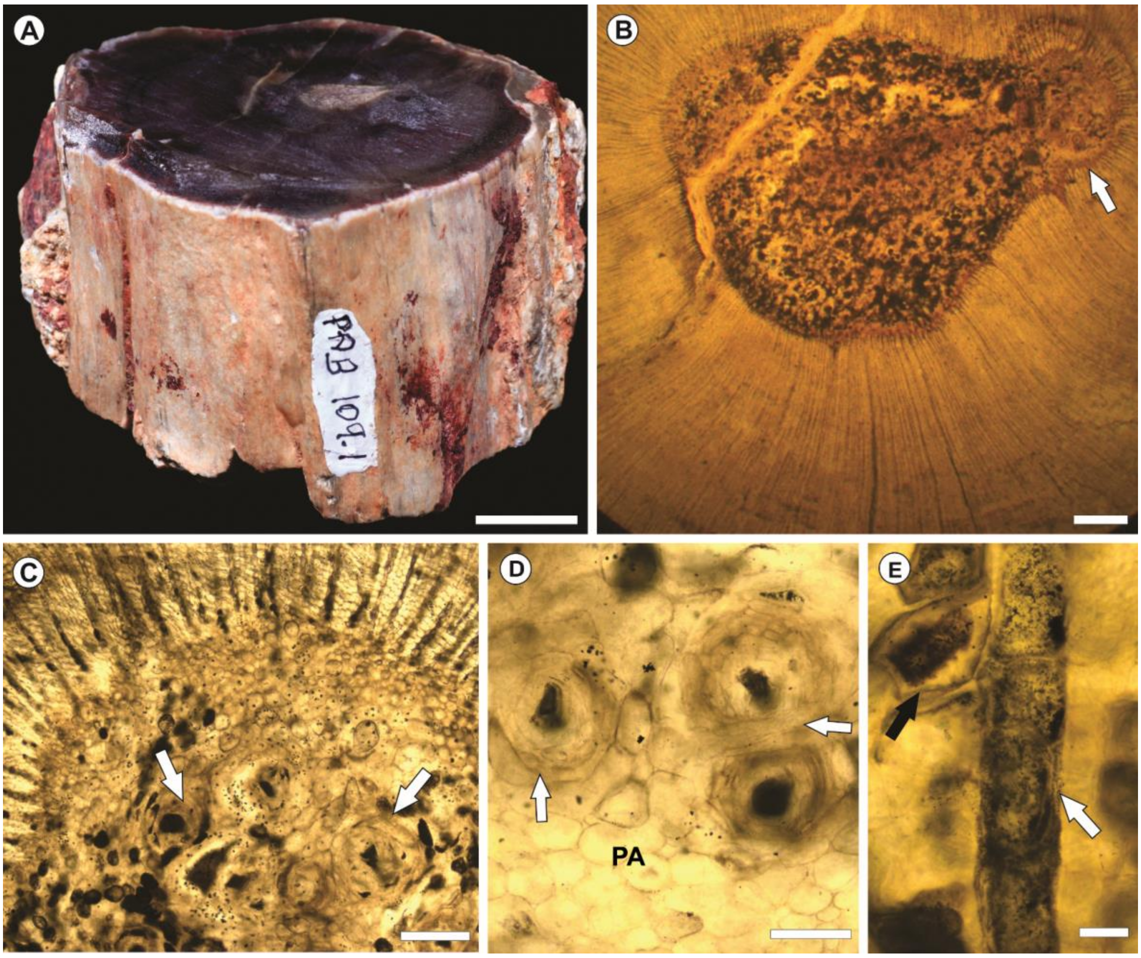


Fig. 3

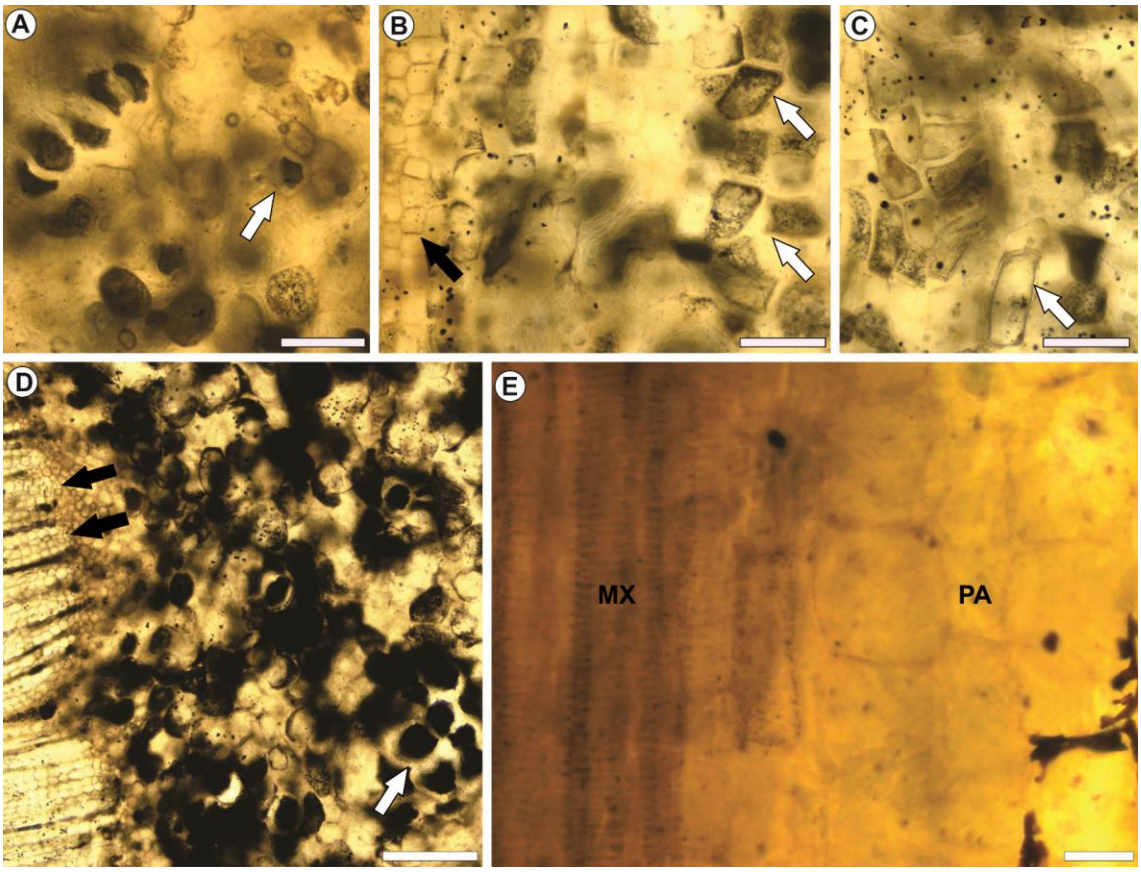


Fig. 4

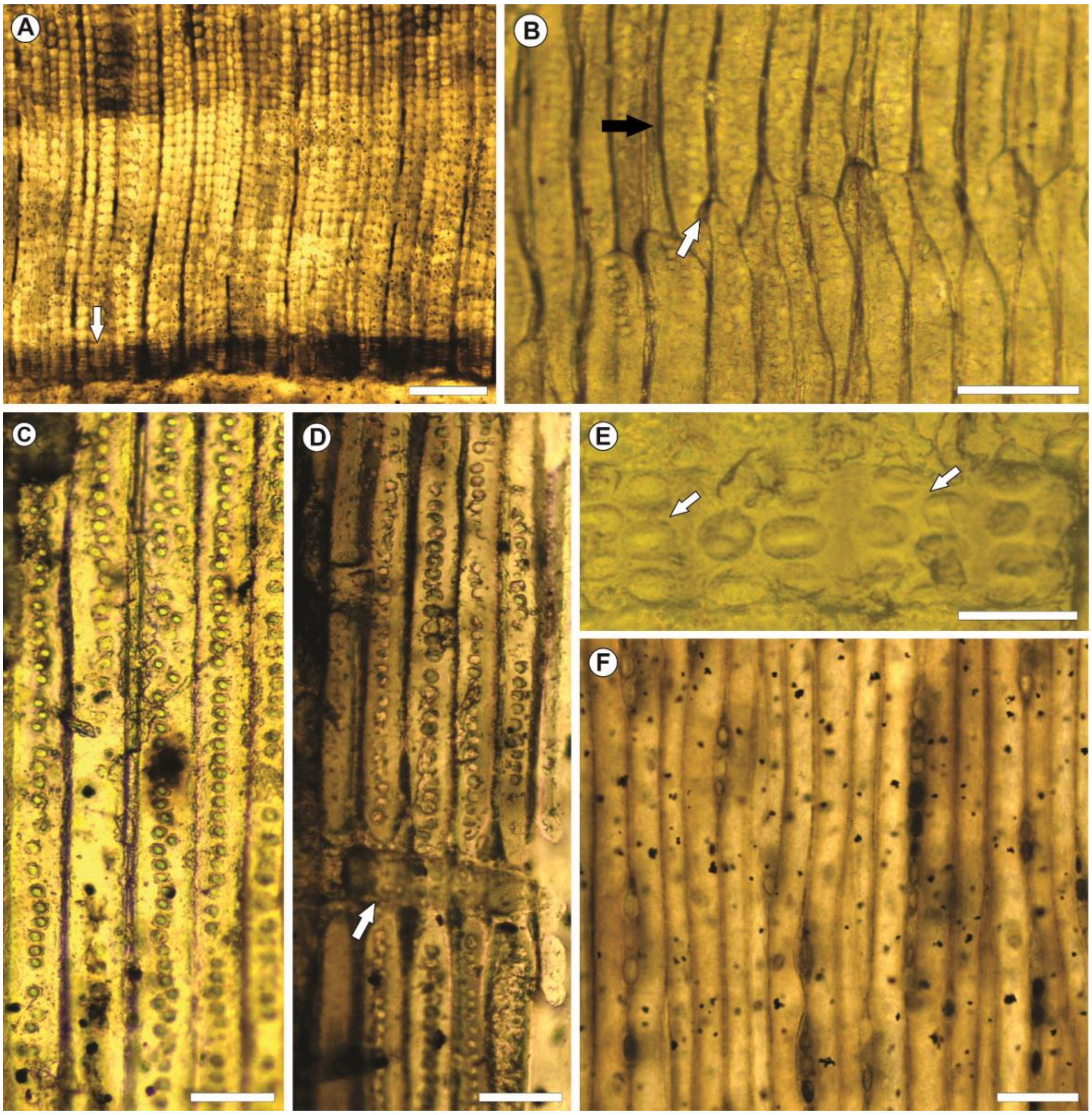


Fig. 5

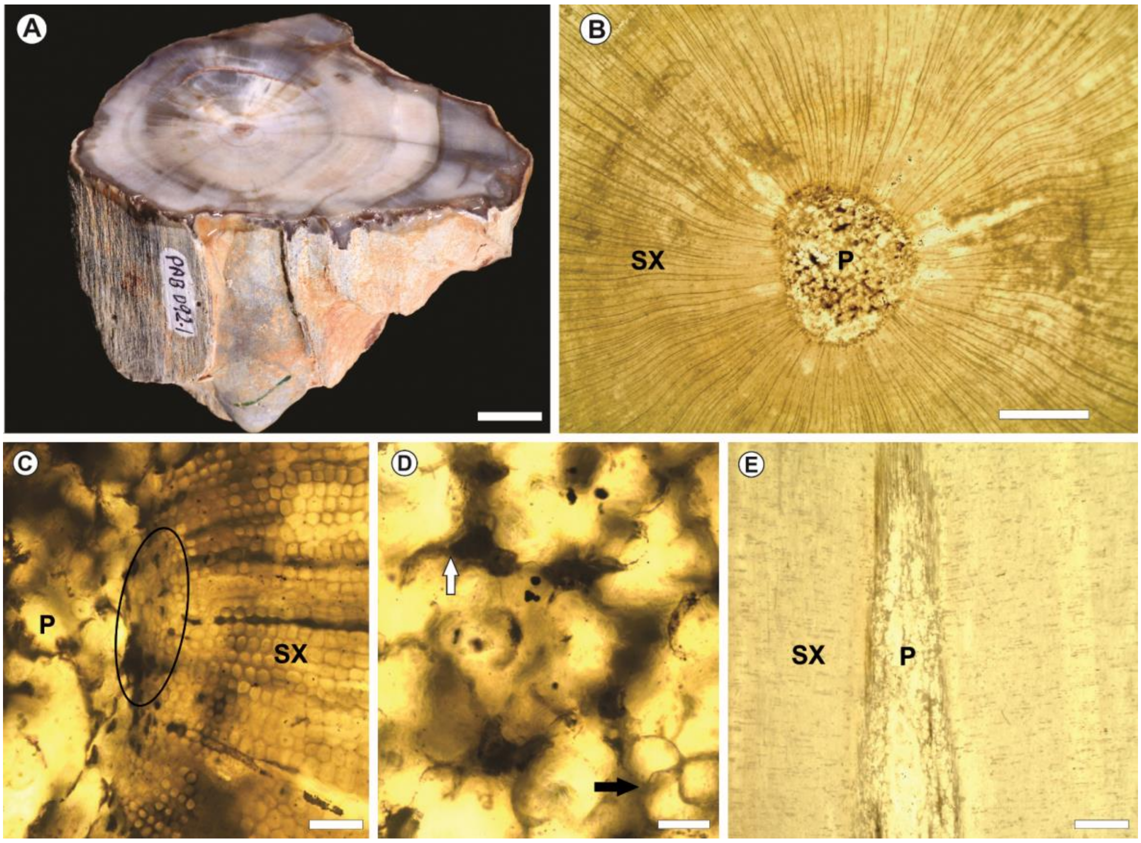


Fig. 6

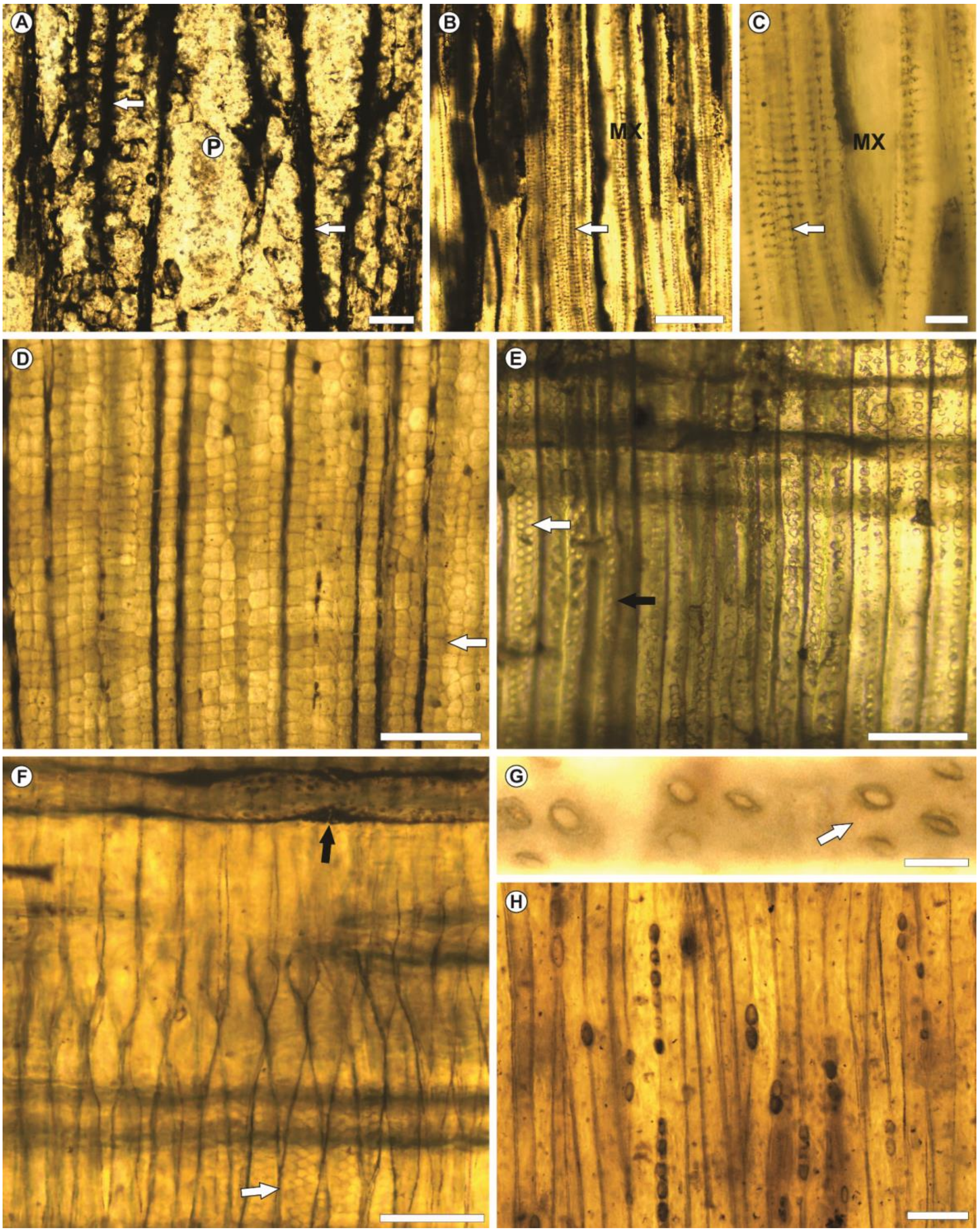


Fig. 7

Table 1. Genera with solenoid and solid piths comparable to *Ductolobatopitys*

Genus	Pith	Primary xylem	Secondary xylem			Type locality and age
			Pitting on radial walls	Cross-field pits	Xylem rays	
Barakaroxylon Surange et Maithy emend. Kulkarni et al., 1971	Solid, solenoid and heterocellular, with secretory cells and sclereids	Endarch	Mixed, uni- to tetraseriate	Araucarioid, up to 7 pits	Uni- to biseriate, rarely triseriate, up to 22 cells high	Kharkhari, India; Barakar; Permian
Parnaiboxylon Kurzawe et Merlotti, 2013	Solid, solenoid and heterocellular, with secretory cells and ducts	Endarch and mesarch	Araucarian, uni- to pluriseriate	Araucarioid, up to 9 pits	Uniseriate, rarely locally biseriate, up to 9 cells high	Tocantins, Brazil; Permian
Catarinapitys Mussa, 1986	Solid, lobulate, solenoid and heterocellular, with sclereids	Endarch and mesarch	Araucarian, uni- to triseriate, with tertiary thickenings	Araucarioid, 4–6 pits	Uniseriate, 1-5 cells high	Rio da Estiva, Brazil; Permian
Ductosolenoxylon Merlotti, 2002	Solid, solenoid and heterocellular, with secretory cells and ducts, and sclereids	Endarch	Uni- to biseriate	Araucarioid	Uniseriate, 1-9 cells high	São Gabriel, Brazil; Permian
Ductoagathoxylon Wan et al., 2017	Solid, heterocellular with grouped or isolated secretory ducts	Endarch and mesarch	Araucarian, uni- to triseriate	Araucarioid, up to 12 pits	Uniseriate, rarely biseriate, 1–12 cells high	Dalongkou, Jimsar County, China; Permian
Ductoabietoxylon Kurzawe et Merlotti, 2013	Solid and heterocellular, with secretory cells and ducts	Endarch	Araucarian, uni- to triseriate	Araucarioid, up to 5 pits	Uniseriate, locally biseriate, up to 37 cells high, and abietoid	Tocantins, Brazil; Permian
Idioxylon Crisafulli, 1995	Solid, solenoid and heterocellular, with secretory cells and sclereids	Mesarch	Mixed, uni- to biseriate	Cupressoid or taxodioid, up to 4 pits	Uniseriate, up to 38 cells high	Arroyo Seco, Uruguay; Permian
Lobatoxylon Kräusel, 1956	Solid, lobulated and heterocellular, with secretory cells and ducts and parenchymal sheath	Endarch	Araucarian, uni- to biseriate	Araucarioid, up to 3 pits	Uniseriate, up to 50 cells high	South Africa; Permian
Megaporoxylon Kräusel emend. Maheshwari, 1972	Solid and heterocellular, with secretory cells and ducts	Endarch	Araucarian, multiseriate	Phyllocladoid, 1 (rarely 2) pit	Uniseriate, up to 14 cells high	Kaokoveld Desert, Namibia; Pennsylvanian
Solenopitys Kräusel et Dolianiti, 1958	Solid, solenoid and heterocellular, with secretory cells	Endarch and mesarch	Mixed, uni- to biseriate	Cupressoid, generally up to 6 pits	Uniseriate, rarely biseriate, up to 13 cells high	Rio Claro, Brazil; Permian
Ductolobatopitys Conceição et Crisafulli, gen. nov.	Solid, solenoid , lobulated and heterocellular, with sclerenchyma nests and ducts	Endarch	Araucarian, uni- to biseriate	Cupressoid, 2–4 pits	Uniseriate, 1 to 12 cells high	Maranhão; Brazil, Permian

Table 2. Genera that have both secondary xylem and pith anatomy most similar to our specimen.

Genus	Pith	Primary xylem	Secondary xylem			Type locality and age
			Pitting on radial walls	Cross-field pits	Xylem rays	
Scleromedulloxylon Doubinger et Margerier, 1975	Irregularly septate, heterocellular with plate-like sclerotic nests and resiniferous cells	Endarch	Araucarian, uni- to biseriate	Cupressoid, 1–3 pits	Uniseriate, 40 cells high	Autun, France; Permian
Austroscleromedulloxylon Mussa, 1980	Irregularly septate, heterocellular with sclerenchyma cells	Endarch	Araucarian, uni- to triseriate	Cupressoid	Uniseriate, 15 cells high	São Paulo, Brazil; Permian
Kaokoxylon Kräusel, 1956	Solid and heterocellular with sclerenchyma cells	Endarch	Araucarian, uniseriate	, Up to 5 pits	Uniseriate, up to 20 cells high	Kaokoveld; Namibia; Triassic
Macdonaldodendron Falcon-Lang, Kurzawe et Lucas, 2014	Heterocellular with sclerotic nests and triangular leaves/ branch	Endarch	Araucarian, uniseriate	Cupressoid, 1, or up to 2–4 pits	Uniseriate, 1–8 cells high	New Mexico, U.S.A.;Permian

Table 3. Species of *Kaokoxylon* Kräusel 1956.

Species	Pith	Secondary xylem			Type locality and age
		Pitting on radial walls	Cross-field pits	Xylem rays	
K. reuningi Kräusel, 1956	Secretory canal; sclerenchyma cells forming short columns near the border	Uniseriate, rarely biseriate	Up to 5 pits	Uniseriate rays, up to 20 cells high	Kaokoveld, Namibia; Africa, Permian
K. durum Kräusel, 1956	Sclerenchyma cells arranged in group in lenticular form?	Uni- to triseriate	Many pits	Up to 20 cells high and tangential pitting	Kaokoveld, Namibia; Africa, Permian
K. farleyense Maheshwari, 1972	Sclerenchyma nests with transverse connections	Uni- to biseriate, rarely triseriate	Up to 7 pits	Uni- to biseriate, 2–21 cells high and tangential pitting	Farley; Australia, Permian
*K. pseudotrimedull*aris Prasad, 1982	Sclerenchyma nests	Uni- to biseriate	Up to 6 pits.	Uniseriate, up to 22 cells high	Kanhargaon Village; India, Permian
K. rioclarense (Mussa) Leiva Verón et al., 2012	Secretory canal scattered, sclerenchymatic cells forming sheath near the periphery, in groups associated with secretory cells	Uni- to triseriate	Up to 4 pits.	Uni- to biseriate with 2–3, commonly 10 cells high	Rio Claro; Brazil, Permian
K. sclerosum Kräusel, 1956	Sclerenchyma cells forming long columns near the periphery	Uni- to biseriate	Up to 4 pits	Uniseriate, up to 33 cells high	Molteno, Namibia; Africa; Triassic
K. zalesskyi Maheshwari, 1967	Sclerenchymatic cells in nests or isolated	Uni- to biseriate	Up to 4 pits	Up to 18 cells high	Bengala, India; Perrmian
Kaokoxylon sp., Gnaedinger et Cúneo, 2009	?	?	?	?	Chubut; Argentina, Jurassic
K. punctatum Kurzawe, Merlotti et Iannuzzi, 2013	sclerenchyma nests and parenchyma cells pitted	Uni- to biseriate	Up to 3 pits	Up to 13 cells high	Rio Claro; Brazil; Permian
K. brasiliensis sp. nov. (this study)	Long and isolated sclerenchyma cells resembling astrosclereids	Uni- to triseriate	Cupressoid, 2–4 pits	Uniseriate, 3 cells high	Maranhão; Brazil, Permian

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First report of Cordaixylon Grand'Eury 1877 in the Permian of South America, Parnaíba Basin, Brazil

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Corresponding Author:	Domingas Maria Conceição Universidade Federal do Rio Grande do Sul BRAZIL
First Author:	Domingas Maria Conceição
Order of Authors:	Domingas Maria Conceição
	Roberto Iannuzzi
	Luiz Saturnino de Andrade
	Mário G. F. Esperança Júnior
	Juan Carlos Cisneros
	Anelise M. Siegloch
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Suggested Reviewers:	Howard J. Falcon-Lang, Dr. h.falcon-lang@es.rhul.ac.uk
	Zhuo Feng jumperfeng@126.com
	Shi-Jun Wang wangsj@ibcas.ac.cn
	Silvia N. Césari scesari@macn.gov.ar
Opposed Reviewers:	

First report of *Cordaixylon* Grand'Eury 1877 in the Permian of South America, Parnaíba Basin, Brazil

Domingas Maria da Conceição[a]*, Roberto Iannuzzi[a], Luiz Saturnino de Andrade[b], Mário G. F. Esperança Júnior[a], Juan Carlos Cisneros[c], Anelise Siegloch[a]

[a] Instituto de Geociências, UFRGS, Avenida Bento Gonçalves 9500, 91501–970, Porto Alegre, RS, Brazil

[b] Instituto de Geociências, UFPA, Rua Augusto Correa 1, 66075–110, Belém, PA, Brazil

[c] Museu de Arqueologia e Paleontologia, UFPI, Ininga, 64049–550, Teresina, PI, Brazil

*Corresponding author: domingasmary@hotmail.com

Abstract

We describe the morphology and anatomy of cordaitalean tree stems preserved in Cisuralian lacustrine deposits of the Pedra de Fogo Formation, Permian of the Parnaíba Basin, northeastern Brazil. The remains consist of seven samples of petrified stems with septate pith (*Artisia* type) and preserved primary and secondary xylem. The anatomic features of these specimens support their classification in the genus *Cordaixylon* Grand'Eury 1877, which is the first evidence of this genus not only in South America but also in Gondwana. The sedimentological indicators suggests climatic seasonality during the deposition of the Pedra de Fogo unit. However, on a local scale, this area may have had a humid to sub-humid regional climate due to the presence of this large lacustrine system, which would allow these plants to grow in similar habitats to their locations in the Northern Hemisphere. The Parnaíba Basin contains a relatively high number of endemic taxa, but this genus is typical of the Euramerican Province and is distributed widely in this basin. The presence of these trees and some forms of tree-ferns also shared with the Euramerican Province suggests the existence of a phytogeographic connection consisting of dispersal through a humid corridor or landscape linkage between the tropics and northern Gondwana. This would make it possible for species to migrate between these two floristic provinces, a hypothesis that can be confirmed through further taxonomic and geological data. Finally, the presence of *Cordaixylon* in the Pedra de Fogo Formation corroborates the Cisuralian age for these rocks.

Keywords: Parnaíba Basin. Cisuralian. Systematics. Cordaitales. Paleoclimatology. Paleophytogeography.

1. Introduction

The Cordaitales are an extinct order of gymnosperms closely related to conifers, and are one of the most conspicuous elements in Late Pennsylvanian and Cisuralian tropical forest ecosystems, especially in the Northern Hemisphere (Rothwell and Warner, 1984; Trivett, 1992; Rothwell, 1993; Šimůnek, 2000; Taylor et al., 2009). Arborescent Cordaitales are tall forest trees, with some forms reaching a height of approximately 30 m, with a straight trunk extending upward for a considerable distance before giving rise to a crown of branches bearing spirally arranged leaves (Harms and Leisman, 1961; Falcon-Lang and Bashforth, 2005; Taylor et al., 2009). Leaves are the most commonly preserved organ of this group; the most complete specimens of foliage, stems and reproductive structures come from the Euramerican (Grand'Eury, 1877; Rothwell and Warner, 1984; Trivett, 1992; Rothwell, 1993) and Cathaysian floral provinces (Wang et al., 2003; Hilton et al., 2009), where some cordaitaleans have been reconstructed as whole plants (see Rothwell and Warner, 1984; Wang et al., 2003).

The presence of this group in the Southern Hemisphere is still under discussion, due to the absence of diagnostic reproductive structures and vegetative organs found in organic connection. However, there is an extensive record of impressions of isolated foliage from numerous Gondwanan basins, in strata ranging from the Pennsylvanian to Cisuralian, that are attributed to Cordaitales, e.g., *Noeggerathiopsis* (Feistmantel) McLoughlin et Drinnan, 1996 (in Chandra and Srivastava, 1991; Archangelsky et al., 1980; McLoughlin and Drinnan, 1996; Degani-Schmidt and Guerra-Sommer, 2019) or *Cordaites* Unger, 1850 (in Millan and Dolianiti, 1981; Millan et al., 1982; Iannuzzi, 2010; Césari and Hünicken, 2013). Recently, Césari and Hünicken (2013) reported *Cordaites* leaves (*Cordaites bifolius*) in organic connection with *Cordaitanthus*-like reproductive structures in Cisuralian strata from Argentina, which shows that the typical forms of Cordaitales found in the Northern Hemisphere tropics are also present in the West Gondwanan terrains.

In terms of anatomically preserved stems, a few genera with septate pith and with a putative cordaitalean affinity were found in the Western Gondwana, e.g., *Carolinapitys* (in Coimbra and Mussa, 1984), *Retemedulloxylon* (in Merlotti, 1998), *Paulistoxylon* (in Mussa, 1982; Crisafulli, 1998), and *Amyelon* root (in Coimbra and Mussa, 1984). The present contribution characterizes petrified cordaitalean wood specimens assigned to the genus *Cordaixylon* Grand'Eury, 1877 from the Permian deposits of the Parnaíba Basin, northeastern Brazil. This discovery provides the first evidence of this genus, not only in South America, but also in Gondwana. We also discuss the paleobiogeographic and biostratigraphic implications of this record, considering that the genus *Cordaixylon* occurs from the Pennsylvanian up to the Cisuralian, and is most abundant in the Pennsylvanian of the Euramerican Province.

2. Geological setting

The succession studied is situated in the Parnaíba Basin, considered an intracratonic basin (Figueiredo and Rala Gabaglla, 1986). The Parnaíba Basin, located in northeastern Brazil, covers a total area of approximately 600,000 km^2 (Fig. 1) (Góes and Feijó, 1994). This sedimentary basin is subdivided into five sedimentary sequences: Silurian (Serra Grande Gr), Middle Devonian-Mississippian (Canindé Gr), Pennsylvanian-Early Triassic (Balsas Gr), Jurassic (Mearim Gr) and Cretaceous (Vaz et al., 2007). The succession is represented by the Balsas Group, composed sequentially of the Piauí, Pedra de Fogo, Motuca and Sambaíba formations (Vaz et al., 2007). According to Góes et al. (1990), the Balsas Group represents the beginning of the continentalization in the Parnaíba Basin.

The stratigraphic succession (Fig. 2 A and B) corresponds to the base of the Pedra de Fogo Formation (Cisuralian), which overlies the Piauí Formation (Pennsylvanian) (Santos and Carvalho, 2009; Vaz et al., 2007; Barbosa et al., 2016; Conceição et al., 2016; Medeiros et al., 2019). The phytofossiliferous record occurs in siliciclastic deposits from the Pedra de Fogo Formation, which are exposed in two main regions in the state of Maranhão: a) along highways and hills (up to 40 m thick) in the municipalities of Coelho Neto and Duque Bacelar; and b) on the banks of the Parnaíba River (Boa Esperança Reservoir), in Nova Iorque municipality (Fig 1). In both regions, the fluvio-eolian sandstones from the Piauí Formation are interrupted and overlain by bedding mudrocks, interbedded with centimeter-thick layers of chert and very fine- to fine-grained sandstones (Fig. 2 A and B). The mudrocks are red to mottled, massive, occasionally laminated, and of variable thickness, locally reaching up to ca 2.5 m. Inside the mudrocks are frequent chert layers or lenses up to 20 cm thick. These cherts are massive, nodular and brecciated (Fig. 2 A and B). The chert breccia was used as a datum for the underlying contact with the Piauí Formation (Conceição et al., 2016; Conceição et al., 2020). Massive tabular and centimetric layers (up to 30 cm thick) of very fine- to fine-grained sandstones occur, generally with flat-lying bases and often laterally amalgamated to form interconnected sandstone sheets. In the northern part of the area, subordinate conglomerates are frequent, alternating with the mudrock beds and chert. Silicified trunks are found predominantly in the mudrocks, some of them in the life position, and some over 5 m long (Conceição et al., 2016). Silicified gymnosperm stems are more frequent (Fig. 2A and E), while tree ferns are subordinate. Locally, small reworked fragments of silicified gymnosperm stems occasionally are inserted in sandstones and conglomerates.

3. Study area

These materials come from two outcrops located 400 km apart in Nova Iorque and Duque Bacelar municipalities, state of Maranhão (Fig. 1), and were recovered from outcrops of the Pedra de Fogo Formation (Fig. 2). The Nova Iorque outcrops are located on the shore of the Boa Esperança Reservoir in southern Maranhão (see Conceição et al., 2020). The majority of the plants present in the area are gymnosperms, but there are also calamitalean and tree-fern stems (*Arthropytis* spp. and *Psaronius* spp., respectively). The Duque Bacelar petrified forest is located in eastern Maranhão and comprises five fossiliferous sites, referred to as “Ladeira do Olho d'Agua”,“Morro das Pedras Brancas”, “Fazendinha”, “Olho d'Agua” and “Morro da Pandora”. The fossil assemblages consist predominantly of large gymnosperm stems, some of them in life position (up to 2.3 m long and 1.15 m in diameter, Fig. 2C), and tree-fern stems (*Psaronius* sp.) in smaller numbers. Conceição et al. (2016) provided more-detailed information about this area.

4. Materials and methods

The material consists of seven petrified gymnosperm stems attributed to the same genus, with preserved septate pith, primary xylem and secondary xylem. Most of these samples have excellent cellular preservation. One of them is fractured into 10 pieces (specimen PAB 018.10).

Specimens were prepared as petrographic thin sections made in the laminating laboratory at the University do Vale do Rio dos Sinos (UNISINOS) in São Leopoldo and at the Federal University of Rio Grande do Sul (UFRGS), Brazil. Petrographic thin sections of the seven specimens were made in the three standard sections used for study of wood anatomy: transverse section, tangential longitudinal section and radial longitudinal section (*sensu* Jones and Rowe, 1999; Merlotti and Rosa, 2002). Large specimens were photographed with a Canon EOS T3i camera with a Sigma 70 mm DG Macro lens. Slides were examined and photomicrographs taken using a Leica MC170 digital camera attached to a Leica DM500 microscope. The cells were measured with the software ImageJ (Rasband, 1997).

The anatomical terminology employed to describe the fossil stems follows the recommendations of Rothwell and Warner (1984), International Association of Wood Anatomists (IAWA Committee, 2004), Falcon-Lang (2003), Falcon-Lang, (2007), Philippe and Bamford (2008). The systematic discussion and comparisons are based on previous descriptions of similar taxa with septate pith found in the different Paleozoic floral provinces, i.e., Gondwana (e.g., Crisafulli, 1998; Crisafulli and Lutz, 2000; Mussa, 1982a, b, 1986; Coimbra and Mussa, 1987; Merlotti, 1989, 1998), Cathaysia (e.g., Hilton et al., 2009; Wang et al., 2003) and Euramerica (e.g., Rothwell and Warner, 1984; Falcon-Lang, 2007) (see Table 1).

In the descriptions, at least 25 measurements, including diameter and length, were taken for each of the anatomical characters analyzed (tracheids, rays, parenchyma cells and cross-field pits). In the descriptions, the measurements of the cells are provided next to the cell type, with the minimum and maximum measurements outside brackets and the means within brackets.

The stems and thin sections are housed in the Museum of Archeology and Paleontology, Federal University of Piauí (UFPI), Teresina, Brazil.

5. Systematic Paleontology

Division: Gymnospermophyta Sternberg, 1820
Order: Cordaitales Stenberg, 1820
Genus*:* *Cordaixylon* Grand'Eury, 1877
Type species: *Cordaixylon dumusum* Rothwell and Warner, 1984

Cordaixylon sp. 1.

Figures 3–5.

Material studied: PAB 078, 137, 140, 142, 150, 151.

Repository: Museum of Archeology and Paleontology, Federal University of Piauí (UFPI), Teresina, Brazil.

Locality: Duque Bacelar, state of Maranhão, northeastern Brazil.

Stratigraphic horizon and age: Pedra de Fogo Formation, Cisuralian.

Descriptions

General features

Species represented by six samples of stems, reaching up to 12 to 14 cm in diameter and no more than 10 cm long. External tissues (e.g., cortex and periderm) are not preserved. The following description is based on observation of thin sections from specimens PAB 151 (Fig. 3 and 5) and 150 (Fig. 4 and 5). The center of the stem shows a large, septate and homocellular pith (ø 2.5–3 cm, Figs. 3A and 4A) surrounded by primary cauline bundles and pycnoxylic secondary xylem.

Pith

In transverse section, the septate pith is circular (Figs. 3A and 4A) and is surrounded by primary xylem cauline bundles. The pith is composed of circular to polygonal resin-filled parenchyma cells with relatively thick cell walls, radial diameter 39 to 119 µm (mean: 82), tangential diameter 43 to 104 µm (mean: 77). In radial section, the pith is subdivided by 15 horizontally arranged septa (bands of parenchyma cells), which extend to the pith margin (Figs. 3B and 4B). They are spaced every 0.2 to 0.4 cm longitudinally and are 1.5 to 2 cm long and 0.02 to 0.05 cm thick. These septa are slender and have pronounced bifurcated endings (Figs. 3B–C and 4B–D).

Primary xylem

The primary xylem consists of 31 discrete cauline bundles, which have endarch maturation (Figs. 3D–E and 4E). In transverse section, the protoxylem comprises small cells in contact with the pith cells, radial diameter 9 to 19 µm (mean: 15) and tangential diameter 6 to 18 µm (mean: 13). Tracheids of the metaxylem are circular to polygonal, radial diameter 20 to 37 µm (mean: 27) and tangential 18 to 35 µm (mean: 27), and shows well-preserved scalariform thickenings (Figs. 3F and 4F).

Secondary xylem

The pycnoxylic secondary xylem is composed of tracheids, arranged in radial rows with about 6 tracheids separating the parenchymatous rays (Fig. 5A–B) and weak growth interruptions (Fig. 5A). The tracheids are circular to polygonal in transverse section, radial diameter 26 to 46 µm (mean: 35), tangential diameter 23 to 42 µm (mean: 37). A double leaf trace is observable in transverse section, diverging from near the pith margin, initially as a single bundle and extending through the secondary xylem as a double bundle (Fig. 3A).

In radial section, the walls of the tracheids have bi- to triseriate, rarely uniseriate araucarian pits that are alternately arranged, contiguous, and circular or hexagonal in outline (Fig. 5C and D); when triseriate, they cover the entire walls of the tracheids (Fig. 5D). The cross-fields are cupressoid with 1–4 pits per field (mean: 2) (Fig. 5E).

In tangential longitudinal section, the parenchymatous rays have thin cell walls and are resin-filled. They are predominately uniseriate, 1–43 (mean: 11) cells high with a mean of 22 rays per mm^2 (Fig. 5F–G). There is a considerable percentage of biseriate rays (29%), ranging from 12–36 (mean: 22) cells high (Fig. 5F).

Comparison and discussion

The anatomically preserved stems characterized by pycnoxylic wood (*i.e.*, dense and forming the main bulk of the stem) and pith with regular septations, such as *Artisia*-type pith, are commonly placed in the following Euramerican genera: *Mesoxylon* Scott et Maslen, 1910, or in *Cordaixylon* Grand'Eury, 1877 (Scott and Maslen, 1910; Rothwell and Warner, 1984). The latter was documented in both the Euramerican and Cathaysian floral provinces (Hilton et al., 2009). More recently, Wang et al. (2003) have reported the presence of the new genus *Shanxioxylon* in the Cisuralian coal-ball assemblage from northern China, which has an *Artisia*-type pith and is directly related to Cordaitales on the basis of reproductive organs found in organic connection (see Wang et al., 2003).

The specimens described here have a large septate pith surrounded by approximately 31 primary xylem bundles of endarch maturation; araucarian radial pits on the tracheid walls, mostly bi- or triseriate; cupressoid cross-field pits; and uniseriate to biseriate xylem rays. Several stem woods with structures similar to septations in the pith are known from the Paleozoic (e.g., Crisafulli, 1998; Crisafulli and Lutz, 2000; Mussa, 1982a, b, 1986; Coimbra and Mussa, 1987; Merlotti, 1998; Feng et al., 2012); however, relatively few stems have septations similar to an *Artisia*-like pith, a structure typically found in cordaitalean plants (see Scott and Maslen, 1910; Rothwell and Warner, 1984; Wang et al., 2003; Falcon-Lang and Bashforth, 2005; Hilton et al., 2009).

In Western Gondwana, the taxa that most resemble our wood include the following Permian genera: *Carolinapitys* Coimbra and Mussa, 1984, from the Parnaíba Basin; and *Retemedulloxylon* Merlotti, 1998 and *Schopfiicaulia* Mussa, 1982b, both from the Paraná Basin. *Carolinapitys* has a pith with irregular septa formed by sclerenchyma cells, and secondary xylem of the taxoid type (Kräusel, 1928), differing from the homogeneous pith and the secondary xylem of our material. *Retemedulloxylon* has a set of mini-lacunae scattered over the entire pith, mixed radial pitting, and fenestriform cross-field pits (Merlotti and Kurzawe, 2011); but it differs from our wood, which has cupressoid cross-field pitting and araucarian radial pitting. *Schopfiicaulia,* similarly to our specimen, has regular septations in the pith and araucarian pitting on the radial tracheid walls. Nonetheless, this genus has *Vertebraria*-like external morphology with adventitious roots. Moreover, it has araucarioid cross-field pits and sclerenchyma cells in the pith (See Merlotti and Kurzawe, 2011; Crisafulli, 2004). These characteristics of *Schopfiicaulia* contrast distinctly from the present material.

Some genera of Paleozoic cordaitaleans from the Northern Hemisphere with septate pith are comparable to the stem described here (Table 1). *Mesoxylon*, despite having regular and well-organized septa in the pith (*Artisia*-like), has primary xylem bundles with mesarch organization and non-sympodial architecture, which are considered the most important diagnostic features of this genus, thus differing from our specimen. *Metacordaites* Renault, 1896 and *Septomedullopitys* Lepekhina, 1972 have septate heterocellular piths with numerous secretory ducts. These characters distinguish them from the present sample, which has homogeneous pith.

Shanxioxylon (in Wang et al., 2003) has a septate pith, but it is solid in the basal and apical regions and the primary xylem maturation of cauline bundles is endarch and mesarch in the leaf traces, therefore differing from our material, which has only endarch primary xylem and septate pith.

The genus *Cordaixylon* Grand'Eury, 1877, from central Europe, was established for specimens with *Artisia*-like piths, sympodial primary vascular architecture, endarch cauline bundles, and woods with araucarian radial pitting and cupressoid cross-field pits. All these characters are seen in the present specimens. Besides, our material is very similar to the forms included in *Cordaixylon*. This genus has been characterized based on stems found in organic connection with roots, leaves and fructifications, unlike our specimens (e.g., Rothwell and Warner, 1984; Wang et al., 2003; Hilton et al., 2009). However, in other cases, isolated petrified stems without septations in the pith have also been referred to this genus (e.g., Wang, 2000; Falcon-Lang; 2007; Césari et al., 2015).

Anatomically well-preserved silicified specimens assigned to the genus *Amyelon* were recorded in the Permian of the Parnaíba Basin by Coimbra and Mussa (1984). This genus corresponds to a cordaitalean root, as stated by some authors (e.g., Cridland, 1964; Stewart and Rothwell, 1993; Wang et al., 2003), and has been found in organic connection with *Cordaixylon* stems in the Euramerican and Cathaysian provinces (Rothwell and Warner, 1984; Hilton et al., 2009).

In view of the above considerations and the fact that the present specimens share their main taxonomic features with *Cordaixylon*, the inclusion of these woods in this genus is clearly justified. The absence of preserved extraxylary tissues and features of the phyllotaxy of the stems makes it impossible to assign the new material to any morphospecies of *Cordaixylon*, since the diagnoses of most species of this genus include these features .The exceptions are *Cordaioxylon houtoumiaoense* Wang, 2000 and *Cordaixylon sahnii* Wang, 2000 (Wang, 2000), and *Cordaixylon andresii* Césari et al., 2015 (Césari et al., 2015), which even has a non-septate pith and was classified based only on the pith and secondary xylem (Table 2). For this reason, we designate our material only as *Cordaixylon* sp. 1.

Cordaixylon sp. 2.
Figures 6–7.
Material studied: PAB. 018.10.
Repository: Museum of Archeology and Paleontology, Federal University of Piauí (UFPI), Teresina, Brazil.
Locality: Nova Iorque, southern Maranhão state, northeastern Brazil.
Stratigraphic horizon and age: Pedra de Fogo Formation, Cisuralian.

Descriptions

General features

The specimen~~s~~ is fragmented into 10 parts, silicified, light brown and decorticated, reaching up to 4 cm in length and 8 cm in diameter. The center of the stem shows a large, septate and homocellular pith (ø 2.5 cm, Fig. 6A–B) surrounded by pycnoxylic secondary xylem (Fig. 7B).

Pith

In transverse section, the septate central pith is circular (Fig. 6A) and is surrounded by primary xylem cauline bundles. At the margin of the pith, the tissue consists of horizontally oriented, circular to rectangular, resin-filled parenchyma cells, apparently the cells of the septa. Circular, resin-filled parenchyma cells are also scattered over the entire pith; their radial diameter is 13 to 59 µm (mean: 42) and their tangential diameter 13 to 67 µm (mean: 52), with relatively thick cell walls. Non resin-filled parenchyma cells are generally circular to polygonal and are wide, with radial diameter 52 to 157 µm (mean: 109) and tangential diameter 63 to 184 µm (mean: 118) (Fig. 6F). In radial section, the pith is subdivided by two files of septa on either margin of the pith (Fig. 6B). They are composed of 11 septa each, alternating with lacunae. The septa (bands of parenchyma cells) start at the pith margins and are arranged horizontally toward the center (Fig. 6B) with connected terminations and subtle bifurcations (Fig. 6C). Horizontal septa are spaced every 0.13 cm longitudinally; they measure 0.5 to 0.7 cm long and 0.08 to 0.14 cm thick. Apparently, the parenchyma cells in the center of the pith were destroyed, since this part is completely recrystallized (Fig. 6B).

Primary xylem

As viewed in transverse section, the primary vascular system appears to consist of about 29 cauline bundles with endarch maturation (Fig.6D–E). In transverse section, the protoxylem cells are poorly preserved, but can be identified by their smaller cells near the margin pith, with some cells reaching up to 12 µm in diameter. Tracheids of the metaxylem are circular to polygonal, with radial diameter 10 to 21 µm (mean: 16) and tangential diameter 5 to 26 µm (mean: 18). In radial section, the walls of the metaxylem cells show poorly visible scalariform thickenings (Fig. 6G).

Secondary xylem

The secondary xylem is pycnoxylic, composed of tracheids, parenchymatous rays and some leaf trace (Fig. 7A and H). The tracheids are circular to polygonal in transverse section, with radial diameter 26 to 42 µm (mean: 28) and tangential diameter 31 to 53 µm (mean: 39). They are arranged in radial rows with about five tracheids separating the rays (Fig. 7B). A double leaf trace is visible in transverse section, diverging from near the pith margin, initially as a single bundle and extending through the secondary xylem as a double bundle and with scalariform thickenings (Fig. 7A and H).

In radial section, the walls of the tracheids have araucarian pits that are alternately arranged, contiguous, and circular or hexagonal in outline (Fig. 7C–D). These pits are bi- to triseriate, rarely uniseriate; when triseriate, they cover the entire walls of the tracheids (Fig. 7D). The cross-fields are cupressoid with 1–5 pits per field (mean: 3) (Fig. 7F–G). In transverse longitudinal section, the parenchymatous rays are narrow and short, with thin cell walls. They are uniseriate or, rarely, biseriate, 1–18 cells high (mean: 7 cells), with 28 rays per mm^2 (Fig. 7I).

Comparison and discussion

As in the above-mentioned Duque Bacelar specimens (*Cordaixylon* sp. 1), the Nova Iorque specimen has a large septate pith (Table 3); primary xylem bundles with endarch maturation; araucarian pits on the radial tracheid walls, mostly bi- or triseriate; cupressoid cross-field pits; but uniseriate, rarely biseriate xylem rays (Table 4). Thus, for the same reasons given for *Cordaixylon* sp. 1, this specimen should be included in the genus *Cordaixylon*. This material cannot be assigned to *Cordaixylon* sp. 1 because of the notable anatomical differences, such as: (a) between the materials of the two regions there are significant differences in the morphology of the septa in the pith, for example, in the Nova Iorque specimen the septa are wider (Table 3 and Fig. 6B–C) with connected terminations and subtle bifurcations (6B–C), while in the Duque Bacelar specimens they are thin and have divided bifurcations and well-developed ends (Figs. 3 B – C and 4B–D).; and (b) in the Nova Iorque specimen the parenchymatous rays are predominately uniseriate, 1 to 18 cells high (mean: 7) cells high (Fig.7I, Table 4), whereas the Duque Bacelar samples have parenchymatous rays, a considerable percentage of which are biseriate (29%) and range from 12 to 36 (mean: 22) cells high (Fig. 5F, Table 4). Therefore, we designate the Nova Iorque specimen as a distinct morphotype, named *Cordaixylon* sp. 2 (see Figs. 3–7 and Table 2).

Remarks:

We are aware that these differences in the morphology of the septa between the two morphotypes, *Cordaixylon* sp. 1 and *Cordaixylon* sp. 2, could be related to different ontogenetic stages of stems. However, to examine this hypothesis further, the stems would need to be more complete, subject to observation through sections from different levels, the basal, middle and apical portions. This would make it possible to recognize the morphoanatomical variations from the proximal to the distal portions and, from there, determine the ontogenetic changes that occur throughout the growth of the plant. However, it was not possible to obtain more-complete specimens. Therefore, these morphological differences of the septa were considered diagnostic, leading to the classification of the specimens from Duque Bacelar and Nova Iorque in two different morphotaxa.

6. Discussion

6.1. Paleoenvironmental reconstruction

The fossiliferous interval of the silicified trunks, in both areas, i.e., the Coelho Neto - Duque Bacelar and Nova Iorque (Boa Esperança Reservoir) municipalities, are associated with predominantly monotonous variegated mudrocks and cherts intercalated with amalgamated sandstone sheets. This is interpreted as a fluvial-lacustrine environment, with deposits on a wetland plain on the shores of large continental lakes (Fig. 2A and B). The large size of some fossil stems (Fig 2C), combined with the extensive lateral coverage of the mudrocks, suggests a sufficiently large hydromorphic surface to support the water requirements of these plants, compatible with humid to sub-humid climatic regimes. On the other hand, the geometry and small vertical dimensions of the sandstone sheet layers indicate deposits from rapid flooding, typical of arid to semi-arid regions. Taken together, these elements suggest a floristic dynamic around the Late Paleozoic in a seasonality regime similar to other parts of Pangea (Driese and Ober, 2005; DiMichele et al., 2009; Lojka et al., 2010). This interpretation is compatible with observations by Conceição et al. (2016) and Conceição et al. (2020). The plant remains became incorporated in the sediments when the lake base level rose rapidly upon the return of wetter climatic conditions in a semi-arid regime and increased hydrological discharge or rainfall. During these flood events, stems were often reworked and transported in shallow channels, while others could be preserved in a life position on the wetland plains surrounding lakes (Fig. 8).

6.2. Paleobiogeography and Paleoclimatology

In the Northern Hemisphere, whole plants of Cordaitales have been reported in many areas throughout the Euromerican and Cathaysia provinces, especially in the Pennsylvanian of the Euromerican (e.g., Rothwell and Warner, 1984; Falcon-Lang, 2007; Hilton et al., 2009; Wang et al., 2003). On the other hand, their presence in the Gondwanan Province is still poorly understood, due to the absence of diagnostic reproductive structures (Césari and Hünicken, 2013). Although several examples of stems with septate pith and leaves and with a putative cordaitalean affinity have been reported from South America (e.g., Paraná Basin deposits, Millan and Dolianiti, 1981; Millan et al., 1982; Mussa, 1982a, b; Merlotti, 1989, 1998b; Iannuzzi, 2010), it remains a challenge to associate these structures directly with the Northern Hemisphere Cordaitales. This problem arises mostly from the absence of leaves in organic connection with reproductive structures, and also from the presence in these stems of irregular septa and other anatomical characters that are not observed in the taxa of the Northern Hemisphere (**see item 4. Systematic Paleontology and Table 1**).

Although our material is not connected to any reproductive structures or other vegetative parts, the medullary septate pith is typically found in Cordaitales stems from the Northern Hemisphere, especially the septations (see Figs 3–7). The presence of *Cordaixylon* in the Permian deposits of the Parnaiba Basin is further supported by the occurrence of the genus *Amyelon* (Coimbra and Mussa, 1984). Leaves (*Cordaites bifolius*) in organic connection with a *Cordaitanthus*-like reproductive structure have recently been reported in the earliest Cisuralian strata of Argentina by Césari and Hünicken (2013), which implies that the same Cordaitales that inhabited the Northern Hemisphere may also have reached and colonized the inner Western Gondwanan terrains.

As discussed by Rößler (2006) and Iannuzzi et al. (2018), due to the intermediate geographical position of the Parnaíba Basin (between the Euramerican and Gondwanan floral provinces), this basin could represent a humid dispersal corridor or landscape linkage between the tropics and northern Gondwana, which would make it possible for many species to disperse while preserving their ecological requirements. Such a corridor would partially explain the presence of both floral and faunal taxa shared with the Gondwanan and Euramerican areas, as shown in some publications (e.g., Mussa and Coimbra, 1987; Rößler and Galtier, 2002; Iannuzzi et al., 2014; Cisneros et al., 2015).

The climate model proposed for the Pennsylvanian-Cisuralian versus the distribution of *Cordaixylon* (Fig. 9) indicates that the occurrence of this genus in the Euroamerican and Cathaysia provinces was limited to the perennially humid tropical belt. In contrast, in the Parnaíba Basin, this genus is recorded in subtropical arid climatic conditions (Fig. 9), although this model represents a macroclimatic scale.

According to Conceição et al. (2020), the predominance of fine-grained siliciclastic sediments interbedded with thin tabular to lenticular layers of fine- to medium-grained sandstone, with associated microbialites and fossil plants, many preserved in their life position, is consistent with an endorheic lacustrine system that was periodically or occasionally subjected to episodic storm and flood events. Notably, the climate models by Rees (2002) and Scotese et al. (2014) do not take into account the presence of this large lacustrine system in the interior of Pangea, specifically in the Parnaíba Basin, such as the system described by Andrade et al. (2014) and Araújo et al. (2016) at the southwest edge of this basin. Conceição et al. (2016a), Conceição et al. (2020) suggested that the plants of the Pedra de Fogo Formation found at the eastern edge of the basin lived on the banks of these large lakes. Therefore, the presence of the lakes may have produced more-humid local climatic and environmental conditions.

Additionally, as discussed by Iannuzzi et al. (2018), although several indicators in the Permian floral record from the Parnaíba Basin point to a seasonally dry climate, there are also other, contradictory factors. These include the arborescent ferns and calamitaleans and most of the gymnosperms, which likely grew over several years to attain their large dimensions, both in diameter (e.g., gymnosperm stems more than one meter in diameter and in height; Conceição et al., 2016a), as well as the quite diverse aquatic vertebrate community described by Cisneros et al. (2015), which would have required permanent water sources (see Iannuzzi et al., 2018). These authors noted that this pattern fits best with the modern ‘tropical summerwet’ biome of Rees et al. (2002), although it contradicts the predictions of climate models (i.e., subtropical arid climate regime) for this region of northern South America during the Cisuralian (Scotese et al., 2014).

Based on changes in sedimentary patterns and paleosols as well as on the general paleobotanical trends, DiMichele et al. (2006) demonstrated that during the Carboniferous-Permian climatic transition, wetland plants were confined to shrinking "wet spots". These plants were found along permanent streams where the vegetation remained undisturbed, living apart from the increasingly depauperate landscape. Environmental conditions would be more humid near the margins of water bodies, enabling the vegetation to grow. Bashforth et al. (2016) demonstrated that cordaitalean trees were present in lowland habitats of the Illinois Basin during a seasonally dry climatic interval. These dryland plants would have been dominant in mesic habitats of equatorial Euramerica during the Pennsylvanian and into the Permian. These scenarios could be analogous to the paleoenvironments interpreted for the Pedra de Fogo Formation, and may explain not only the occurrence of this typically tropical genus in this Gondwanan region, but also the high degree of endemism of the biota of the Parnaíba Basin, as pointed out by Neregato et al. (2017). Similarly, the presence of these large lakes could explain the existence of the lush vegetation discussed by Iannuzzi et al. (2018), as the lakes would have provided the necessary humidity for vegetation growth in a arid region. We note that the models of Rees et al. (2002) and Scotese et al. (2014) are applicable at macroclimatic scales and do not take into account the existence of microclimatic variations in a regional to local context.

6.3. Biostratigraphy

The age of the Pedra de Fogo Formation has long been discussed in many publications, based on data from fossil pollen (Dino et al., 2002), fish remains (Ginter et al., 2005), temnospondyli amphibians (Price, 1948; Cox and Hutchinson, 1991) and other tetrapods (Cisneros et al., 2015), and plants (Iannuzzi et al., 2018). Nevertheless, divergences still persist due to the absence of elements that make it possible to determine age by radiometric methods, and the absence of a more continuous and well-preserved palynological content. Publications have suggested ages from the early up to the late Permian (see discussion by Iannuzzi et al., 2018). Based on the present contribution, the Cisuralian age for the Pedra de Fogo Formation is supported by the presence of *Cordaixylon,* since the occurrence of this genus in the Northern Hemisphere is limited to the interval from the Pennsylvanian to the Cisuralian (see Fig. 9 and Tables 1 and 2). This is in agreement with the recent record of the reptile genus *Captorhinikos* in this formation, also restricted to the Cisuralian of North America (Cisneros et al. in press).

7. Conclusions

The morphology and anatomy of the stems described here suggest that our specimens belong to the genus *Cordaixylon*. These specimens were classified into two morphotypes (*Cordaixylon* sp. 1 and sp. 2), which comprise the first record of these taxa not only in the South American, but also in the Gondwanan Floral Province. This genus was found in two mutually distant outcrops, indicating that these plants occurred over a wide geographical area in the Parnaíba Basin.

These results provide important data for discussing and understanding the presence of Cordaitales in the Southern Hemisphere, since this is still questioned. It remains to be determined whether the cordaitalean plants present in the Gondwana are the same type as in the Northern Hemisphere, or are they other types related to this group? The Gondwanan paleobotanical record is represented mainly by organs without organic connection and the woods are mostly fragments of only secondary xylem, which makes it very difficult to evaluate phylogenetic relationships.

Current models indicate a subtropical arid climate regime for this region of northern South America during the Cisuralian. Nevertheless, regional sedimentological interpretations suggest that, during the deposition of the Pedra de Fogo Formation, this part of the Parnaíba Basin was dominated by large lakes and that these plants lived on their shores. Thus, local conditions may certainly have been more humid than the suggested macroclimate, and could resemble the environmental/climatic conditions in tropical regions of the Northern Hemisphere where these types of plants have been recorded in abundance. The presence of this genus in the Permian deposits of this basin constitutes further evidence for a Cisuralian age for the rocks of the Pedra de Fogo unit. We believe that in order to advance knowledge of the order Cordaitales, it is essential to continue paleobotanical research in the Permian deposits, not only in the Parnaíba Basin, but throughout Gondwana. The information available shows that the Cordaitales was a very diverse group, which existed for approximately 80 Myr and played an important role in shaping terrestrial ecosystems and landscapes through the Pennsylvanian and Cisuralian.

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Figure captions

Figure. 1. General location of the study area. Left insets show the location of the area in relation to South America; gray inset indicates the location of the outcrops where the fossils were found. Large map shows details of the area with geological information on both paleobotanical outcrops studied, i.e. Duque Bacelar and Nova Iorque, in Maranhão state. Modified from Iannuzzi et al. (2018).

Figure 2. Lithostratigraphic logs of the succession, showing the contact between the Piauí Formation (Pennsylvanian) and the Pedra de Fogo Formation (Cisuralian). **A**. Coelho Neto-Duque Bacelar region. **B**. Boa Esperança Reservoir, Nova Iorque region. **C**. Silicified stems in life position (white arrow) and horizontalized (black arrow) at the base of the Pedra de Fogo Formation in Duque Bacelar outcrop. **D** and **E**. Samples of stem that occurs at the base of the Pedra de Fogo Formation in Nova Iorque outcrop (arrows). Scale bar in "**D**" = 10 cm. Terminal Spl.= Terminal Splays. Nears. = Nearshore. Modified from Conceição et al. (2016a) and Conceição et al. (2020).

Figure 3. *Cordaixylon* sp. 1, specimen PAB 151. **A**. General morphology of the stem in transverse section, showing well-developed wood and broad pith and leaf traces (arrows). **B**. Radial section, showing the distribution and morphology of the septa (arrows). **C**. Microscopic view, showing the regular organization and morphology of the septa in radial section (arrows). **D**. Transverse section, showing general view of the pith with resin-filled parenchyma cells (P), cauline bundles with endarch maturation (arrows), and secondary xylem (SX). **E**. Enlargement of D, showing a primary xylem cauline bundle with endarch maturation (ellipse). **F**. Radial section, showing the pith (P) and scalariform/reticulate thickenings of the metaxylem (MX). Scale bars: **A** and **B** = 1 cm; **C** = 1 mm; **D** = 500 µm; **E** = 200 µm; **F** = 100 µm.

Figure 4. *Cordaixylon* sp. 1, specimen PAB 150. **A**. General morphology of the stems in transverse section. **B**. Radial section, showing the morphology of the septa (arrows). **C**. Microscopic view, showing the morphology of the septa in radial section; note the bifurcations (arrows). **D.** Enlargement of C, showing the septa with pronounced bifurcations (arrows). **E**. Transverse section, showing the pith (P), cauline bundles with

endarch maturation (ellipse), and secondary xylem (SX). **F**. Radial section, showing the pith (P) and scalariform/reticulate thickenings of the metaxylem (MX). Scale bars: **A** and **B** = 1 cm; **C** = 2 mm; **D** = 500 µm; **E** and **F** = 200 µm.

Figure 5. *Cordaixylon* sp. 1, specimens PAB 150 and 151. General view of the secondary xylem. **A** and **B**. Transverse section, general view of the pycnoxylic secondary xylem with tracheids and uniseriate rays, note the growth interruptions in A (arrow). **C**. Radial section, showing alternately arranged biseriate pits. **D**. Radial section, showing contiguous triseriate and biseriate araucarian pits (arrows). **E**. Radial section, showing the cupressoid cross-field pitting (arrow). **F**. Tangential longitudinal section, showing uniseriate and biseriate rays (arrow). **G**. Tangential longitudinal section, with only uniseriate rays. Scale bars: **A**–**C** = 100 µm; **D** = 25 µm; **E** = 10 µm; **F** and **G** = 100 µm.

Figure 6. *Cordaixylon* sp. 2, specimen PAB 018.10. **A.** General view of the stem, showing the cauline bundles. Arrows indicate three of the approximately 29 cauline bundles. **B**. Radial section, showing the septate pith; arrows indicate septa. **C**. Microscopic view of the septa in radial section (arrows). **D**. Transverse section, showing the pith (P) with resin-filled parenchyma cells, cauline bundles (arrow) and secondary xylem (SX) **E**. Transverse section, showing primary xylem cauline bundles with endarch maturation (arrow). **E**. Transverse section, showing non resin-filled parenchymal cells of the pith. **G.** Radial section, showing the pith (P), scalariform/reticulate thickenings of primary xylem (MX) and secondary xylem (SX). Scale bars: **A** and **B** = 1 cm; **C** and **D** = 1 mm; **E =** 400 µm; **F** and **G** = 200 µm.

Figure 7. *Cordaixylon* sp. 2, specimen PAB 018.10. General aspect of the secondary xylem. **A**. Transverse section, note the leaf trace diverging from near the pith as a double bundle and extending through the secondary xylem. **B**. Transverse section, general view of the pycnoxylic secondary xylem with tracheids and uniseriate rays. **C**. Radial section, showing biseriate araucarian pits, alternately arranged. **D**. Radial section, showing triseriate araucarian pits. **E.** Radial section, showing general view of the cross-field pitting (arrow). **F** and **G**. Radial section, showing cupressoid cross-field pitting (arrows). **H**. Enlargement of H in A, showing scalariform/reticulate thickenings

of the leaf.). **I.** Tangential longitudinal section, showing uniseriate rays. Scale bars: **A**= 1 mm; **B**=200 µm; **C**=50 µm; **D**= 20 µm; **E**= 100 µm; **F** and **G**=10 µm; **H**= 50 µm; **I**= 200 µm.

Figure 8. Interpretation of the environment of the Pedra de Fogo Formation during the early Permian in the eastern Parnaíba Basin, west-central Pangea. Plants preferentially colonized the wetland area. Many stems were reworked and transported during flood events, while others were preserved in life position in wetlands surrounding lakes. **a.** Lake nearshore. **b**. Marginal wetland. **c**. Active "sheet channel". **d**. Abandoned "sheet channel" petrified-wood forming.

Figure 9. The climate model proposed for the Pennsylvanian-Cisuralian versus the overall distribution of genus *Cordaixylon*. **1-** United States (Trivett, 1992); **2-**United States (Rothwell and Warner, 1984); **3-** Canada (Falcon-Lang, 2007); **4-** Spain (Césari et al., 2015); **5-** France (Grand'Eury, 1877); **6-** Germany (Rößler, 2006) **7-** China **(**Feng et al., 2010) and **8-** (Wang, 2000); **9** northeastern Brazil (this study). Adapted from the model proposed for Sakmarian by Scotese et al. (2014).

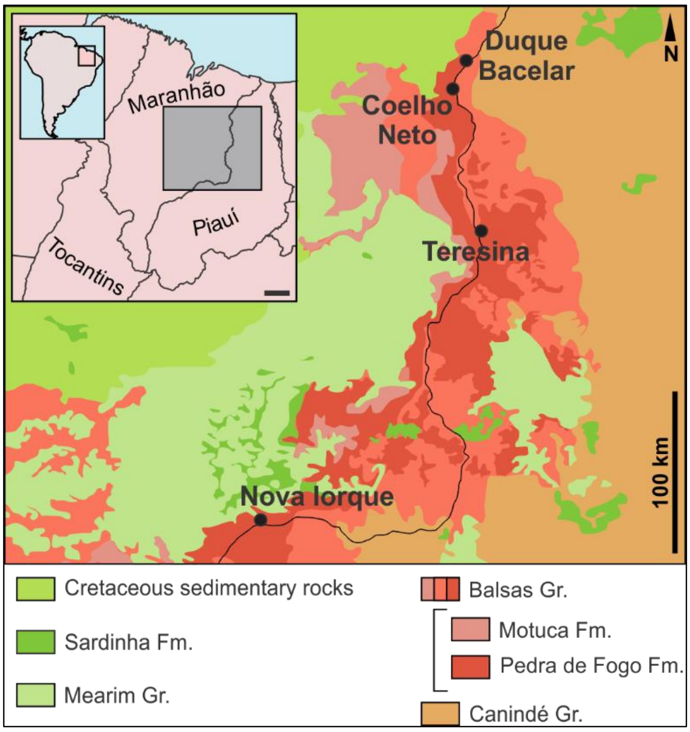

Maranhão
Piauí
Tocantins
Duque Bacelar
Coelho Neto
Teresina
Nova Iorque
N
100 km
Cretaceous sedimentary rocks
Sardinha Fm.
Mearim Gr.
Balsas Gr.
Motuca Fm.
Pedra de Fogo Fm.
Canindé Gr.

Fig. 1

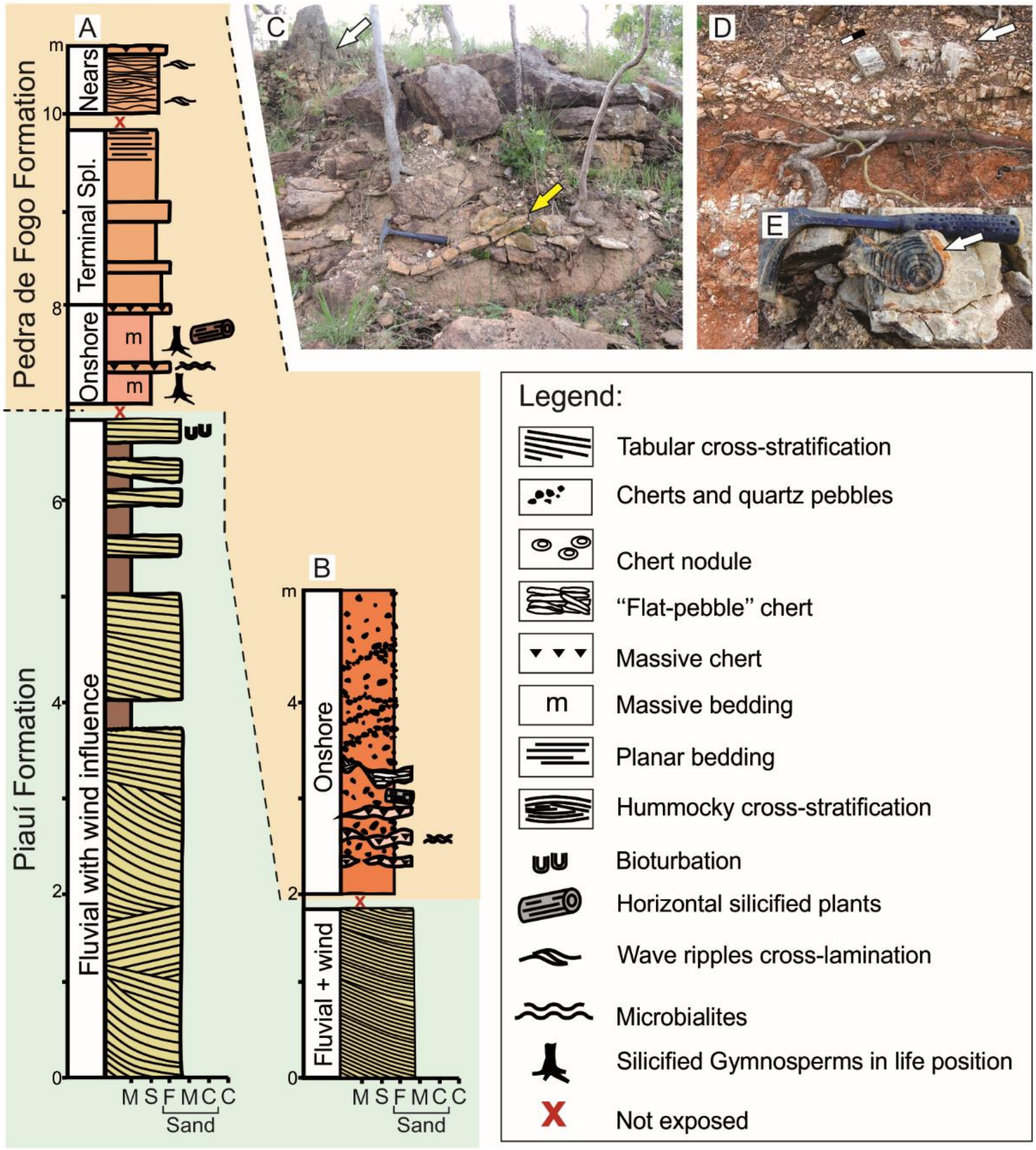

A
B
C
D
E
Pedra de Fogo Formation
Piauí Formation
Nears
Terminal Spl.
Onshore
Fluvial with wind influence
Fluvial + wind
m
m
10
8
6
4
2
0
M S F M C C
Sand
Legend:
Tabular cross-stratification
Cherts and quartz pebbles
Chert nodule
"Flat-pebble" chert
Massive chert
Massive bedding
Planar bedding
Hummocky cross-stratification
Bioturbation
Horizontal silicified plants
Wave ripples cross-lamination
Microbialites
Silicified Gymnosperms in life position
Not exposed

Fig. 2

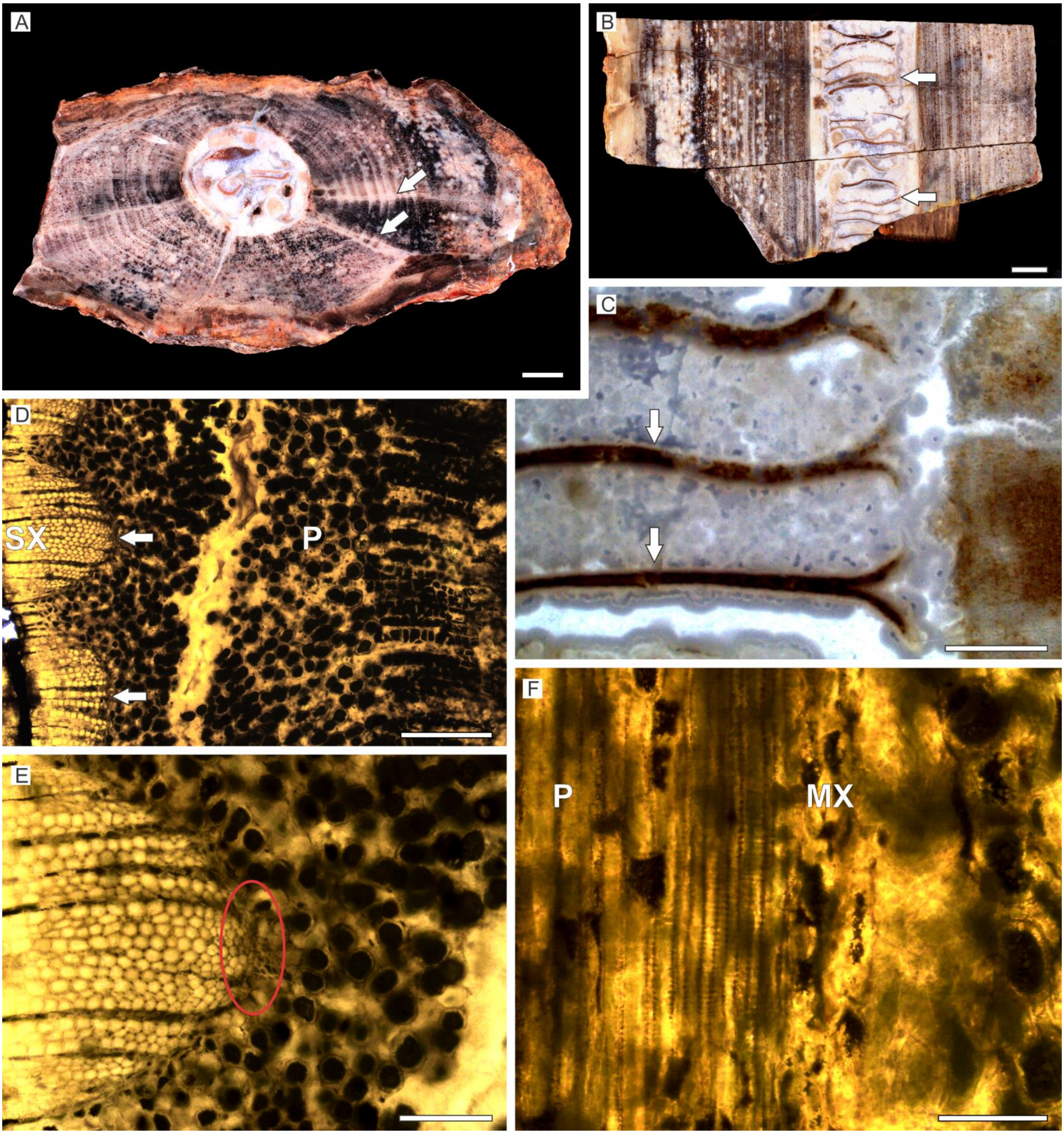


Fig. 3

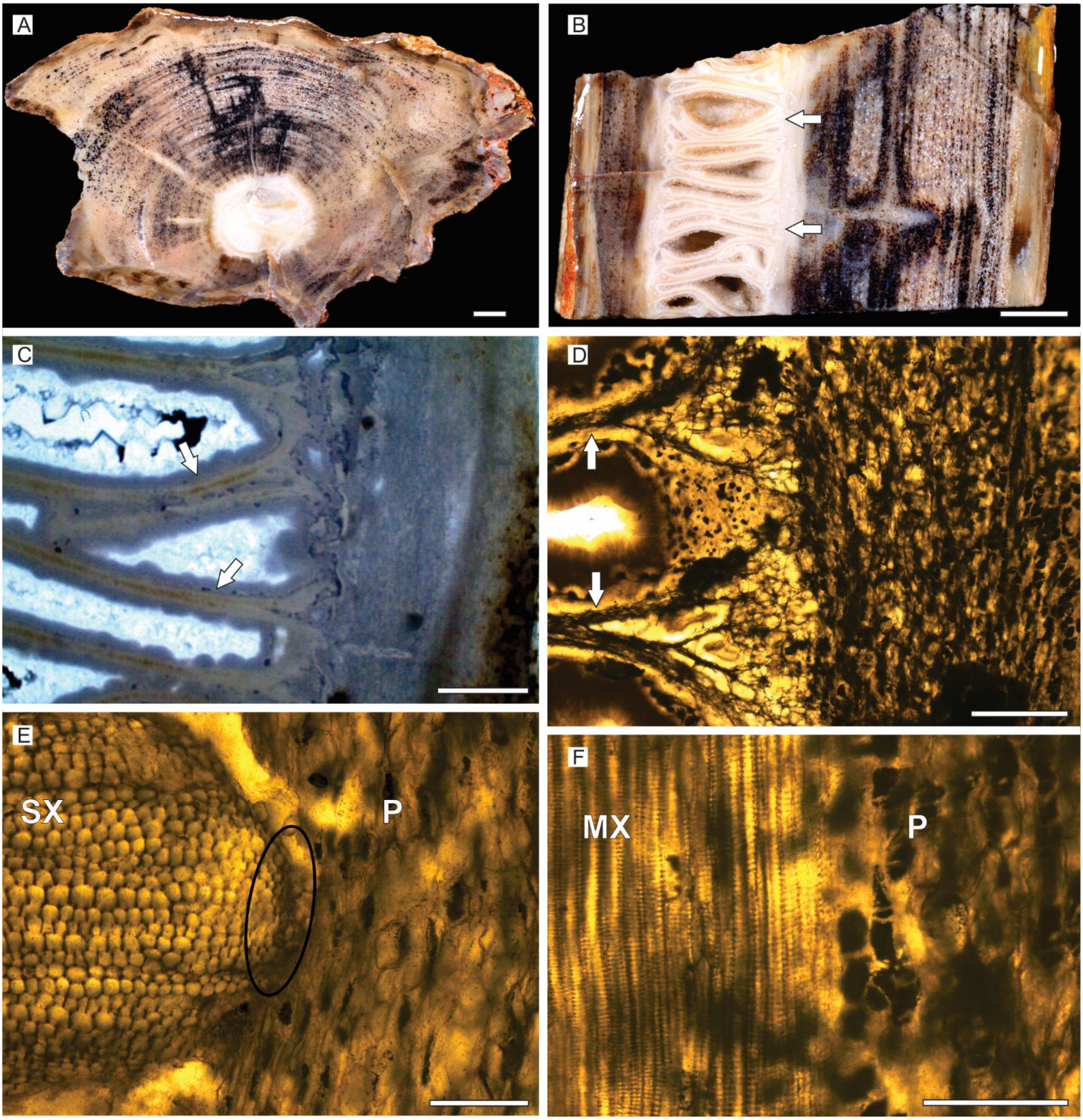


Fig. 4

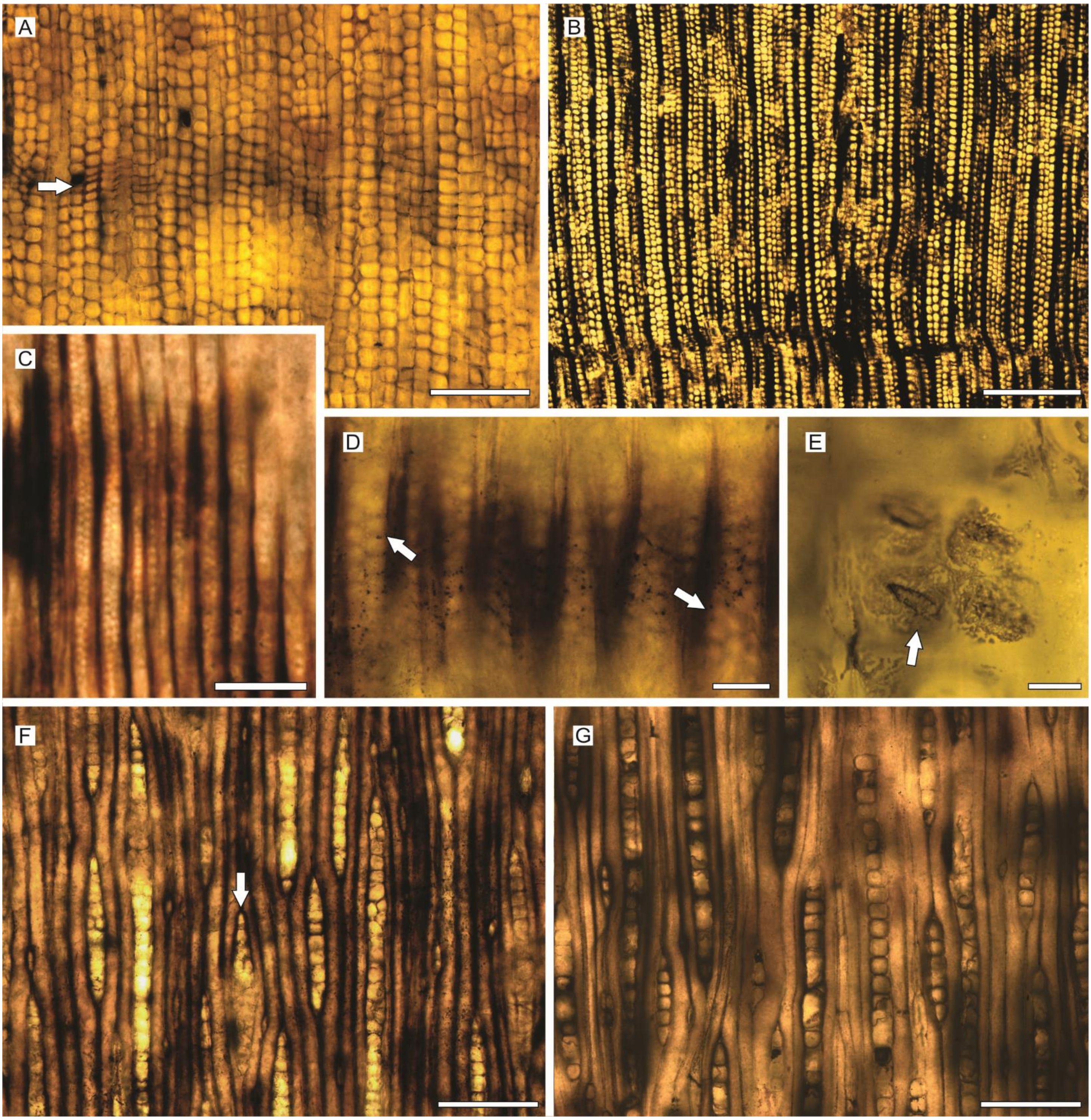


Fig. 5

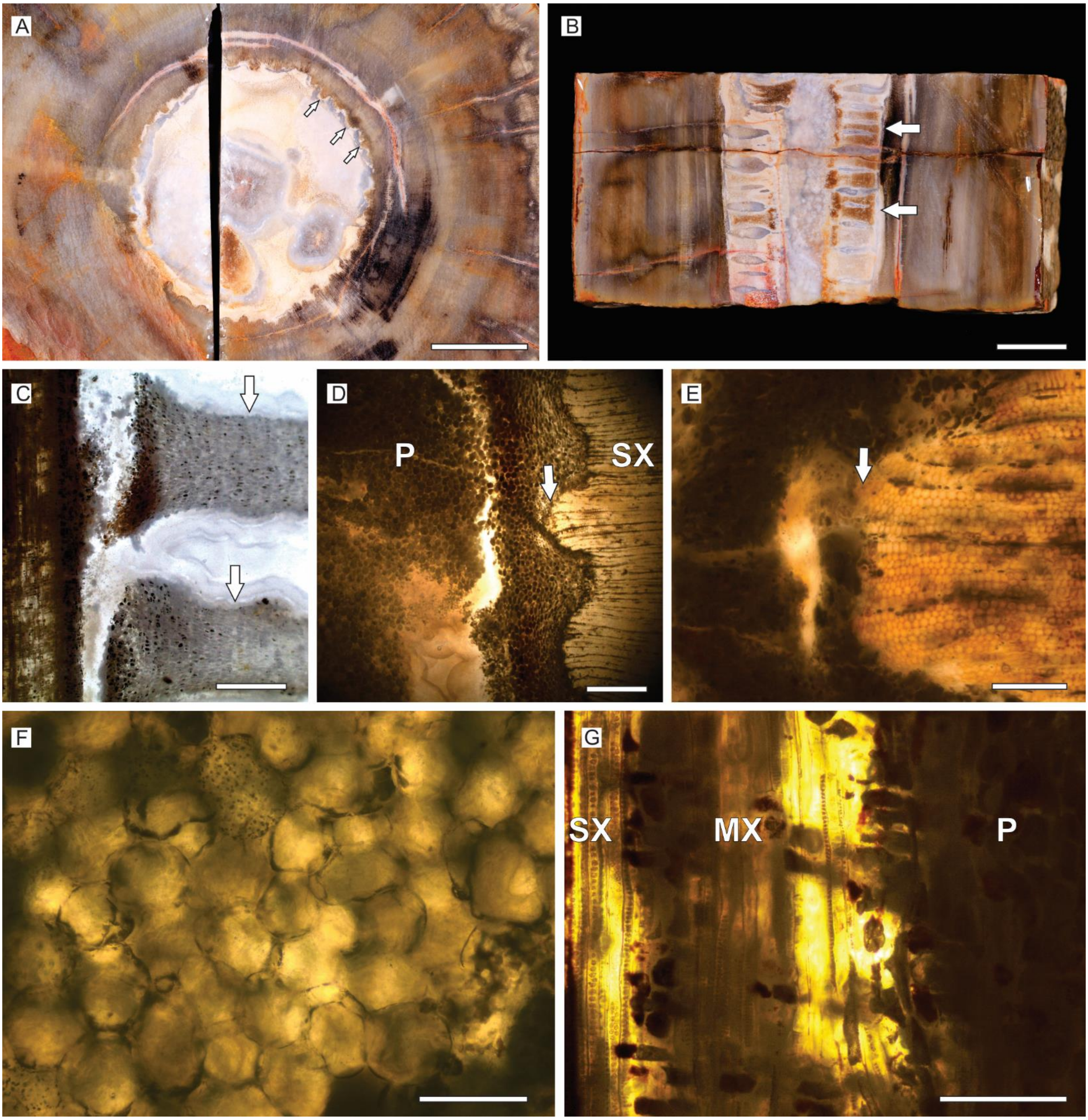


Fig. 6

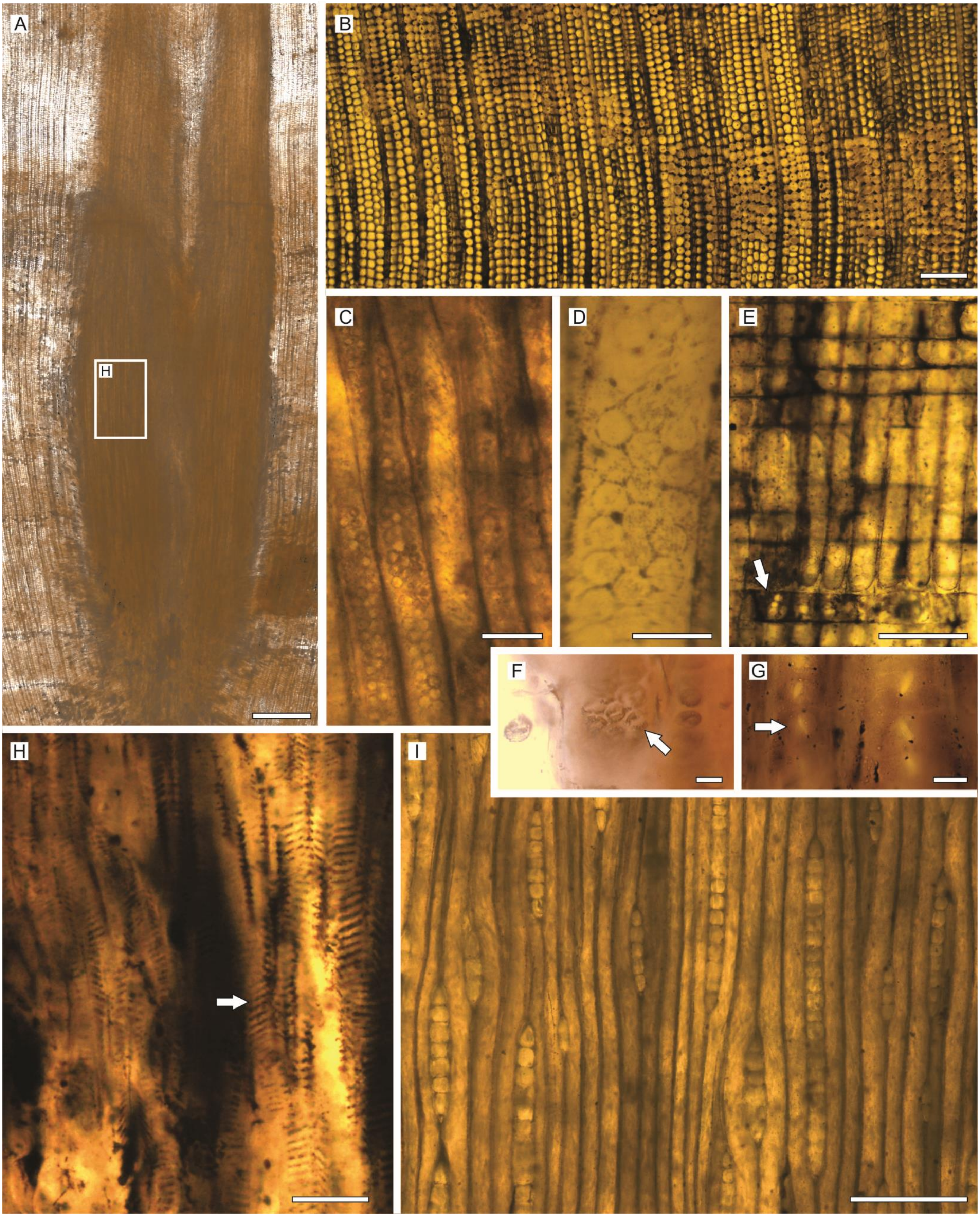


Fig. 7

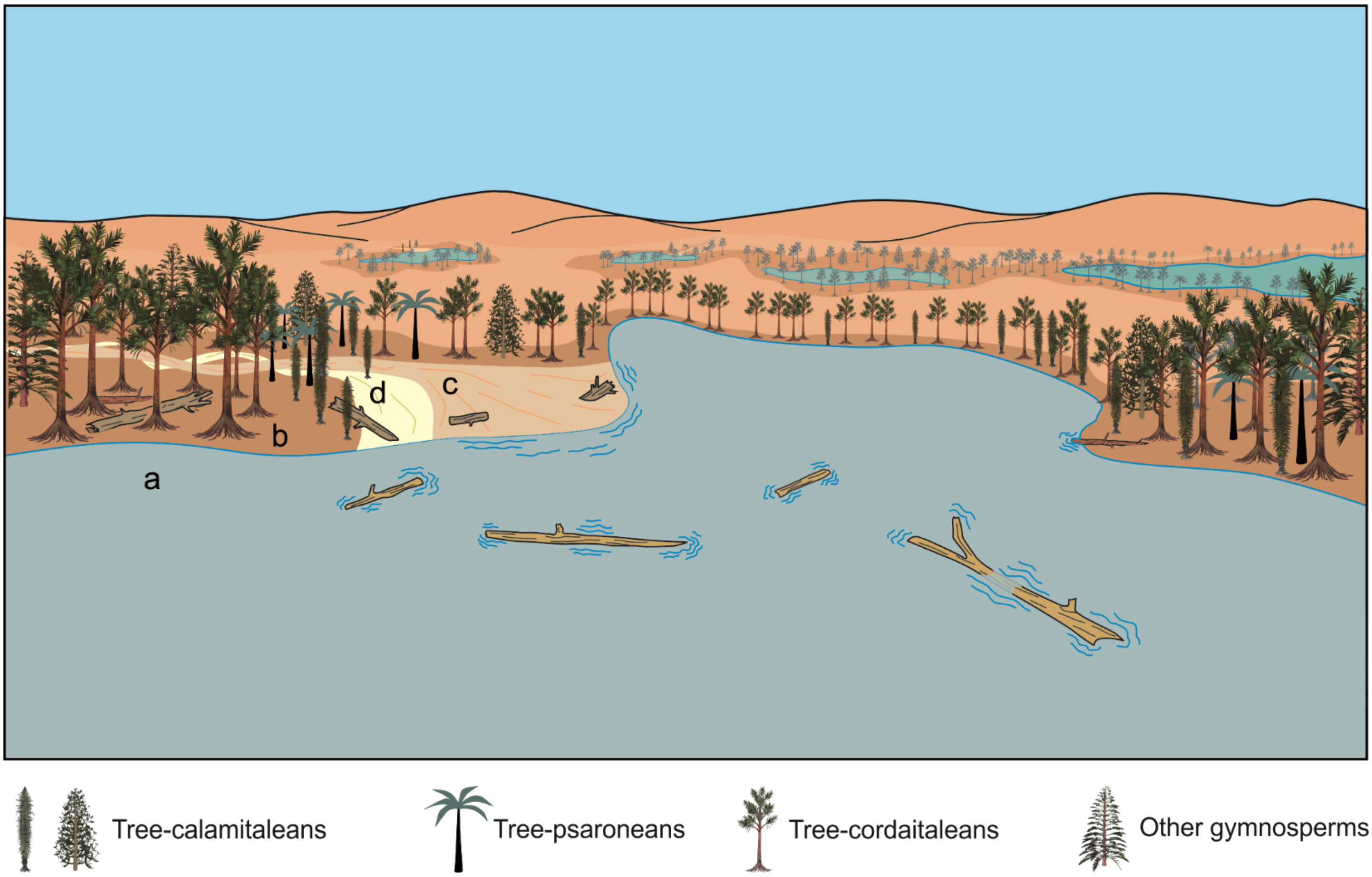

a
b
c
d
Tree-calamitaleans
Tree-psaroneans
Tree-cordaitaleans
Other gymnosperms

Fig. 8

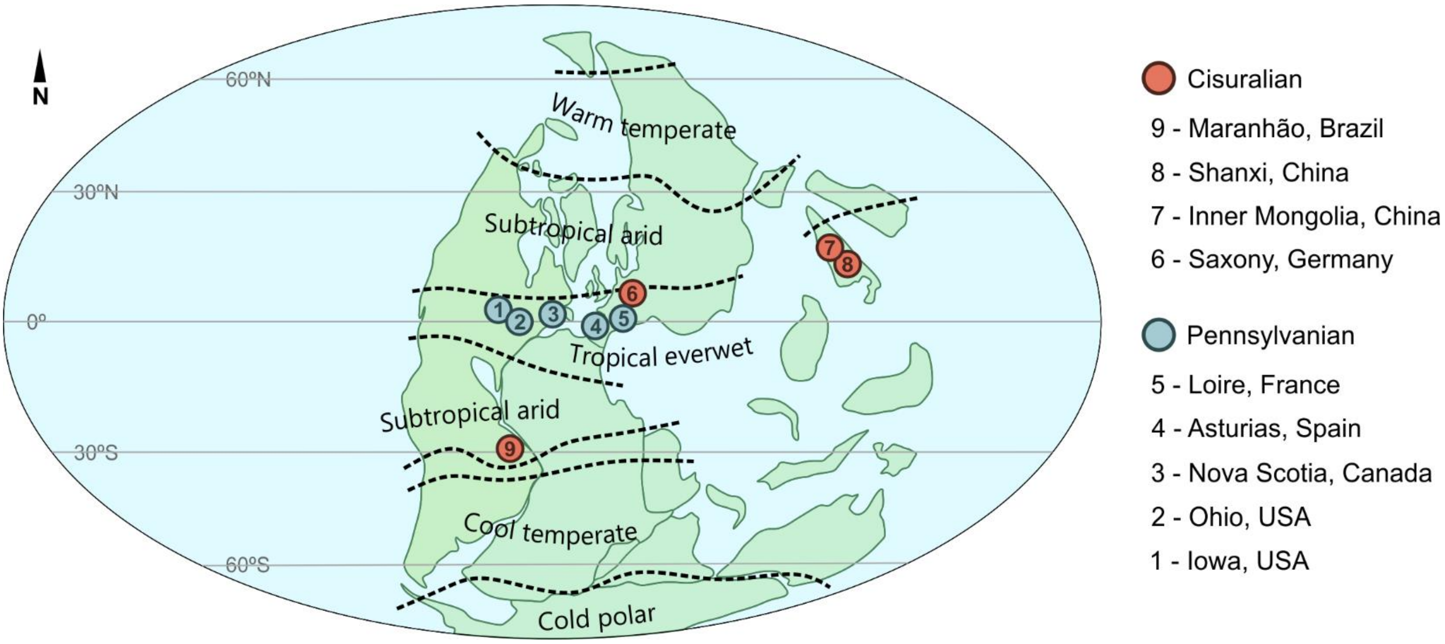

N
60ºN
30ºN
0º
30ºS
60ºS
Warm temperate
Subtropical arid
Tropical everwet
Subtropical arid
Cool temperate
Cold polar
1
2
3
4
5
6
7
8
9
Cisuralian
9 - Maranhão, Brazil
8 - Shanxi, China
7 - Inner Mongolia, China
6 - Saxony, Germany
Pennsylvanian
5 - Loire, France
4 - Asturias, Spain
3 - Nova Scotia, Canada
2 - Ohio, USA
1 - Iowa, USA

Fig. 9

Tables

Table 1. Genera that have both secondary xylem and pith anatomy most similar to our specimens.

Genus	Pith	Primary xylem	Secondary xylem			Type locality and age
			Pitting on radial walls	Cross-field pits	Xylem rays	
Septomedullopitys Lepekhina, 1972	Septate and heterocellular, with secretory canals	Endarch	Araucarian	Simple, 1–2 pits	Uniseriate to biseriate	Kuznetsk Basin,Russian; Permian
Mesoxylon Scott and Maslen, 1910	Homocellular and septate	Mesarch	Araucarian, uni- to multiseriadas	Cupressoid?	Uniseriate-to biseriate, 1-6 cells high	What Cheer,Iowa Pennsylvanian
Schopfiicaulia Mussa, 1982	Heterocellular and septate	Endarch	Araucarian	Araucariod?	Uniseriate, 1-2 cells high	São Paulo, Brazil; Permian
Carolinapitys Coimbra and Mussa, 1984	Heterocellular with irregular septations of Sclerenchyma cells	Mesarch	Araucarian, with tertiary thickenings	Cupressoid?	Uniseriate, 1-12 cells high	Maranhão, Brazil, Perrmian
Metacordaites Renault, 1896	Solid and heterocellular, with parenchyma, secretory ducts and resinferous cells	Endarch	Uniseriate, rarely biseriate	Up to 3 pits	Uniseriate, generally up to 6 cells high	Autun, France; Cisuralian
Retemedulloxylon Merlotti, 1998	Solid to septate	Endarch	Mixed?	Fenestriform?	Uniseriate	Santa Catarina, Brazil, Permian
Shanxioxylon, Wang et al., 2003	Homocellular septate and solid	Endarch and mesarch	Araucarian	Cupressoid	uniseriate	Shanxi Province, China, Permian
Cordaixylon Grand'Eury, 1877	Homocellular and septate	Endarch	Araucarian	Cupressoid	Uniseriate	Loire, France; Pennsylvanian

Table 2. Species of *Cordaixylon* Grand'Eury 1877, including our specimens.

Species	Pith	Primary xylem	Secondary xylem			Extern. tissues	Type locality and age
			Pitting on radial walls	Cross-field pits	Xylem rays		
Cordaixylon dumusum, Rothwell 1993	Homocellular and septate	Endarch	Araucarian?	Cupressoid?	Uniseriate?	Yes	Ohio, U.S Pennsylvanian
Cordaixylon iowensis, Trivett, 1992	Homocellular and septate	Endarch	Araucarian?	Cupressoid?	Uniseriate?	Yes	What Cheer, Iowa, U.S Pennsylvanian
Cordaixylon tianii Wang and Hilton, 2009	Homocellular and septate	Endarch	Araucarian uniseriate	Cupressoid	Uniseriate, 1-3 cells high	Yes	Shanxi Province, China, Cisuralian
Cordaixylon andresii, Césari et al., 2015	Homocellular and no-septate	Endarch	Araucarian, Uniseriate?	Pyllocladoid	Uniseriate, 1-10 cells high and axial parenchyma	No	Asturias, Spain Pennsylvanian,
Cordaixylon birame, Trivett, 1992	Homocellular and septate	Endarch	Araucarian?	Cupressoid?	Uniseriate?	Yes	What Cheer, Iowa, U.S Pennsylvanian
Cordaixylon cf. brandlingii, Walter and Rößler, 2006	?	?	Araucarian	Araucariod?	Uniseriate	No	Saxony, Germany, Cisuralian
Cordaioxylon houtoumiaoense (Zhang et Zheng, 1984) Wang 2000	Homocellular and septate	Endarch	Araucarian, uni-to multiseriate	Simple?	Uniseriate, partly biseriate,1-3 cells high and biseriate 3	No	Inner Mongolia, China, Cisuralian
Cordaixylon sahnii (Hsü et Bose 1952) Wang 2000	Septate	?	Araucarian, uni-to triseriate	Cupressoid 1-4 pits?	Uniseriate, 1-10 cells high	No	Taiyuan, Shanxi, China, Cisuralian

Cordaixylon sp.1 (This study)	Homocellular and septate	Endarch	Araucarian uni-to triseriate	Cupressoid	Uniseriate, 1-18 cells high and biseriate?	No	Maranhão, Brazil, Cisuralian
Cordaixylon sp.2 (This study)	Homocellular and septate	Endarch	Araucarian, uni-to triseriate	Cupressoid	Unisseriados, 1-26 cells high	No	Maranhão, Brazil, Cisuralian

Table 3. Pith-related measurements of *Cordaixylon* sp1 and *Cordaixylon* sp.2.

Sample	Pith diameter		Septa (mean values)		
	Min.	Max.	Length	Thickness	Spacing
Cordaixylon sp.1					
PAB 084	1,6 cm	2,2 cm	1,5 cm	270 µm	2,2 mm
PAB 137	1,4 cm	3,5 cm	1,8 cm	400 µm	1,7 mm
PAB 150	2,1 cm	2,4 cm	1,7 cm	260 µm	2,6 mm
PAB 151	2,5 cm	3,1 cm	1,9 cm	320 µm	3,3 mm
Cordaixylon sp.2					
PAB 018.10	2,4 cm	2,6 cm	0,6 cm	1000 µm	1,3 mm

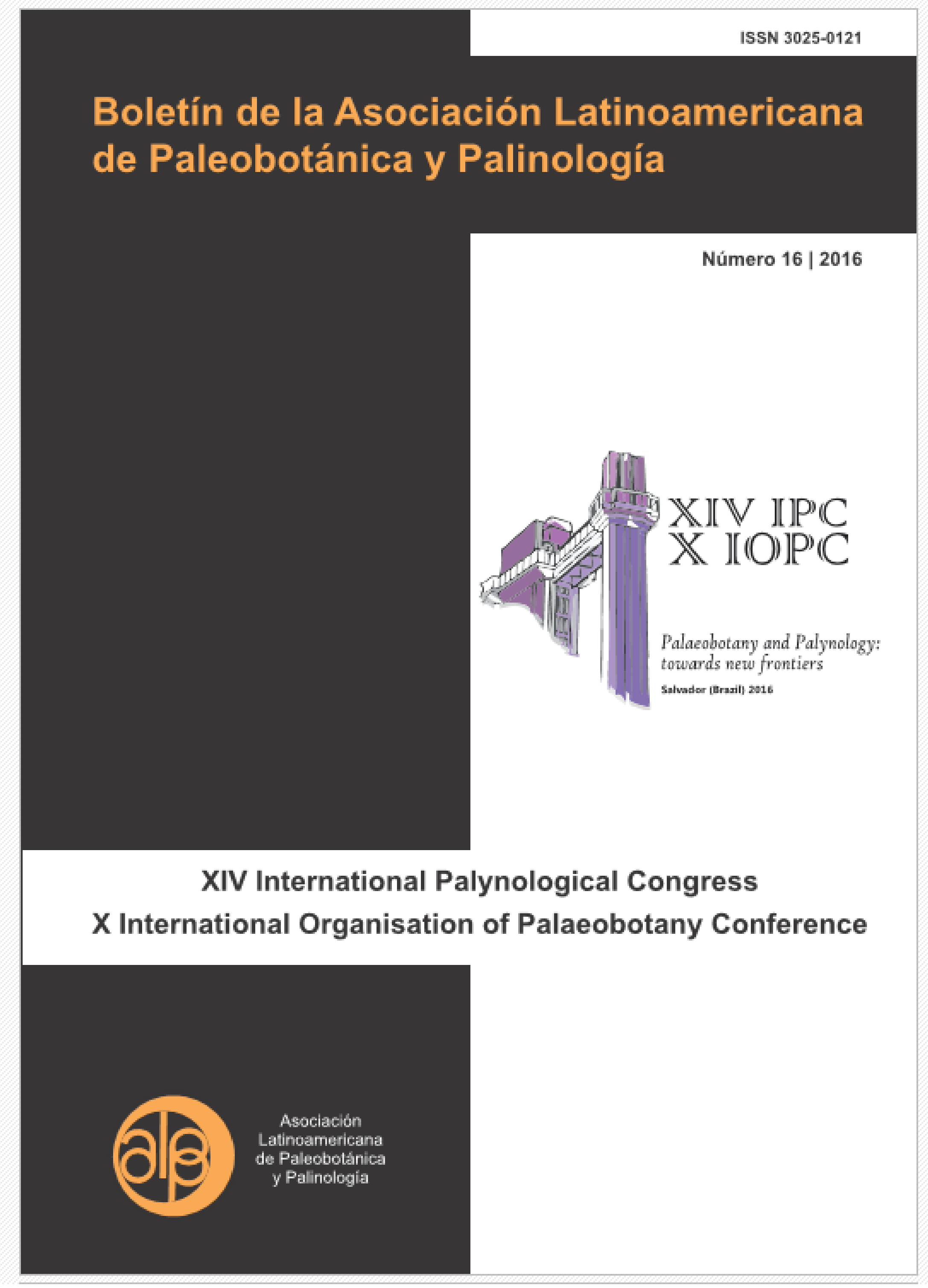
Table 4. Rays-related measurements of *Cordaixylon* sp.1 and *Cordaixylon* sp.2.

Sample	Proportion of uniseriate rays	Mean high of uniseriate rays	Mean high of biseriate rays	Ray density
Cordaixylon sp.1				
PAB 084	68%	11,3 cells	16,1 cells	20 rays/mm^2
PAB 137	72%	6,9 cells	16,7 cells	28 rays/mm^2
PAB 150	66%	13 cells	17 cells	20 rays/mm^2
PAB 151	76%	10,7 cells	24,6 cells	23 rays/mm^2
Cordaixylon sp.2				
PAB 018.10	96%	7 cells	10 cells	28 rays/mm^2

PARTE III

ANEXOS: Resumos em anais de eventos na área de Paleobotânica, e certificados de trabalhos premiados em eventos científicos durante o desenvolvimento da tese e, documentos referentes à submissão dos artigos.

Anexo 1: Publicação em anais de eventos.



ISSN 3025-0121

Boletín de la Asociación Latinoamericana de Paleobotánica y Palinología

Número 16 | 2016

XIV IPC
X IOPC

Palaeobotany and Palynology: towards new frontiers

Salvador (Brazil) 2016

XIV International Palynological Congress
X International Organisation of Palaeobotany Conference

Asociación
Latinoamericana
de Paleobotánica
y Palinología

Georeferencing petrified forests in the eastern margin of the Parnaíba Basin, Lower Permian (Pedra de Fogo Formation)

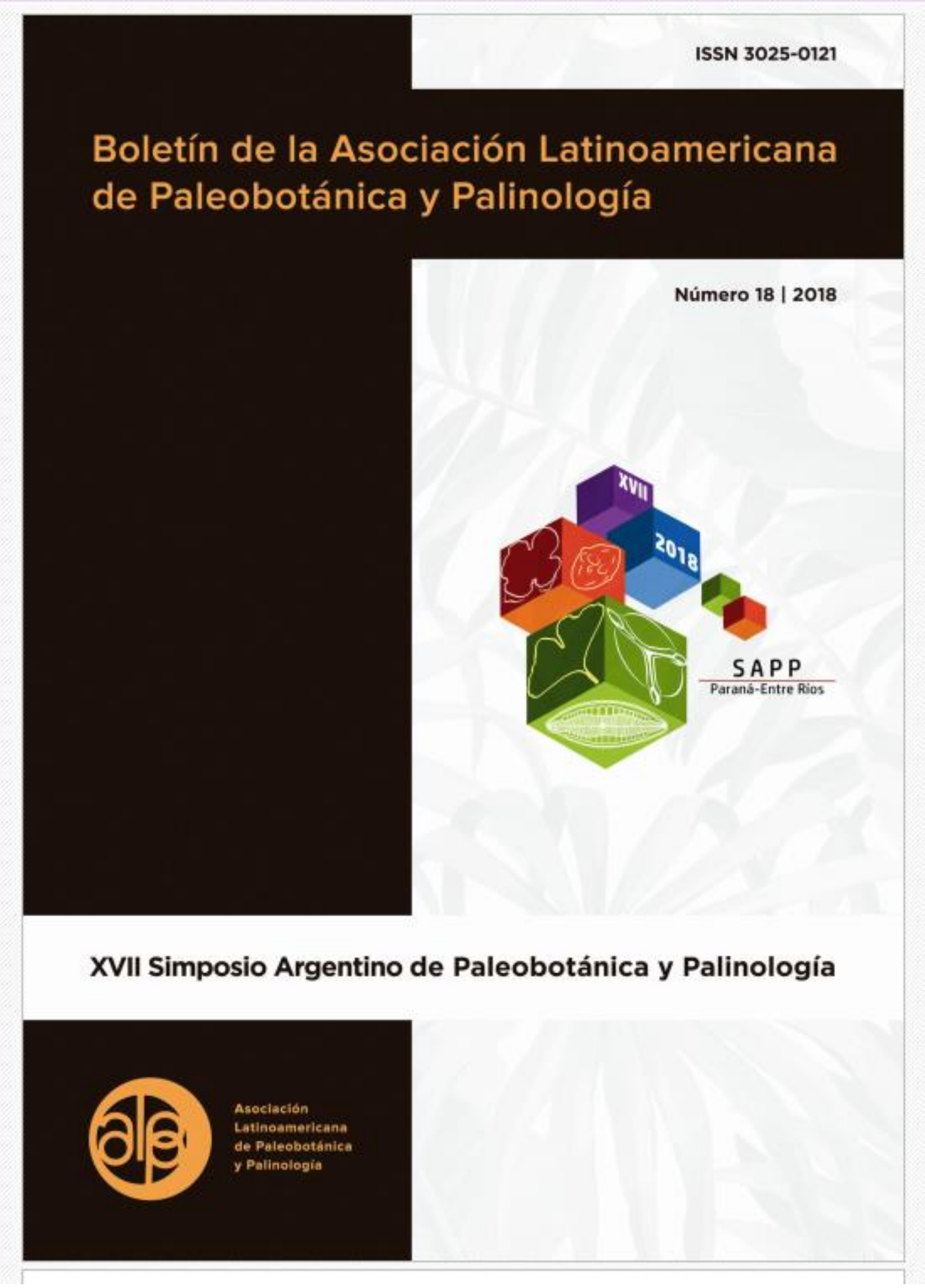
Domingas Maria da Conceição[1], Juan Carlos Cisneros[2], Roberto Iannuzzi[1]

[1] Universidade Federal do Rio Grande do Sul, Brazil, *domingasmary@hotmail.com*
[2] Universidade Federal do Piauí, Brazil

Petrified plant-bearing outcrops of lower Permian strata of the Pedra de Fogo Formation located in the eastern margin of the Parnaíba Sedimentary Basin, are still poorly studied and/or known despite of the abundance of these fossiliferous exposures. The Pedra de Fogo Formation is characterized by rocks with predominance of silicified sandstone and siltstone, abundant layers of chert and limestone, and an abundance of fossil plant associations, especially gymnosperm logs, and also microbialites (ooids, pisoids, bacterial mats and stromatolites). This work aimed the prospection and preliminary analysis of outcrops in the aforementioned margin of the basin. Deposits with fossil plants under consideration are located in the municipalities of Teresina, Monsenhor Gil, Nazária and Altos, in Piauí state; and Duque Bacelar and Coelho Neto, in Maranhão state. The outcrops in Teresina and Altos are dominated by assemblages formed mostly by large gymnosperm woods (over 70 specimens), a number of them being found in life-position. Tree-ferns (petrified fronds and stems) were found in Monsenhor Gil and Nazária. In the Duque Bacelar and Coelho Neto there are more than five exposures mostly formed by large gymnosperm stems, some of them in life position (reaching more than 1.0 m in diameter) and, less often, by tree-fern stems in horizontal position, e.g., *Psaronius* sp. (reaching up to 5 m in length). The plant fossils are commonly well preserved, especially the stems with largest diameters, and despite of considerable fragmentation of several specimens it is possible to recognize certain anatomical features, such as growth ring-like structures. It is worth mentioning that only the site located in Teresina (namely Fossil Florest of Poti River) was already known by the scientific community; all the other outcrops are new. The next step of our research will be the detailed study in terms of taxonomic and taphonomic aspects. This will provide a better knowledge of the fossil plant assemblages of this unit contributing to understanding about the complexity of Paleozoic plant relationships and the depositional environments present during the Permian times in the Parnaíba Basin.

Keywords: Petrified forests, Pedra de Fogo Formation, Parnaíba Basin, Lower Permian.

Anexo 2: Publicação em anais de eventos e certificado de premiação.



ISSN 3025-0121

Boletín de la Asociación Latinoamericana de Paleobotánica y Palinología

Número 18 | 2018

XVII Simposio Argentino de Paleobotánica y Palinología

Asociación
Latinoamericana
de Paleobotánica
y Palinología

La *International Organization of Paleobotany* premia a **Conceição, Domingas María**, ID **2.379.567**, como MEJOR PRESENTACIÓN EN FORMATO POSTER "PRELIMINARY STUDY ON THE GYMNOSPERM PALEOXYFLORA FROM THE PEDRA DE FOGO FORMATION, EARLY PERMIAN OF THE PARNAÍBA BASIN, NORTHEASTERN BRAZIL", en el marco del **XVII Simposio Argentino de Paleobotánica y Palinología.**

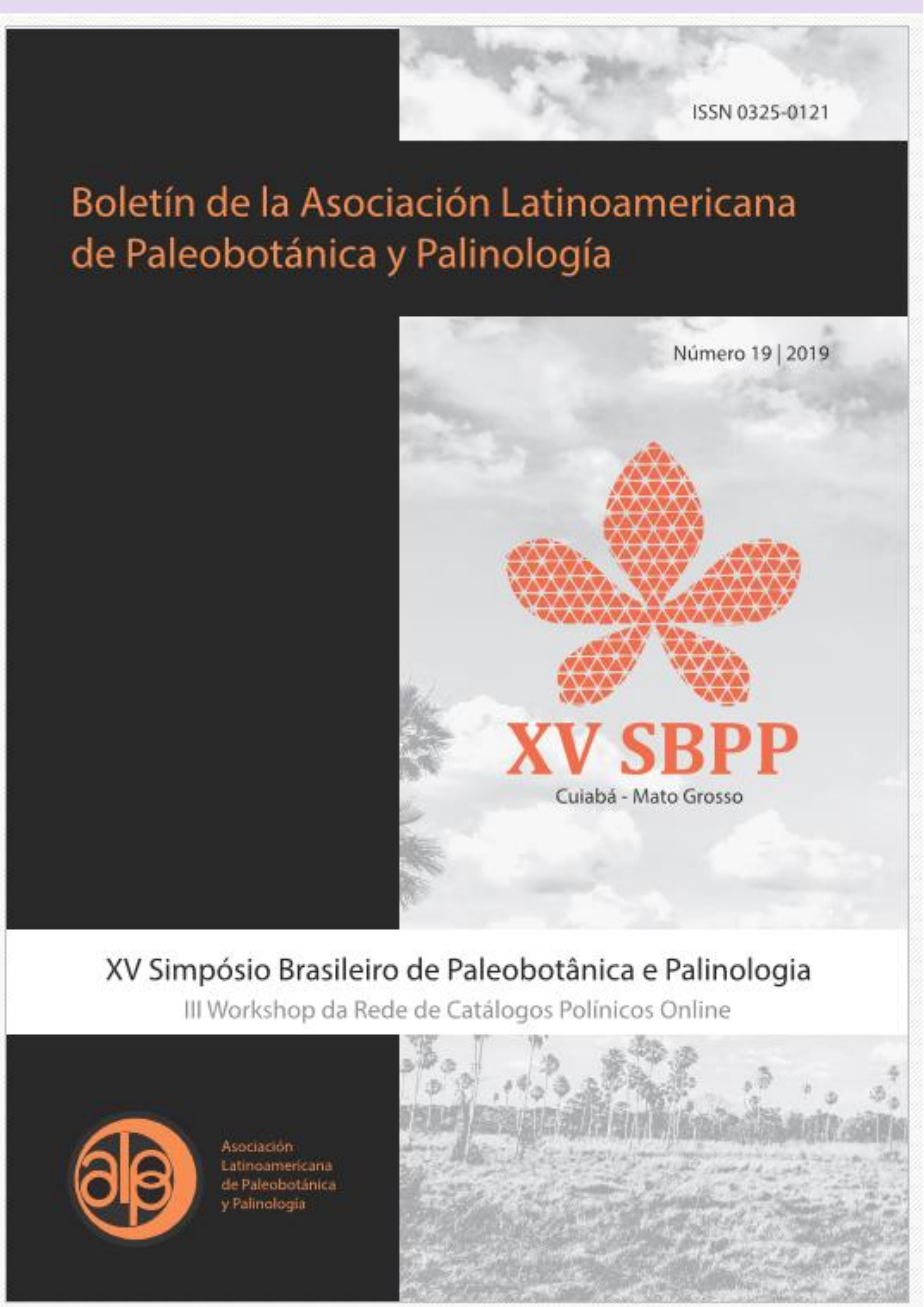
Paraná, 30 de Julio al 3 de Agosto de 2018.

Dr. Jorge Noriega
DECANO FCYT-UADER

Dra. Mercedes Di Pasquo
PRESIDENTE COMISIÓN ORGANIZADORA
PRESIDENTE ALPP (2009-2020)

Bioing. Aníbal J. Sattler
RECTOR

Anexo 3: Publicação em anais de eventos e certificado de premiação.



ISSN 0325-0121

Boletín de la Asociación Latinoamericana de Paleobotánica y Palinología

Número 19 | 2019

XV SBPP
Cuiabá - Mato Grosso

XV Simpósio Brasileiro de Paleobotânica e Palinologia

III Workshop da Rede de Catálogos Polínicos Online

Asociación
Latinoamericana
de Paleobotánica
y Palinología

XV SIMPÓSIO BRASILEIRO DE PALEOBOTÂNICA E PALINOLOGIA

XV SBPP

III WORKSHOP DA REDE DE CATÁLOGOS POLÍNICOS ONLINE

04 a 07 de setembro de 2019
Cuiabá-Mato Grosso

Perspectivas no tempo

CERTIFICADO

Certificamos que **Domingas M. Conceição** foi agraciada com o prêmio de melhor trabalho nível Doutorado apresentado durante o **XV Simpósio Brasileiro de Paleobotânica e Palinologia** realizado de 04 a 07 de setembro de 2019, na Universidade Federal de Mato Grosso, em Cuiabá-MT, Brasil.

Cuiabá- MT, 07 de setembro de 2019

Cláudia Inês da Silva
Coordenadora da RCPol

Silane A. F. Silva Caminha
Presidente do XV Simpósio Brasileiro de Paleobotânica e Palinologia

Mercedes di Pasquo
Presidente da ALPP

REALIZAÇÃO

UFMT

APOIO

RCPol

PATROCÍNIO

FAGEO FACULDADE DE GEOCIÊNCIAS

NÚCLEO CENTRO-OESTE

ZEISS

UNISELVA

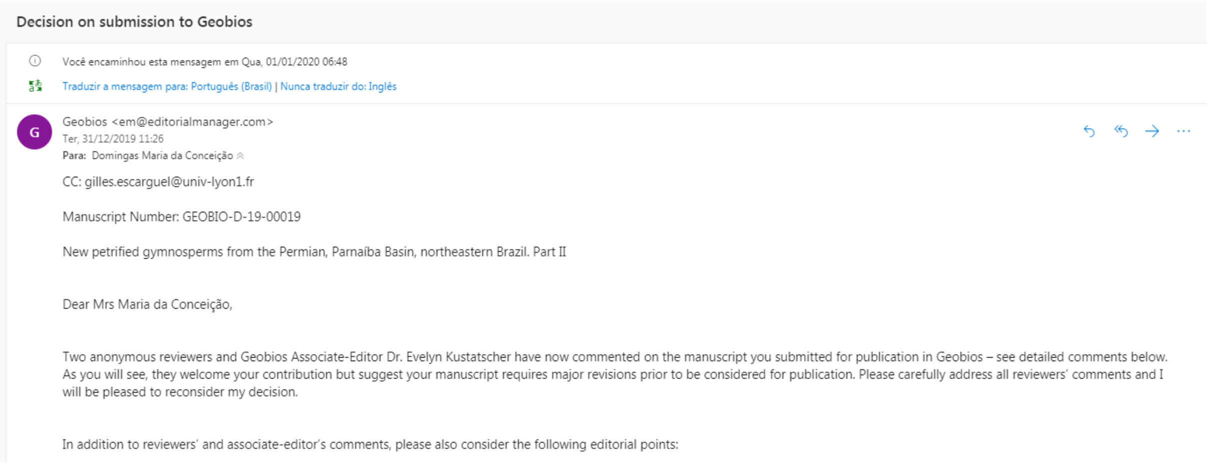
PERMIAN CORDAITALEAN WOODS FROM THE PEDRA DE FOGO FORMATION, PARNAÍBA BASIN, BRAZIL

Conceição, D.M. (1); Neregato, R.(1); Iannuzzi, R.(1); Alexandra Crisafulli (2); Juan C. Cisneros (3)

(1) Universidade Federal do Rio Grande do Sul: domingasmary@hotmail.com; rodrigoneregato@hotmail.com; roberto.iannuzzi@ufrgs.br; (2) Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste: alexandracrisafulli@hotmail.com; (3) Universidade Federal do Piauí, Museu de Arqueologia e Paleontologia: juan.cisneros@ufpi.edu.br

Although Permian fossils plants from the Parnaíba Basin have been known since the nineteenth century, they have received little attention in the last decades, principally the Permian flora from the Pedra de Fogo Formation (PFF). Besides, there is a significant gap in our knowledge regarding petrified gymnospermous woods from the PFF, especially in comparison to other Upper Paleozoic units in the Southern Hemisphere. Among the gymnosperms, the Order Cordaitales represents an extinct group, whose records span from the Carboniferous to the Permian. The most complete Cordaitales specimens were registered in the Euroamerica and Cathaysia terrains. Otherwise, few putative woods with possible cordaitalean affinity were found in the Gondwanan continent. Generally, stems belonging to these plants display regular septations, such as *Artisia*-type pith, commonly placed in *Mesoxylon* Scott et Maslen 1910, or in *Cordaixylon* Grand'Eury 1877, the latter documented in the both Euramerican and Cathaysian floral provinces. In the last few years, several prospections have been carried out in the PFF, with special attention to the eastern and southeastern portions of the Parnaíba Basin, where were found important plant occurrences, mainly gymnosperm woods, some of them still in life position. This contribution presents the first Cordaitales described in these localities. The woods were cut in three distinct planes: cross-section, tangential longitudinal and radial longitudinal; following the standard procedures for woody taxonomy studies. These sections were prepared at the Lamination Laboratory in the University of Vale do Rio dos Sinos (UNISINOS), São Leopoldo, Brazil. These petrified woods present large septate pith, surrounded by approximately 29 primary xylem bundles of endarch organization and sympodial architecture. Bordered pits on radial tracheid walls are mostly bi- to triseriate, cross-fields cupressoid pits and uniseriate xylem rays. The studied specimens may be assigned to *Cordaixylon* rather than *Mesoxylon*, which is characterized by mesarch cauline bundles. The botanical affinity to *Cordaixylon* reinforces the idea that Permian flora of the Parnaíba Basin sheltered several tropical Euroamerican taxa. In addition, the flora includes some temperate taxa known in Southwest Gondwana and endemic taxa, mainly in specific level. (CNPq PQ 312747/2017-9)

Anexo 4: "Aceite" Artigo 1 (Geobios)



Decision on submission to Geobios

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Geobios <em@editorialmanager.com>
Ter, 31/12/2019 11:26
Para: Domingas Maria da Conceição

CC: gilles.escarguel@univ-lyon1.fr

Manuscript Number: GEOBIO-D-19-00019

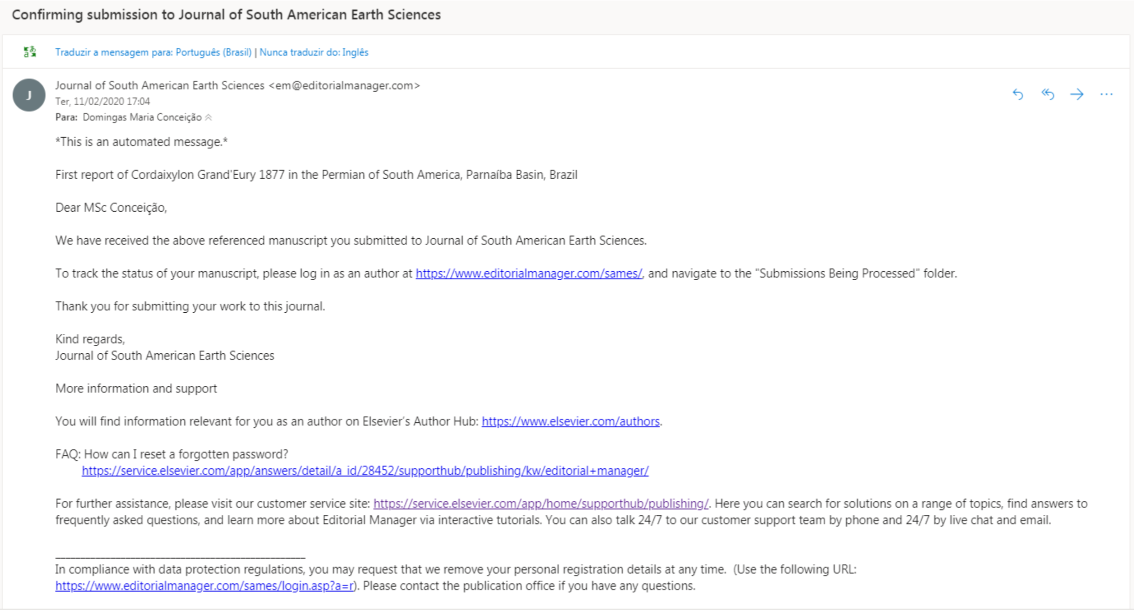
New petrified gymnosperms from the Permian, Parnaíba Basin, northeastern Brazil. Part II

Dear Mrs Maria da Conceição,

Two anonymous reviewers and Geobios Associate-Editor Dr. Evelyn Kustatscher have now commented on the manuscript you submitted for publication in Geobios – see detailed comments below. As you will see, they welcome your contribution but suggest your manuscript requires major revisions prior to be considered for publication. Please carefully address all reviewers' comments and I will be pleased to reconsider my decision.

In addition to reviewers' and associate-editor's comments, please also consider the following editorial points:

Anexo 5: Carta de Submissão do artigo 3 (Journal of South American Earth Sciences)



Confirming submission to Journal of South American Earth Sciences

Journal of South American Earth Sciences <em@editorialmanager.com>
Ter, 11/02/2020 17:04
Para: Domingas Maria Conceição

This is an automated message.

First report of Cordaixylon Grand'Eury 1877 in the Permian of South America, Parnaíba Basin, Brazil

Dear MSc Conceição,

We have received the above referenced manuscript you submitted to Journal of South American Earth Sciences.

To track the status of your manuscript, please log in as an author at https://www.editorialmanager.com/sames/, and navigate to the "Submissions Being Processed" folder.

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Journal of South American Earth Sciences

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ANEXO I

Título da Tese:

“XILOFLORAS PERMIANAS DAS MARGENS NORDESTE E LESTE DA BACIA DO PARNAIBA: TAXONOMIA, PALEOAMBIENTES E PALEOFITOGEOGRAFIA”

Área de Concentração: Paleontologia

Autor: **Domingas Maria da Conceição**

Orientador: Prof. Dr. Roberto Iannuzzi

Examinadora: Dra. Francine Kurzawe

Data: 28/02/2020

Conceito: A - excelente

PARECER:

A aluna anexou três artigos completos na tese. O primeiro já foi publicado on-line e o segundo já foi aceito, ambos em revistas internacionais revisadas por pares, o que atesta a qualidade dos mesmos. Nestes dois artigos a doutoranda teve como resultado de suas pesquisas quatro novos taxa de lenhos fossilizados para a Formação Pedra de Fogo, Permiano, Bacia do Parnaíba. Estes novos taxa são importantes, pois há uma falta de pesquisas de lenhos de gimnospermas nessa formação. Além da taxonomia, a autora discute Paleobiogeografia e Paleoecologia. O terceiro trabalho, ainda não submetido, também é de ótima qualidade, descrevendo um gênero nunca antes encontrado no Hemisfério Sul. Além de taxonomia, o trabalho engloba Paleoclimatologia, Paleoecologia e Paleobiogeografia. A tese de Domingas é ampla, discutindo um tema ainda pouco explorado na Paleobotânica brasileira.

Assinatura: Francine Kurzawe Data: 28/02/2020

Ciente do Orientador:

Ciente do Aluno: