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

ANÁLISES EM LENHOS FÓSSEIS DE CONÍFERAS INTEGRADAS A ANÁLISES GEOQUÍMICAS EM SEDIMENTOS ASSOCIADOS COMO PROXIES PARA INTERPRETAÇÕES PALEOBIOGEOGRÁFICAS E PALEOAMBIENTAIS NO INTERVALO APTIANO DAS BACIAS DO ARARIPE (FORMAÇÃO SANTANA) E SERGIPE-ALAGOAS (FORMAÇÃO MACEIÓ)

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ORIENTADORA: Profª Drª Margot Guerra Sommer

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DEDICATÓRIA

Aos grandes mestres
da minha vida:
MEUS PAIS

AGRADECIMENTOS

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CAPÍTULO II: artigos ciêntíficos

Sobre a Estrutura da Tese:

A estrutura da presente tese de doutorado segue a Norma 118 do Regimento Interno do Programa de Pós-Graduação em Geociências da Universidade Federal do Rio Grande do Sul (PPGGEO-UFRGS), e é composta por 1 artigo publicado (Qualis- CAPES - A2) e 2 artigos submetidos em periódicos classificados nos estratos Qualis-CAPES A3. O volume segue a seguinte organização:

Capitulo I. Texto Integrador: a) introdução; b) objetivos da pesquisa; c) o estado da arte do tema da pesquisa; d) materiais e métodos; e) contexto geológico; f) resumo dos principais resultados obtidos e discussão integradora dos resultados; g) conclusões; h) referências bibliográficas.

Capítulo II. Artigos científicos: constituído pelos artigos escritos pela autora durante o desenvolvimento de seu doutoramento (conforme o item 1.2 da norma 118).

Artigo 1: Santos, Â.C.S., Guerra-Sommer, M., Degani-Schmidt, I., Siegloch, A.M., de Souza Carvalho, I., Mendonça Filho, J.G. & Mendonça, J.O. 2020. Fungus–plant interactions in Aptian Tropical Equatorial Hot arid belt: White rot in araucarian wood from the Crato fossil Lagerstätte (Araripe Basin, Brazil). *Cretaceous Research*, *114*, 104525. (**Qualis -CAPES A2**).

Artigo 2: Santos, Â.C.S., Siegloch, A.M., Guerra-Sommer, M., Degani-Schmidt, I. & Carvalho, I.S., 2021. *Agathoxylon santanensis* sp. nov*.* from the Aptian Crato fossil Lagerstätte, Santana Formation, Araripe Basin, Brazil. *Journal of South American Earth Sciences* (**Qualis -CAPES A3**).

Artigo 3: Santos, Â.C.S., Guerra-Sommer, M., Siegloch, A.M., Degani-Schmidt, I., Carvalho, I.S, Mendonça Filho, J.G. & Mendonça, J.O. 2021. Record of Pinaceae woods in the Aptian of Sergipe-Alagoas Basin (Maceió Formation) and geochemical analysis in associated sediments as proxies for paleobiogeographic and paleoenvironmental interpretations. *Journal of South American Earth Sciences.* (**Qualis – CAPES A3**).

RESUMO

Análises anatômicas em lenhos fósseis de coníferas, integradas a análises geoquímicas em fácies sedimentares a eles associadas, foram desenvolvidas tendo como objetivos principais interpretações paleobiogeográficas, paleoclimáticas e paleoambientais no intervalo Aptiano em duas bacias do nordeste brasileiro. O morfotaxon *Agathoxylon santanensis nov. sp.*, procedente do Membro Crato (Crato Lagerstätte) da Formação Santana, (Bacia do Araripe), definido a partir de padrões de xilema, apresenta características anatômicas no floema e padrões morfológicos de uma folha organicamente conectada, que indicam afinidade com a família Araucariacea. A presença de *Agathoxylon* Hartig com afinidade araucariana no Cinturão Climático Equatorial Quente e Árido, considerando outros registros previamente documentados nos cinturões contemporâneos subtropical e temperado, indica que a ocorrência dessas coníferas não era climaticamente controlada durante o Aptiano. As assinaturas de padrões de crescimento no lenho indicaram zonas de interrupção causadas por estresse hídrico, implicando em períodos intermitentes de seca sob um clima megatérmico. O processo de preservação identificado como geleificação no lenho proveniente da Formação Maceió (Bacia de Sergipe-Alagoas), apesar de gerar alterações na arquitetura celular em alguns tecidos, preservou também tecidos não comprimidos que permitiram a caracterização anatômica diagnóstica da família Pinaceae. O primeiro registro de Pinaceae na Bacia Sergipe –Alagoas, respaldado pela presença de grãos de pólen de tipo *Cedripites* em sedimentos associados, traz implicações palebiogeográficas relacionadas à fase de ruptura do Gondwana no Cretáceo. Os resultados permitiram inferir que as Pinaceae teriam provavelmente se irradiado a partir de massas de terra do sul da Província de Laurásia (atual Península Ibérica) para o norte da Província Gondwana, estabelecendo-se em massas de terra norte - africanas durante o Eocretáceo, tornando-se componentes comuns nas províncias florísticas terrestres do Norte do Gondwana durante o Aptiano e registradas atualmente em bacias sedimentares do Norte da África e nordeste do Brasil. A composição da matéria orgânica particulada em sedimentos associados, caracterizada pela dominância de fitoclastos e cutículas, e a baixa contribuição de esporomorfos terrestres, além da ausência de microplâncton aquático, sugere deposição em fácies distais de canal em um complexo fluviodeltaico, dentro de

amplo sistema turbidítico. A identificação de perileno no lenho e também como elemento disperso em sedimentos associados ratifica a associação entre este biomarcador químico e a atividade de fungos degradadores de lenho. Evidências de padrões de decomposição do xilema mostram que coníferas afins a Araucariaceae e Pinaceae foram hospedeiras disponíveis para interações lenho-Basidiomycota sob condições climáticas quentes e áridas na faixa equatorial durante o Aptiano, provavelmente em processos patogênicos e saprofíticos. A identificação da interação planta-fungo implica em algumas forças ambientais, representadas por janelas de oportunidade que impulsionaram a regulação da disponibilidade hídrica em ambientes aeróbios, sob condições gerais de baixa umidade e alta temperatura.

Palavras-chave: Lenhos fósseis, Araucariaceae, Pinaceae, Aptiano, Brasil

ABSTRAT

Anatomical analysis of fossil coniferous woods, integrated with geochemical analysis of associated sedimentary facies, were conducted with the main goals of establishing paleobiogeographic, paleoclimatic and paleoenvironmental interpretations for the Aptian interval in two basins in northeastern Brazil. The morphogenus *Agathoxylon santanensis* nov. sp., described for the Crato Member (Crato Lagerstätte) of the Santana Formation, (Araripe Basin) defined from xylem patterns, shows anatomical characteristics in the phloem and morphological patterns of an organically connected leaf, which indicate affinity with the Araucariacea family. The presence of *Agathoxylon* Hartig with Araucarian affinity in the equatorial Warm Arid Climate Belt, considering other records previously documented in the contemporary subtropical and temperate belts, indicates that these conifers were   not climatically controlled during the Aptian. Signatures of growth patterns in the wood indicated interruption zones caused by water stress, implying intermittent periods of drought under a megathermal climate. The preservation process identified as gelification in the wood from the Maceió Formation (Sergipe-Alagoas Basin), despite generating changes in the cell architecture of some tissues, also preserved uncompressed tissues that allowed the diagnostic anatomical characterization of the Pinaceae family. The first record of Pinaceae in the Sergipe -Alagoas basin Brazil, supported by the presence of

Cedripites pollen grains in associated sediments, brings palebiogeographic implications related to the Gondwana rupture phase in the Cretaceous. The results indicated that the Pinaceae would have probably radiated from landmasses in southern Laurasian Province (present-day Iberian Peninsula) to the north of the Gondwanan Province, in North African terrestrial   masses during the Early Cretaceous, becoming common components in the terrestrial floristic provinces of northern African and Brazilian Gondwana during the Aptian. The composition of the particulated organic matter in associated sediments, characterized by the dominance of phytoclasts and cuticles, and the low contribution of terrestrial sporomorphs, in addition to the absence of aquatic microplankton, suggest deposition in distal canal facies in a fluviodeltaic complex, within a broad turbiditic system. The identification of perylene in the wood and as a dispersed element in associated sediments ratifies the association between this chemical biomarker and the activity of wood-degrading fungi. Evidence of xylem decomposition patterns shows that conifers related to Araucariaceae and Pinaceae were available hosts for wood-Basidiomycota interactions under warm and arid climatic conditions in the equatorial belt during the Aptian, probably in pathogenic and saprophytic processes. The identification of the plant-fungus interaction implies the occurrence of environmental forces represented by windows of opportunity that boosted the regulation of water availability in aerobic environments under general conditions of low humidity and high temperature.

Key-words: Fossil woods, Araucariaceae, Pinaceae, Aptian, Brazil

Capítulo I: Texto Integrador

1. INTRODUÇÃO

Diferenças fundamentais na distribuição dos oceanos e massas de terra no Hemisfério Norte e Hemisfério Sul ao longo do Mesozoico tiveram um impacto potencial nos padrões de diversidade biológica nas duas áreas.

O Cretáceo (145–65 Ma) foi uma época de extremo aquecimento global (Skelton et al., 2003), com temperatura média anual global superior a 10°C (Haywood et al., 2004), gerada principalmente pelos altos níveis de dióxido de carbono atmosférico superiores a 1000 ppm (Haworth et al., 2005). As calotas polares eram mínimas (Price, 1999) e consequentemente as florestas temperadas expandiram-se até a proximidade dos polos (Spicer & Parrish, 1986).

Nesse intervalo de tempo geológico ocorreram grandes mudanças evolutivas nos ecossistemas terrestres, onde passam a dominar as angiospermas (Crane et al., 1995) caracterizando a "Revolução Terrestre do Cretáceo" (Lloyd et al., 2008). A história evolutiva das coníferas oferece uma oportunidade para explorar essas dinâmicas, porque a maioria das espécies de coníferas existentes pertencem a linhagens que foram amplamente confinadas ao hemisfério norte ou sul durante o Cretáceo.

Lenhos fósseis constituem fontes de dados confiáveis na avalição de padrões biogeográficos em escala continental com base em três motivos: 1. Espécimes macroscópicos de lenhos petrificados têm potencial de transporte muito inferior aos outros órgãos (e.g. palinomorfos) e são mais resistentes do que fragmentos de folhas (Philippe et al., 1998, 2003, 2004); 2. A ocorrência desses lenhos frequentemente em fácies sedimentares relacionadas a paleoambientes marginais, permite estabelecimento de correlações com fósseis-índice autóctones incluídos em ambientes aquáticos, que servem a propósitos bioestratigráficos; 3. Dado o caráter conservador das taxas de evolução em padrões anatômicos de lenhos, esses fósseis são bons indicadores de variações regionais na flora em distintos intervalos temporais.

Philippe et al. (2004), a partir de uma robusta base de dados sistemáticos, plotada em mapas paleoclimáticos de Rees et al. (2000), relacionaram a distribuição genérica e biogeográfica de coníferas no intervalo Jurássico-Cretáceo, durante as fases de pré-ruptura e ruptura do Gondwana e definem

critérios de expansão e retração de diferentes famílias das coníferas durante a fase de fragmentação do Gondwana.

Essa temática é retomada por Peralta-Medina & Falcon-Lang (2012) que estabelecem também considerações de caráter paleobiogeográfico a partir dos mapas paleoclimáticos globais de Scotese, (2011) amparados em compilações de sedimentos sensíveis ao clima. Os resultados dessa compilação e plotagem demonstram que de coníferas com lenho afim às Araucariaceae foram cosmopolitas ao longo do intervalo estudado, enquanto outros táxons relacionados a Pinaceae demonstraram um maior grau de provincianismo e vários morfogêneros endêmicos são reconhecíveis. Foi constatado também que, embora em raros casos a dispersão possa ter percorrido largas distâncias (Kershaw & Wagstaff, 2001), a maioria dos gêneros de coníferas provavelmente permaneceram circunscritos a "jangadas tectônicas" (Page, 1990).

Adicionalmente, estudos em lenhos fósseis fornecem, além de subsídios paleobiogeográficos, assinaturas climáticas derivadas de fatores bióticos e abióticos vigentes no paleoambiente que influenciaram a planta-mãe. Dessa forma, caracteres anatômicos presentes no lenho permitem análises estatísticas para determinar a sazonalidade e extensão da estação de crescimento (Pole & Bergen, 2006).

Inferências paleoclimáticas a partir de padrões de crescimento em lenhos de coníferas, mesmo no intervalo "green house" caracterizado para o Cretáceo globalmente, são proxies confiáveis no estabelecimento de parâmetros em cinturões climáticos tropicais, temperados tanto no Hemisfério Norte (e.g. Falcon Lang, 2003) quanto no Gondwana ocidental (e.g. Pires & Guerra Sommer, 2011; Del Fueyo et al., 2021,).

Uma evidência frustrante em todas as análises globais para o Juro-Cretáceo **e que delimita o grande problema** a ser solucionado gradualmente através do desenvolvimento de projetos inter -institucionais integrados, constitui-se na escassez e, em alguns intervalos temporais, até na ausência de dados anatômicos detalhados sobre diferentes táxons de lenhos fósseis no intervalo Jurássico-Cretáceo nas diversas bacias mesozoicas brasileiras, o que tem impedido o desenvolvimento de sínteses confiáveis.

O presente projeto centrou-se na **hipótese** de que lenhos fósseis são proxies confiáveis na definição de afinidades botânicas, e na avaliação de padrões paleobiogeográficos, paleoclimáticos e paleoambientais no intervalo de tempo

Aptiano em diferentes bacias sedimentares. Dessa forma, considerando a viabilidade de desenvolvimento de pesquisa que teste a hipótese aqui apresentada, foi desenvolvido projeto de pesquisa com temática e objetivos propostos a seguir.

2. OBJETIVOS

2.1 Objetivo Geral

Estabelecer análises em lenhos fósseis de coníferas como fontes de dados para definir afinidades botânicas e avaliar os padrões paleobiogeobiogeográficos, paleoclimáticos e paleoambientais vigentes durante o Aptiano em bacias sedimentares do Nordeste brasileiro.

2.2 Objetivos Específicos

- Definir padrões anatômicos que permitam caracterizar a participação de diferentes famílias de coníferas na configuração das associações vegetais desenvolvidas no Aptiano em diferentes bacias sedimentares;

- Correlacionar os resultados de caráter sistemático com padrões globais para o intervalo Aptiano, ratificando ou não critérios paleobiogeográficos suportados por base de dados centrada em lenhos fósseis;

- Identificar assinaturas anatômicas nos lenhos que atuem como proxies para caracterização paleoclimática;

- Caracterizar o tipo de fossilização ocorrente nos espécimes estudos relacionando-os sempre que possível a condicionantes paleoambientais;

- Identificar processos de interação entre organismos e lenhos e tentar relacionar esses processos a condicionantes ambientais vigentes no Cinturão Equatorial Quente e Árido no Aptiano;

- Desenvolver análises em sedimentos associados aos lenhos que permitam o estabelecimento de relações entre os lenhos e a interpretação das fácies sedimentares em que estes se incluem.

3. ESTADO DA ARTE

3.1 Lenhos fósseis do Jurássico-Cretáceo

3.1.1 Dados Globais

Lenhos fósseis fornecem uma das melhores fontes de dados para avaliar padrões biogeográficos em escala continental. Todavia, o registro de lenhos fósseis do Mesozoico do Gondwana é escasso e está distribuído irregularmente. Além disso, os lenhos são frequentemente descritos de acordo com estruturas nomenclaturais e taxonômicas conflitantes.

Philippe et al. (2004) plotaram gêneros de lenhos fósseis coletados globalmente no intervalo Juro-Cretáceo em cinco zonas climáticas com base nos mapas de Rees et al. (2000) assim definidas: verão úmido, deserto, inverno úmido, clima temperado quente e zonas temperadas frias, estabelecidas com base em dados geológicos independentes. Essa plotagem permitiu reconhecer que determinados táxons eram cosmopolitas enquanto que outros eram endêmicos, e oportunizou a elaboração da tabela que demostra as preferências climáticas dos diferentes morfogêneros (Tabela 1).

Tabela 1. Distribuição dos morfogêneros em cinco zonas climáticas no Cretáceo, com o número de registros correspondentes. Modificado de Phillipe et al. (2004).

Idade	Verão úmido	Deserto	Inverno úmido	Temperado quente	Temperado frio
Cretáceo Inferior	Agathoxylon 19, Brachyoxylon 16, Metapodocarpoxylon 28, Protocircoporoxylon 3, Protophyllocladoxylon 4, Protopodocarpoxylon 3	Agathoxylon 2	Agathoxylon 3, Brachyoxylon 3, Cupressinoxylon 1, Ginkgoxylon 1, Podocarpoxylon 11	Agathoxylon 26, Brachyoxylon 7, Circoporoxylon 2, Cupressinoxylon 1, Podocarpoxylon 15, Protocircoporoxylon 4, Protocupressinoxylon 3, Protopodocarpoxylon 4, Shanioxylon 9, Taxaceoxylon 5	Agathoxylon 9, Araucariopitys 3, Circoporoxylon 1, Podocarpoxylon 3, Protocircoporoxylon 1, Taxodioxylon 1
	6 gêneros **103 registros (30%)**	**1 gênero** **2 registros (0,57%)**	**5 gêneros** **19 registros (5,46%)**	**10 gêneros** **72 registros (21, 84%)**	**6 gêneros** **18 registros (5,17%)**
Jurássico Superior	Agathoxylon 3, Brachyoxylon 1, Metapodocarpoxylon 5	Agathoxylon 1, Brachyoxylon 1	Agathoxylon 1, Taxaceoxylon 1	Circoporoxylon 1	Agathoxylon 7, Protopodocarpoxylon 6
	3 gêneros **9 registros (62,59%)**	**2 gêneros** **2 registros (0,57%)**	**2 gêneros** **2 registros (0,57%)**	**1gêneros** **1 registros (0,29)**	**1 gêneros** **1 registros (0, 29%)**
Jurássico Inferior	Agathoxylon 4, Brachyoxylon 10, Metapodocarpoxylon 7	No data	Agathoxylon 7, Protelicoxylon 1, Prototaxylon 2	Agathoxylon 4, Brachyoxylon 2, Podocarpoxylon 1	Agathoxylon 7, Protopodocarpoxylon 6
	3 gêneros **21 registros (6,03%)**		**3 gêneros** **10 registros (2,87%)**	**3 gêneros** **7 registros (2,01%)**	
Jurássico Inferior	Agathoxylon 4, Brachyoxylon 5	Agathoxylon 1, Baieroxylon 1, Protopodocarpoxylon 1	Agathoxylon 4, Brachyoxylon 2	Agathoxylon 4, Cupressinoxylon 1, Ginkgoxylon 1, Podocarpoxylon 3, Taxaceoxylon 4	Agathoxylon 3
	2 gêneros **9 registros (2, 59%)**	**3 gêneros** **3 registros (0,86%)**	**2 gêneros** **6 registros (1,72%)**	**5 gêneros** **13 registros (3,74%)**	**1 gênero** **3 registros (0,86%)**

O gênero *Agathoxylon* Hartig, quando registrado no Mesozoico, tem sido relacionado a padrões anatômicos ocorrentes em diferentes gêneros atuais da família Araucariaceae (e.g. Del Fueyo et al., 2021). Esse taxon era onipresente no Gondwana e também difundido no Hemisfério Norte. O longo intervalo de tempo e a distribuição cosmopolita deste tipo de madeira implica na hipótese de que as plantas-mãe colonizaram a Pangeia antes de sua fragmentação, permanecendo como componentes de associações florísticas em todas as zonas climáticas desde o Jurássico Inferior ao início Cretáceo. É importante porém, ressaltar que embora entre as coníferas atuais apenas as Araucariaceae possuem lenho do tipo

Agathoxylon, no Jurássico-Cretáceo outros grupos de plantas apresentam lenhos com padrão semelhante a *Agathoxylon,* como por exemplo, Pteridospermales e Cheirolepidiaceae.

No decorrer do intervalo Jurássico Inferior - Cretáceo Inferior foi detectada a ocorrência de mais gêneros endêmicos no hemisfério norte do que no hemisfério sul (Tabela 2) sugerindo **padrões de distribuição** climaticamente controlados.

Tabela 2. Comparação de lenhos endêmicos da Gondwana e Laurásia no Cretáceo. Modificado de Phillipe et al. (2004).

Gêneros endêmicos para Gondwana		Gêneros endêmicos para Laurasia
Gêneros amplamente distribuídos	*Araucariopitys*	*Simplicioxylon*
Gênero local	*Metapodocarpoxylon*	*Xenoxylon*
		Pinaceae-like woods
		Keteleerioxylon
		Palaeopiceoxylon/ Protopiceoxylon
		Piceoxylon
		Pityoxylon/Pinoxylon/ Pinuxylon
		Lenhos restritos a altas latitudes ao norte
		Yatsenkoxylon
		Phoroxylon
		Anomaloxylon
		Semelhante a bosques de Cupressaceae
		Protoglyptostroboxylon
		Protosciadopityoxylon
		Tetraclinoxylon
		Outros
		Lhassoxylon

De acordo com a base de dados e os mapas climáticos, os lenhos boreais semelhantes a Pinaceae nunca alcançaram regiões equatoriais no passado geológico, embora *Pinus merkusii* ocorra hoje em Sumatra.

Os resultados indicam que os gradientes de diversidade em coníferas do Gondwana não foram invariáveis latitudinalmente, mas alteraram-se durante o início do Jurássico para o início Cretáceo, e os padrões de diversidade do Mesozoico diferem do que se observa atualmente.

Os dados relacionados a padrões de lenho em diferentes cinturões paleoclimáticos sugeriram a Philippe et al. (2004) a ocorrência de um provincialismo adicional significativo dentro de Gondwana no intervalo Jurássico Superior-Cretáceo Inferior. Quatro zonas foram delimitadas pela paleolatitude: Zona 1: Caracterizada pela presença de *Metapodocarpoxylon* (zona úmida de verão), com

baixa diversidade relativa; Zona 2: baixíssima diversidade (zona de deserto); Zona 3: Presença de *Podocarpoxylon e Taxaceoxylon* e madeiras semelhantes a Taxaceae (inverno chuvoso e zonas temperadas quentes); Zona 4: em altas latitudes (zona fria temperada) com *Araucariopytis.* Estas zonas concordam de maneira geral com zonas macroflorais intra-Gondwana propostas por McLoughlin (2001).

Peralta-Medina & Falcon-Lang (2012) retomam a temática paleobiogeográfica, utilizando padrões globais de composição de associações de coníferas do Cretáceo usando um banco de dados abrangente de madeira fóssil (n= 2238). Para determinar a composição das associações florestais, os diferentes táxons foram agrupados de acordo com sua afinidade botânica, e plotados em paleomapas georreferenciados (Scotese paleomap Project).

A análise de padrões de composição das associações vegetais foi feita com base em lenhos fósseis em detrimento de outros tipos de fósseis vegetais tais como folhas, estruturas reprodutivas ou pólens porque apenas os lenhos fornecem evidências inequívocas sobre morfotipos formadores de copada que indicam o desenvolvimento de florestas.

Os resultados demonstraram que coníferas araucarianas e podocarpoides foram globalmente codominantes no Cretáceo Inferior, especialmente em biomas tropicais úmidos e paratropicais, reduzindo-se drasticamente o registro tanto em número e extensão durante o Cretáceo Superior.

Coníferas cupressoides, que eram mais comuns em latitudes médias sazonalmente secas e coníferas pinoides, que foram associadas a condições temperadas nas latitudes mais altas do hemisfério norte, também restringiram sua ocorrência, embora menos acentuadamente.

Esses resultados sugerem que a grande recessão de florestas de coníferas (especialmente araucaroides) esteve relacionada a expansão de angiospermas co-ocorrentes nas associações vegetais a partir do Cretáceo Superior.

A comparação com dados relacionados às floras atuais mostrou que a produtividade das florestas no Cretáceo era significativamente elevada em paleolatitudes médias e altas, ocorrendo um deslocamento da zona temperada em direção aos pólos em > 15 °.

Os taxa de conífera foram assim agrupados de acordo com padrões vigentes no xilema secundário:

- **Araucarioides** (26,2%) compreende: *Agathoxylon, Araucarioxylon, Araucariopitys*, alguns *Brachyoxylon, Dadoxylon, Dammaroxylon*, e alguns *Planoxylon.*

- **Podocarpoides** (13,9%) compreende: *Circoporoxylon, Metapodocarpoxylon, Phyllocladoxylon, Podocarpoxylon, Protocircocarpoxylon, Protophyllocladoxylon, e Protopodocarpoxylon.*

- **Cupressoides e cheirolepidoides** (11,9%) compreendem: *Chamaecyparixylon, Cupressinoxylon, Cupressoxylon*, alguns *Elatides,* alguns *Frenelopis, Juniperoxylon, Metacupressinoxylon, Paracupressinoxylon, Protocupressinoxylon, Prototaxodioxylon,* alguns *Pseudofrenelopsis, Sequoioxylon, Taxaceoxylon, Taxodioxylon, e Thujoxylon.*

- **Pinoides** (7,7%) compreende: *Abiocaulis, Cedroxylon, Keteleerioxylon, Laricioxylon, Palaeopiceoxylon, Piceoxylon, Pinoxylon, Pityoxylon, Protocedroxylon, Protopiceoxylon e Protopinuxylon.*

A distribuição nos mapas paleogeógraficos foi efetuada em três intervalos, respectivamente: T1: Berriasiano–Hauteriviano (145.5–125 Ma); T2: Aptiano–Albiano (126–99 Ma); T3: Cenomaniano–Santoniano (99–83 Ma); T4: Campaniano–Maastrichtiano (84–65.5 Ma). (Fig. 1).
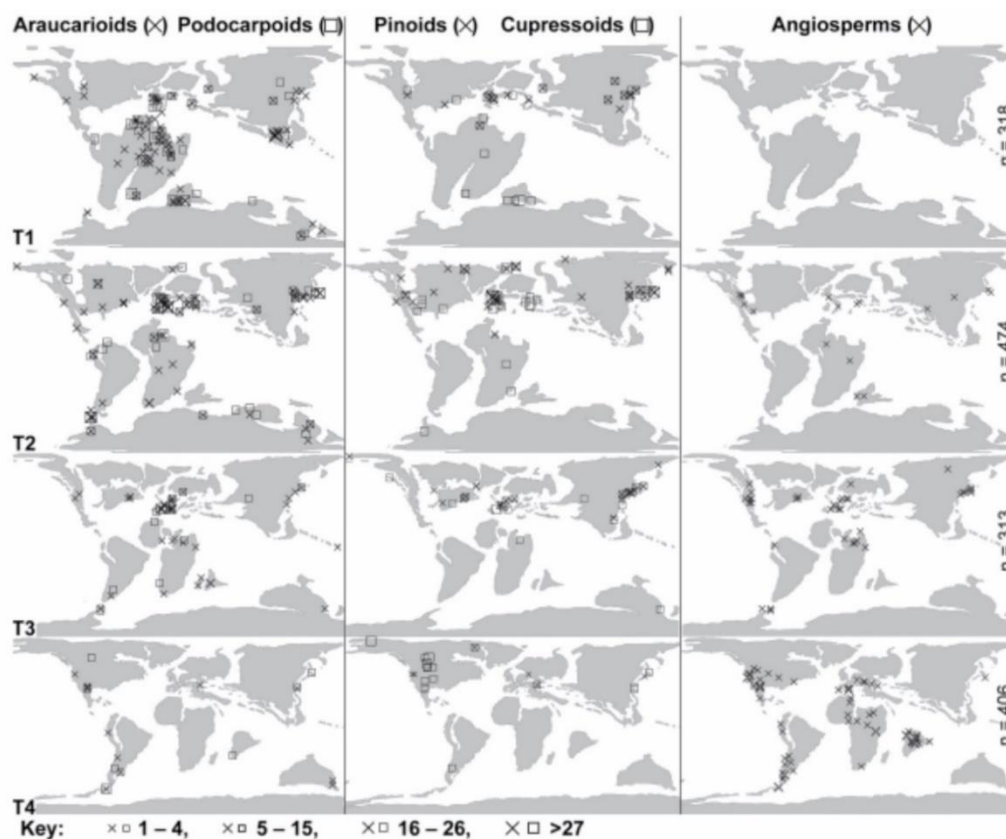
Figura 1. Distribuição paleogeográfica das Coníferas do Cretáceo plotadas com Esri ArcMap(Http:www.esri.com/soft-ware/arcgis/index.html). Coluna (1) Araucarioides e podocarpoide, (2) Cupressoide e pinoide, e (3) Angiospermas. T1: Berriasiano-Hauteriviano (145.5-125 Ma); T2: Aptiano-Albiano, (126-99 Ma); T3: Cenomaniano-Santoniano (99-83Ma); T4:, Campaniano-Maastrichtiano (84-65.5Ma). Retirado de Peralta-Medina & Falcon-Lang (2012).

Peralta Medina & Falcon-lang (2012) demonstraram que coníferas araucarioides e podocarpoides dominaram no Aptiano –Albiano, mas todos os grupos de coníferas sofreram declínio durante o período do Cretáceo Superior quando a contribuição de coníferas araucarianas e, em menor grau, podocarpoides, reduziu-se drasticamente. No Campaniano-Maastrichtiano, a proporção de angiospermas aumentou de 32% para 78%.

3.2 Lenho do Jurássico-Cretáceo nas bacias Brasileiras

Embora lenhos fósseis sejam abundantes em algumas unidades estratigráficas de diferentes bacias brasileiras (e.g Formação Missão Velha e Formação Romualdo na bacia do Araripe), são extremamente raras as análises que estabeleçam afinidades sistemáticas formais.

Análises de padrões de xilema secundário em lenhos da Formação Missão Velha (Jurássico Superior, Bacia do Araripe) levaram Pires & Guerra Sommer (2011) a identificação de dois padrões, um deles araucariano, que levaria a afinidades com lenhos de araucariaceae, e outro abietiano que apontaria para afinidades com lenhos de Pinaceae. Todavia, estudos de caráter taxonômico formal não foram realizados.

Eventuais atribuições ao gênero *Dadoxylon,* atualmente abandonado (Philippe et al., 2011) para designar lenhos procedentes do Mesozoico brasileiro não refletem qualquer tipo de afinidade e devem ser desconsideradas.

Padrões de xilema com potencial afinidade com Pinaceae foram registrados anteriormente para a Formação Botucatu do Cretáceo Inferior da bacia do Paraná, (Pires et al., 2011). A afinidade foi baseada na descrição original do gênero *Paleopinuxylon* Mussa, 1974, descrito para afloramentos dessa mesma unidade estratigráfica no município de Uberlândia, MG.

O gênero foi incluído na família Protopinaceae definida por Kraüsel, 1917, que considerava a hipótese de que as Protopinaceae tinham grande significado

filogenético, sendo um elo evolutivo entre o Paleozoico e as coníferas modernas. No entanto, de acordo com Bamford et al. (2016) Protopinaceae corresponde a um agrupamento artificial e como tal não pode ser associado a padrões genéricos sensu ICBN, porque não representa um grupo filogeneticamente significativo.

Araújo et al. (2011) vinculam padrões gimnospérmicos de uma assembleia de lenhos procedentes da Formação Alcântara (Albiano Superior-Cenomaniano Inferior, norte do Estado do Maranhão, NE, Brasil) como eminentemente araucarianos, provavelmente ligados a Araucariaceae, em detrimento de raros fragmentos com padrão abietoide, relacionados, com dúvidas, à Taxaceae. Todavia, análises taxonômicas formais não foram estabelecidas no material.

Batista et al. (2017) sugeriram a ocorrência de xilema com padrão araucariano no Crato Lagerstätte, através de vinculações de padrões de superfície externa de um ramo atribuído a *Brachyphyllum obesum* e padrões anatômicos internos de madeira do tipo *Agathoxylon.* No entanto, análises formais não foram propostas e a preservação deficiente do xilema impede qualquer abordagem taxonômica ou sistemática.

3.3.2 *Processos de Preservação em Lenhos ricos em Carbono Orgânico*

Investigações a respeito do processo de preservação de macro espécimes de lenho com alto teor de matéria orgânica são muito comuns, principalmente em amostras procedentes de linhitos mesozoicos, cenozoicos e até em material procedente de turfeiras atuais (George, 1982; Russel, 1984; Stout & Spackman, 1987; Betchel et al., 2007).

Análises de macro fragmentos de lenho de coloração escura, potencialmente ricos em matéria orgânica, procedentes das formações Crato, Ipubi e Romualdo (bacia do Araripe,) estabelecidas por Lima et al. (2019), centradas em Microscopia Eletrônica de Varredura, levaram a estabelecer afinidade desses fragmentos com macrocharcoal de acordo com os critérios de Scott (2010). Essa identificação levou a inferir a ocorrência de incêndios durante a deposição dos sedimentos. Não foram desenvolvidas, todavia, análises de petrografia orgânica, relacionados a identificação de macerais e refletância, que permitissem ratificar essas conclusões.

3.3 Processos de interação fungo-lenho

Atualmente, os fungos estão amplamente distribuídos em todos os ecossistemas terrestres, mas as relações entre latitude e diversidade de possíveis fungos patogênicos de plantas indicam que as forças climáticas impulsionam fortemente esses processos, com mudanças marcantes na diversidade em torno das latitudes médias (Wang et al., 2019).

Um modelo de evolução do hospedeiro sugerido por Krah et al. (2018) mostra que fungos que produzem a podridão parda (brown fungi) em floras atuais são generalistas ou especialistas em gimnospermas, enquanto a maioria dos fungos que produzem podridão branca (white rot) são especialistas em angiospermas.

Martínez et al. (2005) indicaram que a capacidade de degradar ou modificar a lignina é um processo enzimático que se originou no Devoniano Superior em paralelo com a evolução das plantas vasculares, corroborando os resultados de Nelsen et al. (2016) que concluíram que os dados genômicos são diretamente consistentes com a evolução da lignina no Devoniano.

A evidência indireta mais antiga do envolvimento de Basidiomycophyta (podridão branca) em processos de degradação de paredes celulares ocorreu em *Callyxylon* (Stubblefield et al., 1985) do Devoniano Superior (EUA). No entanto, os registros de corpos de Basidiomycophyta mais antigos no Paleozoico são os de Krings et al. (2011) para o Mississipiano da França e de Dennis (1969, 1970) para o Pensilvaniano da América do Norte.

Uma detalhada busca de referências identificou estudos que reportam evidências de decomposição de lenhos por podridão branca (Basidiomycophyta), documentadas por diferentes autores em diferentes biomas globais. Esses estudos, relacionados na Tabela 3, somam diferentes cinturões paleoclimáticos incluíndo climas tropicais, quentes, frios desde o Devoniano até o Eoceno.

Tabela 3. Registro direto e indireto de degradação por podridão branca em lenhos do Devoniano ao Eoceno. Santos et al. (2020).

Intervalo	Evidência		Zonas Climáticas (scotese 2011, 2014)	Referências
	Direta	Indireta		
Devoniano Superior	x	x	Quente/Árido	Stubblefield et al., (1985)
Mississipiano	x		Tropical	Krings et al., (2011)
Pensilvaniano Inferior	x		Tropical	Dennis (1969, 1970)
	x	x	Tropical	Wan et al., (2017)
	x	x	Tropical	Barthel (2010)
	x	x	Temperado Frio	Wei et al., (2016)
Permiano Inferior	x	x	Temperado Frio	Stubblefield and Taylor (1986)
		x	Quente	Diéguez and López-Gomez (2005)
	x	x	Temperado Frio	Wan et al. (2016)
		x	Temperado Frio	Wei et al. (2019)
Permiano Superior	x	x	frio	Weaver et al. (1997)
Triassico Inferior		x	quente	Stubblefield and Taylor (1986)
Triassico Superior		x	Tropical	Creber and Ash (199)
	x	x	Temperado Quente	Gnaedinger et al. (2012)
	x	x	Quente	Feng et al. (2015)
Jurássico Inferior	x	x	Quente	García-Massini et al. (2012)
Jurássico Superior	x	x	Quente	Sagasti et al. (2019)
Cretáceo Superior	x	x	Tropical Boreal	Tian et al. (2020)
Cretáceo Inferior		x	Frio	Falcon Lang et al. (2001)
Eoceno Superior		x	Quente	Pujana et al (2009)
Cretáceo Inferior	x	x	Árido	Este trabalho

No Intervalo Jurássico- Cretáceo em bacias brasileiras, evidências de fitofagia atribuídas a insetos, especificamente em folhas de pteridófitas, gimnospermas e angiospermas, são relatadas por Santos Filho et al. (2017) para o membro Crato da Formação Santana (bacia do Araripe).

Processos de fitofagia em xilema foram atribuídos à artrópodes (Pires & Guerra Sommer, 2011; Turman et al., 2021) em lenhos da Formação Missão Velha de idade Jurássico Superior (bacia do Araripe).

Descrições de processos de interação lenho-fungos para o Mesozoico brasileiro restringem-se somente ao estudo de Araújo et al. (2011) que registram intensa atuação de fungos em lenhos petrificados da Formação Alcântara (Albiano Superior-Cenomaniano inferior do norte do Estado do Maranhão). A degradação do lenho por fungos é evidenciada pela presença de hifas e esporos no lúmen celular além de alterações da parede celular. Todavia, os padrões encontrados não são vinculados a processos de interação mais específicos.

4. MATERIAIS E MÉTODOS

No decorrer do projeto, foram efetuadas abordagens em distintos tipos de vegetais fósseis e também em sedimentos a eles relacionados. Essas análises encontram-se detalhadas no corpo dos manuscritos que compõem esse volume, mas para uma compreensão mais integrada são sintetizadas a seguir.

4.1 Tipos de preservação do material fóssil

4.1.1 Lenho procedente do membro Crato, Formacão Santana, Bacia do Araripe (manuscritos 1 e 2)

Tipo de preservação: Permineralização (petrificação) Schopf (1975)

A composição elementar das paredes celulares e preenchimentos da lumen celular foram analisados usando um detector de espectroscopia dispersiva de energia (EDS) acoplado a um MEV Inspecione F50 FEI localizado no Centro de Microscopia e Microanálises IDEIA da Pontifícia Universidade Católica do Rio Grande do Sul.

4.1.1.1 Análise Anatômica

As análises e fotos de lâminas petrográficas delgadas com espessura de 40 my foram efetuadas sob microscópio estereoscópico Leica S8 APO com câmera acoplada um axiososcópio Zeiss. Uma câmera AxioCam MRc da Universidade Federal do Rio Grande do Sul (UFRGS) foi usada para produzir as fotos do microscópio de luz transmitida.

O software Zeiss Axio Vision 4.8.1 foi usado para as medições e o Adobe Photoshop CS3Extended foi aplicado para compor as placas. A transformação das imagens foi feita por corte, rotação, ajustes de contraste, empilhamento de foco e composição de imagem. A terminologia utilizada para fornecer os detalhes anatômicos da madeira seguiu as recomendações do IAWA Committee (2004), Decombeix et al. (2019), Schweingruber, (1992 1996) e Falcon Lang (2003).

4.1.2   Lenho procedente da Formação Maceió, Bacia do Sergipe Alagoas (manuscrito 3)

Tipo de preservaçao: Geleificação (Stach et al., 1982)

Obtida por análise petrográfica realizada em blocos polidos sob óleo (Immersol 518 F) utilizando microscópio Axioskop 2 Plus Zeiss equipado com espectrofotômetro J&M (MSP 200) por meio de objetiva ×50. O microscópio foi calibrado com um padrão Sapphire (0,595% Ro). Os mesmos blocos foram analisados para obter dados de refletância como um proxy visando estimativas de temperatura de carbonização, (McParland et al., 2009).

Observaçoes sob MEV foram realizadas visando   comprovar ou não o processo de homogeneização de parede celular que é típico em processos de charcoalificação (Scott & Jones, 1991; Jones and Rowe, 1999; Scott, 2010; McGinnes et al.,1971).

4.1.2.1 Análise anatômica

Foi realizada em microscopia eletrônica de varredura (MEV) acoplada a um Inspetor F50 FEI SEM localizado no Centro de Microscopia e Microanálises IDEIA da Pontifícia Universidade Católica do Rio Grande do Sul, revestido em ouro. A terminologia utilizada para fornecer os detalhes anatômicos da madeira seguiu as recomendaçoes do IAWA Committee (2004), Decombeix et al. (2019), Schweingruber, (1992 1996) e Falcon Lang (2003).

4.2 Análises do lenho e sedimentos associados

Foram realizadas no lenho e em sedimentos sobrepostos e sotopostos ao lenho procedente da Formação Maceió, Bacia de Sergipe Alagoas

4.2.1 Palinofácies

Foram selecionadas para análises de palinofácies amostras em fácies circundantes ao fóssil. A preparação envolveu procedimento não oxidativo da matéria orgânica sedimentar (Mendonça Filho et al., 2010). As amostras foram fragmentadas e inicialmente tratadas com HCl e HF, seguido de líquido pesado (ZnCl$_2$) para concentração da matéria orgânica, que foi então montada em lâminas.

A caracterização da matéria orgânica foi baseada no exame qualitativo da matéria orgânica particulada por meio de técnicas de microscopia. Um total de 300 a 500 partículas foram contadas para cada amostra, e normalizadas em percentis (Mendonça Filho et al., 2010).

4.2.2 Análise de Carbono Orgânico Total (COT):

As determinações do carbono orgânico total e do enxofre foram realizadas nas amostras de sedimento, no aparelho SC 144 da LECO. O método adotado foi o ASTM D 4239 (American Society for Testing and Materials - ASTM, 2008) e NCEA-C-1282 (United States Environmental Protection Agency-US EPA, 2002).

4.2.3 Biomarcadores

A matéria orgânica solúvel foi extraída das amostras de sedimento e do fragmento de lenho (50 g) com diclorometano e fracionada por cromatografia líquida de coluna aberta de sílica gel ativada. Para identificação das frações aromáticas o programa de temperatura do forno do GC foi: de 40°C por 5 min e então 4°C/min a 290°C por 30 min. O MS foi operado pelo modo de ionização por impacto de elétrons a 70 eV; temperatura iônica a 290°C; temperatura da interface a 300 °C; temperatura do quadrupolo a 150 °C. A identificação dos compostos foi feita usando a comparação da biblioteca MS e dados disponíveis na literatura.

5 SÍNTESE GEOLÓGICA DAS BACIAS DO ARARIPE E SERGIPE/ALAGOAS COM ÊNFASE NO CRETÁCEO INFERIOR

Os eventos associados ao rifteamento do Gondwana e a abertura do Atlântico atuaram de formas diferenciadas e a reativação de estruturas antigas do

embasamento Pré-cambriano condicionou, a forma e a localização das bacias interiores e marginais do Nordeste do Brasil (Assine, 2007).

Tendo em vista os objetivos e a temática proposta no projeto, são aqui sintetizados as características gerais das bacias do Araripe e Sergipe Alagoas.

Figura 2. Mapa das bacias sedimentares brasileiras com destaque para as bacias abordadas. (Modificado de Milani et al., 2007).

5.1 Bacia do Araripe

A Bacia do Araripe é a mais extensa das bacias interiores do Nordeste Brasileiro e a que apresenta, dentre elas, história geológica mais complexa. Com aproximadamente 243 km^2 de comprimento e 83 km^2 de largura, compreende os estados do Piauí, Pernambuco e Ceará (Assine, 2007).

A configuração estrutural da Bacia do Araripe abrange os estratos tabulares que formaram o Planalto do Araripe, uma importante feição geomorfológica E-W do nordeste do Brasil. Assine (2007) integrou diferentes propostas de Ponte & Appi (1990); Assine (1990, 1992); Ponte & Ponte Filho (1996) identificando quatro grandes unidades delimitadas por inconformidades (Fig. 3).
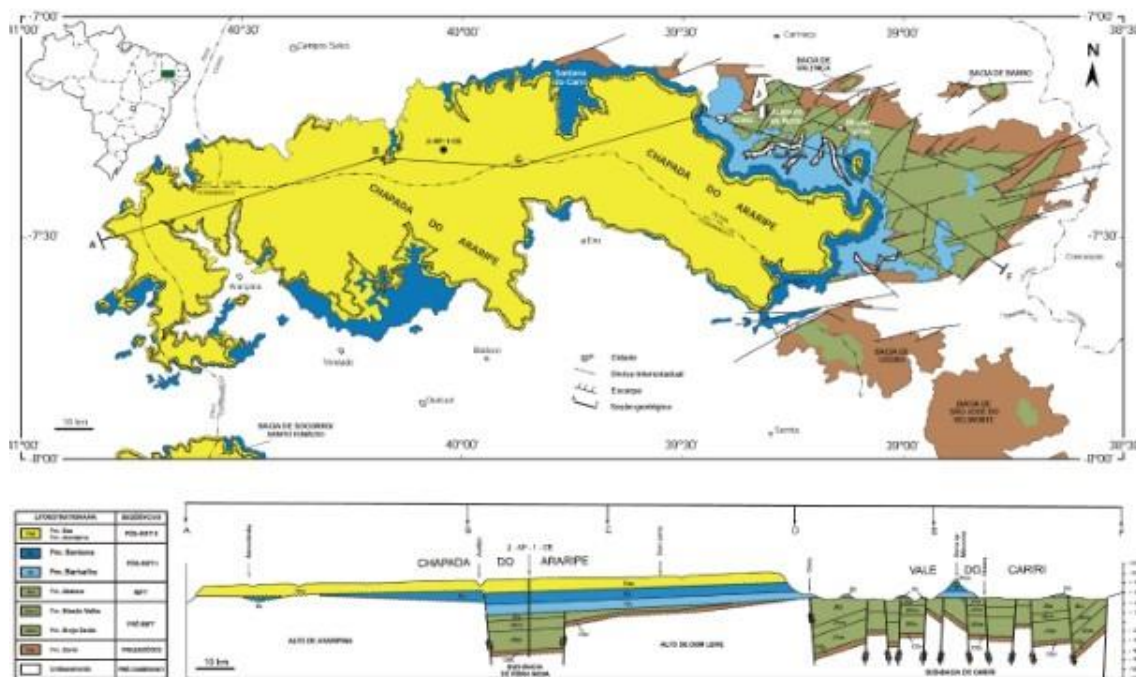
Figura 3. Mapa Geológico da Bacia do Araripe (Assine 1990).

A Sequência Paleozoica é representada pelos depósitos aluviais da Formação Cariri de idade Siluriano-Devoniano (Beurlen, 1962; Assine, 1992, 2007; Arai, 2006) foi interpretado como depósitos residuais de uma grande bacia intracratônica. A supersequência pré-rifte do Jurássico Superior corresponde às formações Brejo Santo (pelitos vermelhos) e Missão Velha (arenitos). A supersequência rifte é representada pela Formação Abaiara do Cretáceo Inferior, formada por uma sucessão de arenitos intercalados com folhelhos calcíferos (Fambrini et al. 2012). A supersequência pós-rifte, subdividida em duas sequências respectivamente a sequência pós-rifte I (Aptiano-Albiano), correspondente à Formação Barbalha e a Formação Santana (Membros Crato, Ipubi e Romualdo) e a sequência pós-rifte II (Albiano-Cenomaniano), que é caracterizada por sedimentos aluviais das formações Araripina e Exu, indicativos de reativação tectônica.

Face ao objetivo proposto no presente estudo, que remete a uma abordagem das unidades aptianas em diferentes bacias do Nordeste, a abordagem será restrita à Supersequência Pós-rifte, sequência k40-k60 conforme os critérios de Assine (2007).

5.1.1 Supersequência Pós-Rifte

A sequência Neoaptiana- Neoalbiana registra o advento do estágio pós-rifte da bacia do Araripe resultado de subsidência flexural térmica e assenta-se em discordância angular sobre as sequências sotopostas. Essa discordância conhecida como pré Alagoas, é reconhecida em todas as bacias da margem leste brasileiras, que envolve na bacia do Araripe uma lacuna no registro sedimentar com duração de 17 Ma, desde o andar Buracica ao andar Alagoas Inferior (Assine, 2007).

Essa sequência materializa um ciclo transgressivo-regressivo, reflexo de subsidência térmica e de eventos eustáticos globais de elevação do nível do mar, que criaram espaço de acomodação para a deposição e preservação de depósitos marinhos no interior do Nordeste. Trata-se de um ciclo quase completo, uma vez que é truncado no topo, faltando as fácies dos tratos de sistemas de mar alto do final do ciclo (Assine, 2007).

A parte basal da supersequência pós-rifte inclui os depósitos Aptiano /Albianos da Formação Santana, abrangendo, em ordem crescente os membros Crato, Ipubi e Romualdo (sensu Assine et al., 2007) que registram configurações lacustres a costeiras (Membro Crato), costeiras evaporíticas (Membro Ipubi) e plataformas (Membro Romualdo).

Os calcários micríticos laminados do Membro Crato da Formação Santana ocorrem ao final do segundo ciclo de granodecrescência ascendente da Formação Barbalha sotoposta, formando bancos descontínuos com espessuras que ultrapassam duas dezenas de metros, interdigitados lateralmente com folhelhos verdes.

De acordo com os critérios de Martill et al. (2007) essa unidade, caracterizada como Formação é composta respectivamente por Membro Nova Olinda, Membro Caldas, Membro Jamacaru e o Membro Casa de Pedra, sendo que o membro inferior Nova Olinda é o Konservat-Lagerstätte que tem sido estudado extensivamente.

O Membro Nova Olinda, com até 13 m de espessura e duas macrofácies distintas: finamente laminada, ritmitos de carbonato de argila marrom enferrujado, com quantidades variáveis de matéria orgânica, e macrofácies de calcário do tipo "plattenkalk" (Neumann et al., 2003).

O membro Caldas, compreendendo folhelhos pretos finos bem estratificados, folhelhos siltosos, argilas variegadas e arenitos com finos calcários laminados e micríticos. Além de raros bivalves e mal preservados, ocorrem alguns horizontes excepcionalmente rico em ostracodes e conchostraceos (Martill & Heimhofer, 2007).

O Membro Jamacaru, apresenta litologia semelhante ao membro Nova Olinda, geralmente com uma unidade de calcário basal separado do calcário principal por um leito de folhelho siltoso com registros fósseis restritos a *Dastilbe* sp. conchostraceos, e madeiras fósseis (Martill & Heimhofer, 2007).

O Membro Casa de Pedra, composto por xisto piritoso laminado preto, com algumas camadas finas de areia, e folhelho negro rico em algas, ostracodes e *Dastilbe* sp. (Martill & Heimhofer, 2007).

Neumann et al. (2003), consideram uma origem bacteriana em condições anóxicas para os carbonatos. Esta hipótese é aceita por Catto et al. (2016) que considera a ampla procedência da sucessão carbonática como decorrente de atividade de organismos que reduziam compostos sulfetados, o que promoveu concentração atípica de sulfetos por indução biológica. Condições de crescente aridez em direção ao topo das seções (Assine et al., 2014; Heimhofer et al., 2010; Martill et al., 2007; Neumann, 1999) são inferidas partir da ocorrência de pseudo - morfos de halita nos calcários laminados.

Registros de carapaças de microforaminíferos imediatamente subjacentes às "Camadas de Ipubi" indicam para Goldberg et al. (2019) o aumento da influência marinha na Bacia do Araripe, em porções restritas da bacia.

As camadas de gipsita formam o Membro Ipubi Beurlen (1971) que compreende um intervalo de evaporito (gesso e anidrita) de 12-30 m de espessura associado a folhelhos pretos, totalizando 30 a 40 m em 125 de espessura (Neumann & Assine, 2015; Fambrini et al., 2017). Na região da fronteira sudoeste da Bacia do Araripe, esta unidade se sobrepõe diretamente às unidades do embasamento pré-cambriano (Lucio et al., 2020) e na região nordeste da bacia sobrepõe-se ao calcário da Membro Crato ou unidades tectôno-sedimentares mais antigas da bacia (Neumann & Cabrera, 1999; Assine et al., 2014; Fambrini et al., 2017).

O topo do Membro Crato, redefinido com a inclusão da associação que contém as camadas de gipsita, é marcado por descontinuidade erosiva de curta duração, caracterizando um contato diastêmico com o Membro Romualdo.

A parte inferior do Membro Romualdo caracteriza se pela presença de arenitos interestratificados com folhelhos (Chagas, 2006). O empilhamento é transgressivo no topo e os arenitos costeiros sucedem-se por folhelhos verdes. A ocorrência dos gêneros *Spiniferites (*Mantell) e *Subtilisphaera* (Jain & Millepied) indicam a influência marinha nesse nível (Arai & Coimbra, 1990).

Os folhelhos adquirem colorações mais escuras e são caracterizados pela presença de um nível com concreções que ocorre em toda a bacia e que corresponde a importante marco estratigráfico. As concreções encerram rica paleoictiofauna considerada marinha (Silva Santos & Valença, 1968; Price, 1971, Price, 1973; Campos & Kellner, 1985). Alguns metros acima do nível das concreções ocorre uma camada de coquinas, que pode atingir um metro de espessura.

A seção superior da Formação Santana, em particular nos arredores da cidade de Arajara, é caracterizada por intercalações de arenitos finos com lâminas e clastos de argila nos forests e nos limites dos sets. Esta seção foi correlacionada, por Ponte & Appi (1990), à seção de ritmitos e arenitos que ocorre no extremo oeste da bacia, classificada como o membro inferior da Formação Exu (Beurlen, 1963).

Datações relativas com base em análises palinológicas definiram duas palinozonas para a Formação Santana: a Zona *Sergipea variverrucata* (Formações Barbalha e Crato) e a Zona *Cicatricosisporites avnimelechi* (formações Ipubi e Romualdo; Coimbra et al., 2002; Rios Neto et al, 2012). No entanto, microfósseis (por exemplo, *Pattersoncypris angulata, Pattersoncypris micropapillosa, Alicenula leguminella*) sugerem que as formações Ipubi e Romualdo foram depositadas durante o Aptiano e Albiano (Regali, 1990; Coimbra et al., 2002).

Todavia, a obtenção de idades absolutas tem contrastado com datações relativas. Dessa forma, uma idade absoluta de 123 ± 3,5 Ma foi obtida por Lucio et al. (2020) para a Formação Ipubi. Essa idade restringe a deposição para o intervalo Barremiano Superior ao Aptiano Inferior.

Por outro lado, duas idades U-Pb foram obtidas por Celestino et al. (2021) em mineralizações de veias carbonáticas respectivamente 94,9 ± 3,8 Ma (Cenomaniano a Turoniano) e 80,2 ± 3,0 Ma (Campaniano), relacionadas a episódios de reativação da Zona de Falha do Triunfo e a entrada de fluidos de diferentes composições durante a deformação pós-rifte da Bacia do Araripe.

5.2 Bacia de Sergipe – Alagoas

A Bacia de Sergipe-Alagoas é a bacia da margem leste brasileira que possui o registro sedimentar mais completo, apresentando todos os estágios evolutivos da ruptura do Pangea e surgimento do oceano Atlântico: Sinéclise Paleozoica, Pré-Rifte, Rifte, Transicional e Drifte (Feijó, 1994; Mohriak et al., 1997; Souza-Lima et al., 2002; Cruz, 2008).

Embora a Bacia de Sergipe-Alagoas seja comumente abordada como uma bacia única, Feijó (1994) individualizou as bacias de Sergipe e Alagoas Campos Neto et al. (2007) apresentam duas cartas estratigráficas como representativas da bacia, considerando que o preenchimento sedimentar e o estilo tectônico na bacia variam da porção sergipana para a alagoana, conceito esse adotado no presente projeto.

As sub-bacias de Sergipe e Alagoas apresentam embasamentos distintos. O embasamento da Sub-Bacia de Sergipe é representado pelo Sistema Orogênico Sergipano (Província Borborema) em praticamente toda a sua totalidade e pelo embasamento arqueano-paleoproterozoico (Craton do São Francisco), no extremo sul dessa sub-bacia.

A sub-bacia de Alagoas (Fig. 4) apresenta embasamento constituído majoritariamente pelo Domínio Pernambuco Alagoas, maior domínio da Província Borborema. Esse domínio está localizado entre a Zona de Cisalhamento Pernambuco e os terrenos neoproterozoicos Sergipano e Riacho do Pontal, dividindo-se em parte leste e oeste, separadas pela Bacia de Jatobá (Silva Filho, 2008). A porção leste representa cerca de 75% do complexo, sendo a região com ocorrência dos maiores batólitos graníticos da Província Borborema (Silva Filho et al., 2014). Em grande escala, o Domínio Pernambuco – Alagoas está subdividido em dois complexos (i) Cabrobró, formado por rochas supracrustais e (ii) Belém do São Franscisco, rochas ortoderivadas migmatizadas (Silva Filho, 2008).

A deposição da Formação Maceió representa o último pulso tectônico do rifte que envolveu três fases distintas (Petrobrás, 1960 segundo Souza-Lima et al., 2002). A deposição envolveu fases de leques aluviais e sistemas turbidíticos lacustres de idade neoaptiana (Campos Neto et al., 2007).

O conteúdo fossilífero desta unidade é rico e variado. Foraminíferos, nanofósseis calcários, palinomorfos ostracodes foram registrados para essa

formação por Feijó, (1993) além de conchostráceos cizicídeos, (Carvalho & Arai, 2001).
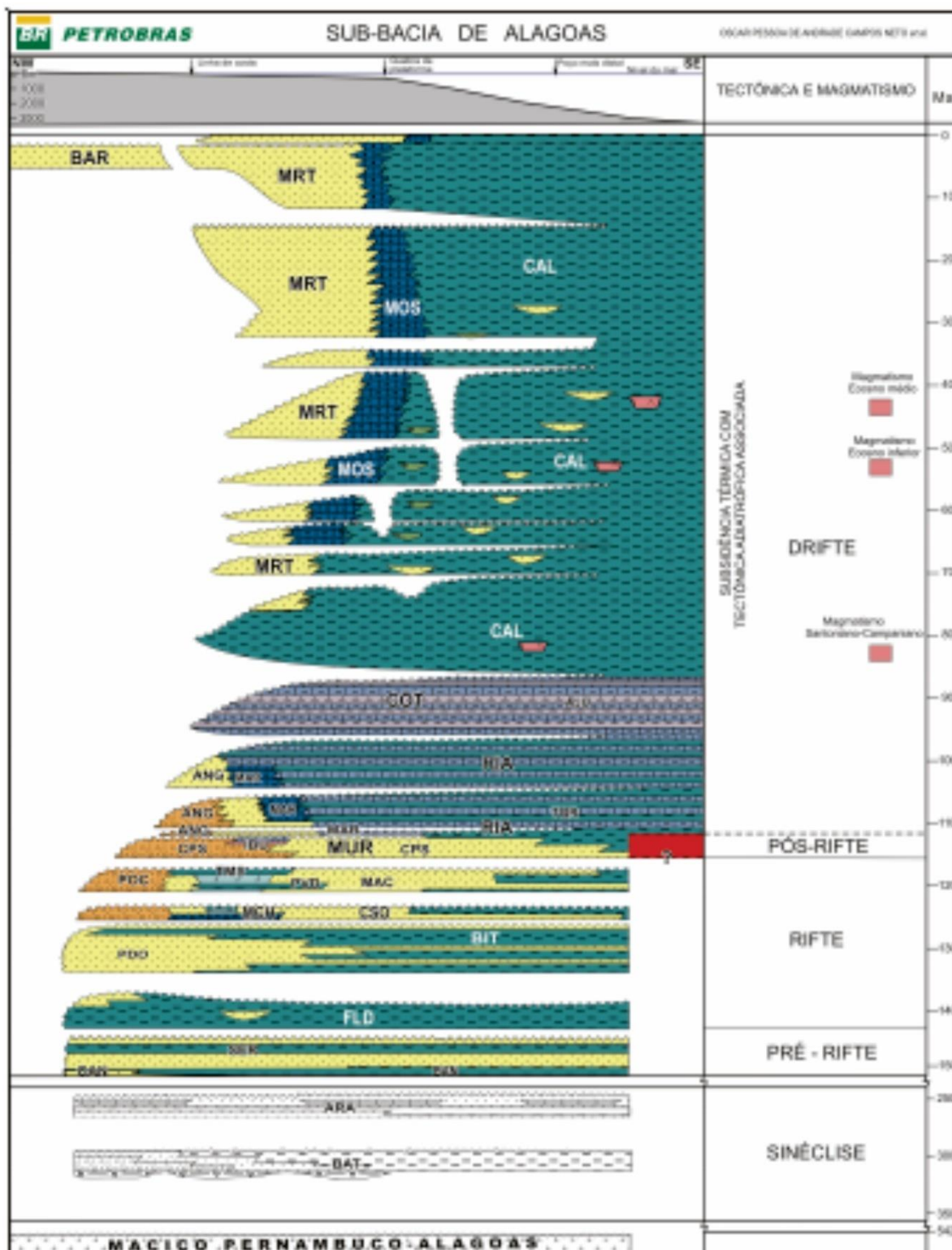
Figura 4. Carta estratigráfica da sub-bacia de Alagoas.

Peixes osteíctes actinopterígeos: *Vinctifer punctatus* (Santos), *Cladocyclus alagoensis* (Jordan), foram registrados por Nascimento; Filho (2005), além de *Ellimma brannneri* (Jordan) e *Dastilbe crandalli* (Jordan) de águas dulcícolas, registrados por Carvalho & Lima (2002) e *Ellimmichthys* sp, registrado por Malabarba et al (2002).

Níveis de mortandade em massa foram registrados por Viana et al. (2001) na localidade de Barreira da Bica (município de Japaratinga) em que se intercala a dominância conchostráceos cizicídeos no nível inferior com dominância de restos de *Dastilbe* no nível intermediário e formas juvenis de clupeomorfos no nível superior.

Fragmentos vegetais associados aos três níveis são designados como indeterminados, em contraposição ao registro taxonômico de fósseis de ambiente aquático,   confirmando a inexistência de estudos de detalhe de material paleobotânico para essa unidade.

Os mais importantes afloramentos da Formação Maceió ocorrem na Praia de Japaratinga, Barreiras do Boqueirão e Morro de Camaragibe no norte do Estado de Alagoas (Almeida et al., 2017). O material analisado no presente projeto procede do afloramento Morro do Camaragibe, que é detalhado a seguir.

O afloramento de Morro de Camaragibe (09°20'06,43"S, 35°26'25,97"W) corresponde a um anticlinal com extensão de aproximadamente 800m com uma complexa arquitetura estrutural que dificulta a correlação e interpretação de todo o conjunto de fácies ao longo do afloramento (Almeida et al., 2017).

O afloramento foi compartimentado por Almeida et al. (2017) em três partes principais (Fig. 5): norte, central e sul. O setor norte do anticlinal apresenta um mergulho das camadas variando entre 15° a 20° para SW com direção preferencial NW/SE, já o setor sul mostra um mergulho de camadas entre 6° a 15° para NW, com direção preferencial NE/SW (Siqueira, 2002), enquanto que a porção central não apresenta grande mergulho aparente.

A porção norte do afloramento apresenta, na base, uma fácies interacamadada com alternância de lâminas de arenito fino com *ripples* e siltito argiloso cinza escuro de aspecto maciço a laminado e rico em matéria orgânica para o topo, com estruturas em chama, apresentando *ripples* em geral unidirecionais, para sudoeste, associado a paraconglomerado de matriz arenosa média a grossa contendo clastos e blocos de lamitos aparentemente oriundos do rompimento de camadas de folhelhos (deformação intraestratal). Acima dessas

fácies encontra-se um arenito grosso conglomerático mal selecionado acamadado e com porções gradacionais, por vezes exibindo estratificação tabular e passam a estratificação plano-paralela no topo (Almeida et al., 2017).

A parte central desse afloramento, objeto de estudo no presente estudo, possui basicamente três fácies: arenito fino a médio, moderadamente selecionado, com estratificação plano-paralela na base da seção, passando para *ripples* no topo, com vários fragmentos de matéria orgânica escura; paraconglomerado de matriz arenosa de composição lítica, contendo grânulos e seixos de granitoides, blocos de arenito fino a médio, blocos de siltitos e arenitos vermelhos e de lamitos cinza escuro com matriz mal selecionada preenchendo feição canalizada e; arenito muito grosso na base do estrato, passando a grosso e por vezes a médio em direção ao topo, muito mal selecionado, maciço, com blocos de lamitos dispersos no topo (Almeida et al., 2017).

Na porção sul observam-se arenito cinza escuro, maciço, muito mal selecionado, com blocos dispersos decimétricos de lamitos e carvão, próximo ao topo dessa fácies há uma porção fina com *climbing ripples* fluidizadas e cristas colapsadas.

Sobre esse pacote encontra-se uma camada de arenito médio a grosso maciço de coloração cinza esverdeada com fragmentos de carvão dispersos que grada para um arenito fino com *climbing ripples* de paleocorrente SW (Almeida et al., 2017).
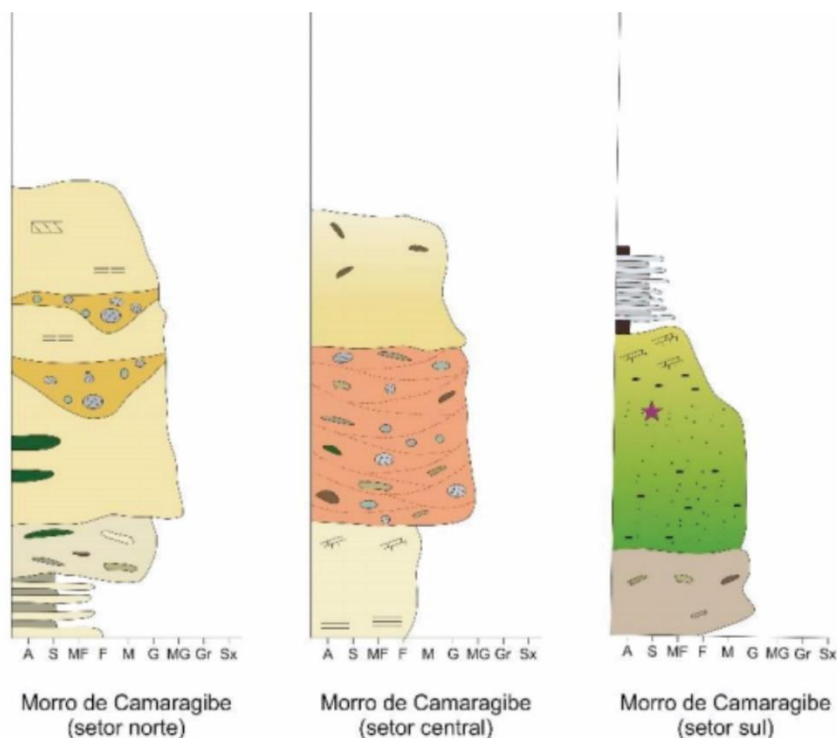
Figura 5. Perfis estratigráficos esquemáticos (sem escala vertical) mostrando as principais fácies dos afloramentos estudados. **A:** argila; **S:** silte; **MF:** areia muito fina; **F:** areia fina; **M:** areia média; **G:** areia grossa; **MG:** areia muito grossa; **Gr:** grânulo; **Sx:** seixo). Modificado de Almeida et al. (2017).

6. ANÁLISE INTEGRADORA DOS RESULTADOS

Tendo em vista a contextualização da pesquisa que se centrou em análises de lenhos fósseis e sedimentos associados no contexto de diferentes bacias sedimentares no intervalo Aptiano, a presente discussão integradora é apresentada dentro dos tópicos temáticos abordados a seguir, constantes dos três manuscritos que compõem a tese:

6.1 Características Anatômicas X Afinidade Botânica

Análises nos lenhos procedentes de sedimentos Aptianos de duas distintas bacias sedimentares da região Nordeste do Brasil, respectivamente a sub bacia marginal de Alagoas e a bacia interior do Araripe, permitiram a identificação de padrões anatômicos distintos.

O lenho procedente de sedimentos turbidíticos da Formação Maceió, na Bacia de Sergipe Alagoas, sub bacia de Alagoas (Fig. 6) tem características típicas de

xilema secundário gimnospérmico relacionado, com segurança, à família Pinaceae, embora não suficientes para designação genérica.

Figura 6. Lenho geleificado coletado no Afloramento Morro do Camaragibe, Formação Maceió, Bacia de Sergipe-Alagoas.

A correlação sistemática baseou-se nos seguintes padrões:

- xilema secundário com um padrão homoxílico picnoxílico;

- pontoações areoladas unisseriadas com bordas circulares, isoladas contíguas e parcialmente bisseriadas nas paredes radiais dos traqueídeos, associadas a pontoações semi areoladas piceoides nos campos de cruzamento (2 a 4 por campo) ocorrendo pontoações areoladas nas filas marginais dos campos;

- Presença de canais axiais intercelulares dispersos aleatoriamente no xilema, isolados ou em grupo de dois canais, mostrando lumen circular internamente revestidos por células epiteliais. Ocorrência também de canais com lumen circular, circundados por células epiteliais incluídos nos raios parenquimáticos unisseriados.
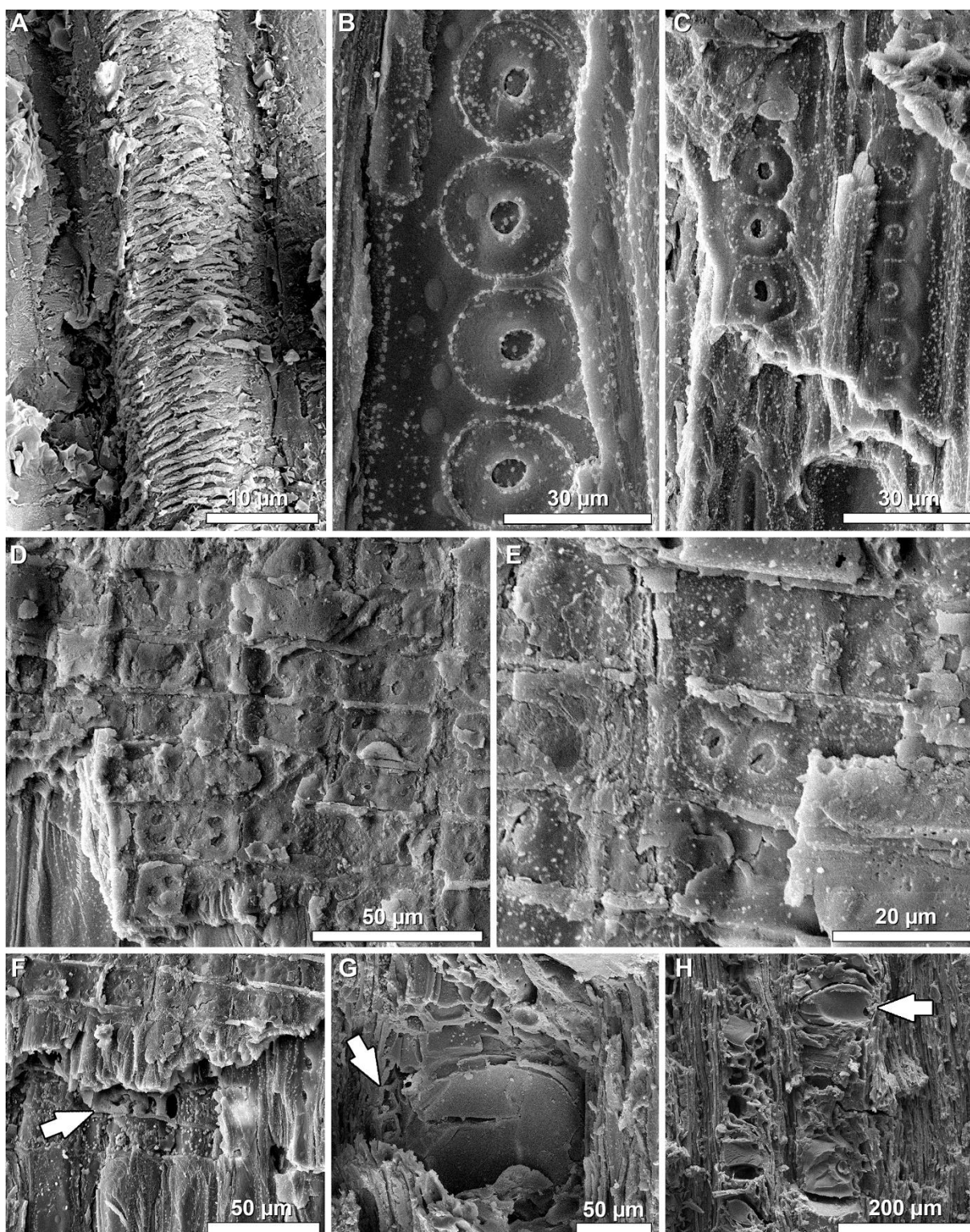
Figura 7. Seção Radial: xilema primário e secundáriodo do lenho procedente da Formação Maceió, Bacia Sergipe Alagoas. (A) Xilema primário com espessamento espiralado a reticulado (B) Pontoações unisseriadas, isoladas com bordas circulares; (C) Pontoações unisseriadas, contíguas com bordas circulares; (D), (E) Pontoações dos campos de cruzamento com arranjos do tipo piceoide; (F) Campos de cruzamento contornando a margem dos raios(seta). (G) Vista longitudinal de um lumem do canal axial (seta); (H) Canais radiais paralelos à orientação das células parenquimáticas dentro dos raios (seta).

O lenho procedente do Membro Crato (Formação Santana, bacia do Araripe) corresponde a um ramo, partido em fragmentos ao ser isolado do sedimento (Fig. 8)

Figura 8. Fragmentos de lenho procendentes da Formação Santana, Bacia do Araripe.

Análises microscópicas revelaram a ocorrência de um padrão homoxílico composto por medula muito pequena com limites irregulares, circundada por xilema secundário maciço estando também preservados, floema e casca. A presença de uma folha ligada organicamente ao eixo, permitiu a identificação do espécime como um ramo de última ordem.

As características anatômicas do xilema secundário que levaram a identificação de uma nova espécie do *Agatoxylon santanensis,* são as seguintes:

- Xilema secundário com um padrão homoxílico picnoxílico e traqueídeos com contorno quadrangular em seção transversal;

- pontoações areoladas com bordas hexagonais trisseriadas, alternas densamente arranjadas nas paredes radias dos traqueídeos; raios parenquimáticos homogêneos, com a pontoações semi-areoladas com arranjo araucarioide nos campos de cruzamento (2 a 4 por campo).

- Frequente presença de plugs de resina.
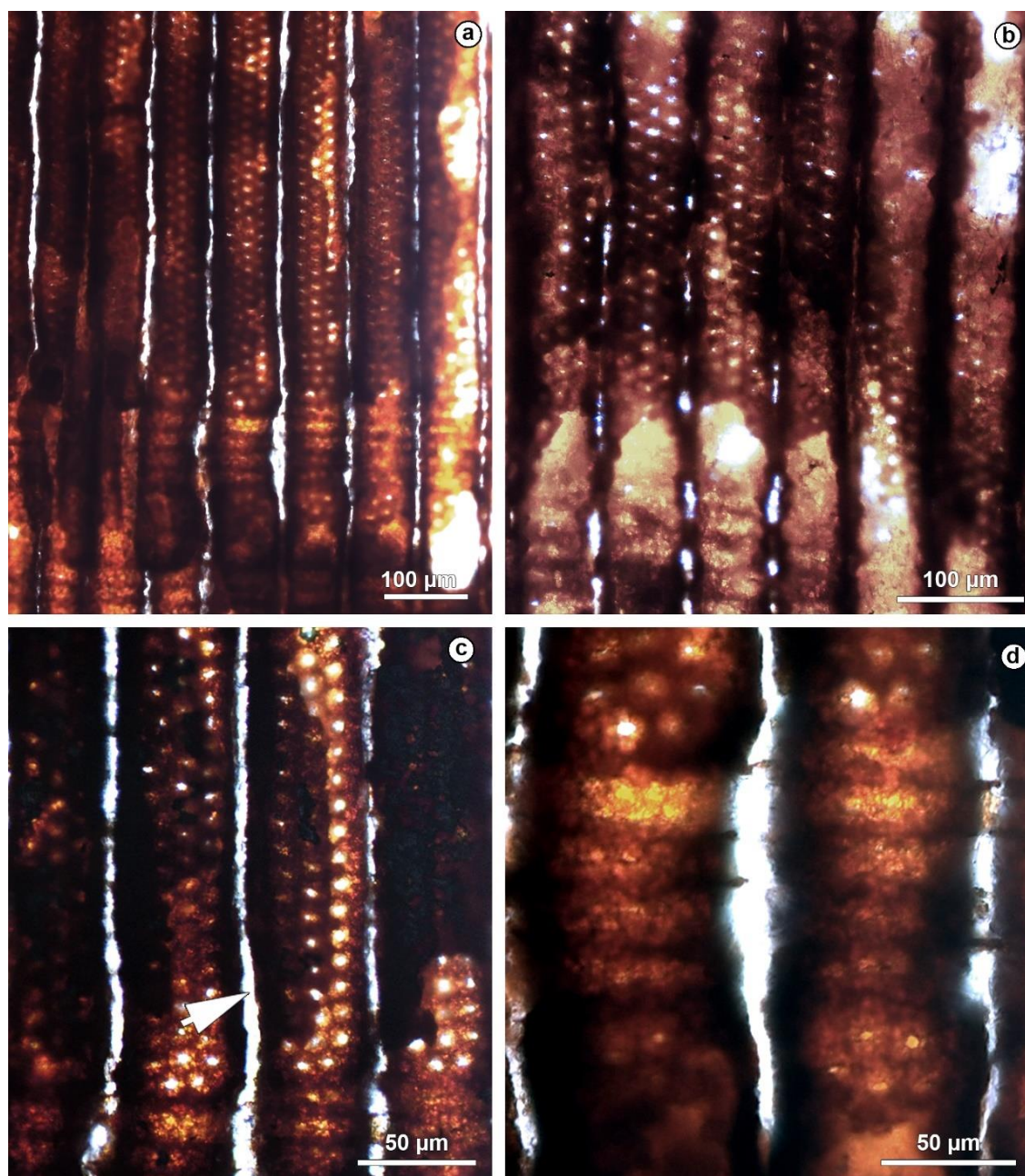
Figura 9. Principal Padrão Anatômico do lenho em seção radial do lenho procendente da Formação Santana, Bacia do Araripe. (A). Vista geral de traqueídeos com pontoações multiserriadas hexagonais e campos de cruz e campos de cruzamento com pontoações do tipo araucarioide. (B-C). Traqueideos com pontoações multiseriadas hexagoanis alternas, em arranjo compacto e degradação contínua da lamela média por podridão branca (seta). (D) Detalhe de (a) mostrando pontoações com organização do tipo araucaripoide nos campos de cruzamento.

Embora o morfogênero *Agathoxylon* designe critérios exclusivamente morfométricos (i.e. Sem estabelecimento de vinculações filogenéticas) de acordo com os critérios de Philippe & Bamford (2008) sua afinidade com Araucariaceae tem sido fortemente defendida, com base em material procedente do Gondwana Ocidental no intervalo Jurássico Superior-Cretáceo Inferior (Zamuner & Falaschi,

2005; Vera & Cesari, 2012; García-Massini et al., 2012; Gnaedinger et al., 2015; Kloster & Gnaedinger, 2018; Greppi et al., 2020; Del Fueyo et al., 2021).

No espécime estudado, além da organização do xilema, a presença de canais axiais e um cinturão de esclereídos no floema secundário apontam para o padrão de floema de Araucariaceaceae (Chan, 1986; Castro et al., 2006). A inserção séssil de uma folha na porção externa do espécime   que apresenta venação paralela e padrão epidérmico onde ocorrem estômatos   com quatro células subsidiárias reforçam essa afinidade (Andruchow-Colombo et al., 2018).

6.2 Afinidade Sistemática X Inferências Paleobiogeográficas e Paleoclimáticas

A presença de *Agathoxylon* no cinturão Equatorial Quente Árido, também comum nos cinturões subtropicais e temperados frios contemporâneos do Cretáceo Inferior do Gondwana Ocidental indica que coníferas com afinidade araucariana não eram climaticamente controladas no Aptiano. A ocorrência cosmopolita desse gênero no Cretáceo, em diferentes zonas climáticas mais raramente em ambientes equatoriais áridos já é registrada por Philippe et al. (2004) ao estabelecer a distribuição de lenhos fósseis em cinco faixas climáticas caracterizadas nos paleomapas de Rees et al. (2000).

Essas evidências são ratificadas pelos resultados obtidos por Peralta Medina & Falcon Lang (2012) usando metodologia semelhante, que demonstraram ser as coníferas araucaroides os táxons mais abundantes e globalmente difundidos (80 °N a 80 °S), no Aptiano–Albiano.

Os dados referentes a presença de *Agathoxylon* no Aptiano da bacia do Araripe, obtidos pela primeira vez   no presente estudo, confirmam a distribuição paleogeográfica global de coníferas araucarianas do Cretáceo conforme a base de dados utilizada por Philippe et al. (2004); Peralta-Medina & Falcon-Lang (2012). Todavia, o registro de Pinaceae na sub bacia de Alagoas suporta algumas implicações paleogeográficas no contexto de fragmentação do Gondwana e da abertura do Atlântico Sul durante o Aptiano.

Nos quatro intervalos temporais definidos por Peralta-Medina & Falcon-Lang (2012) (Berriasiano-Hauteriviano, Aptiano-Albiano, Cenomaniano-Santoniano e Campaniano-Maastrichtiano)   as   coníferas   pinoides   foram   confinadas principalmente a paleolatitudes médias a altas (principalmente 40°- 65°)

exclusivamente no Hemisfério Norte. A única ocorrência de Pinaceae para o Gondwana registrada no nordeste do continente aficano.

A identificação de biotas de vertebrados terrestres Aptianos apresentando fortes semelhanças, comuns entre bacias brasileiras e africanas, como por exemplo as faunas de saurópodes e celacantos, já foram consideradas como dados consistentes para Calvo & Salgado (1996) sobre a proximidade dessas áreas continentais durante este intervalo.

Os novos dados aqui apresentados sobre a distribuição paleogeográfica de Pinaceae no Aptiano levaram à inferir que esse grupo de coníferas, muito concentrado no Hemisfério Norte, teria se irradiado durante o Cretáceo Inferior de extensões de terra da Província Ibérica para áreas continentais hoje correspondentes ao norte do continente africano e nordeste do Brasil (Fig. 11).
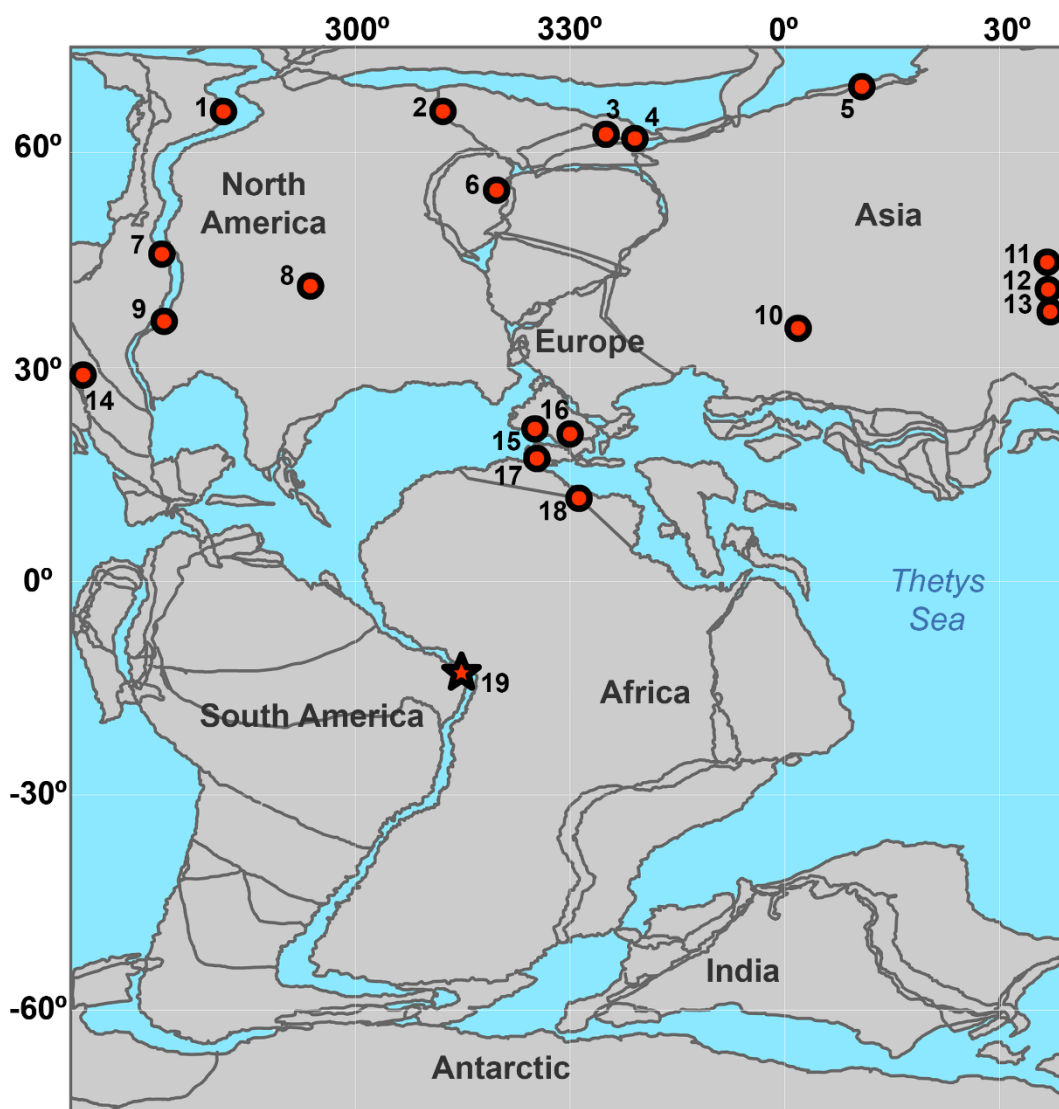
Figura 10. Distribuição paleogeográfica de lenhos de Pinaceae nas massas continentais no Aptiano-Albiano (126–99 Ma) depois da distribuição geral de Coníferas registradas por Peralta-Medina & Falcon-Lang (2012) e referências citadas a seguir. Mapa geral modificado de Arai (2014). Locality

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references: 1. Bailey, 1933; 2. Bannan & Fry, 1957; 3, 4, 6. Harland et al., 2007; 5. Blokhina & Afonin, 2007; 7. Tidwell et al., 1967; 8. Berry, 1911; 9. Tidwell & Thayn, 1985; 10. Peralta-Medina & Falcon-Lang, 2012; 11, 12. He, 1995; 13. Shimakura, 1937; 14. Beck, 1871; 15. Stopes, 1915; 16. Fliche, 1897; Lignier, 1913; Carpentier, 1943; Pons 1973,1974,1975; Desplats, 1976; Koeniguer, 1981; Pons et al., 1993; 17. Del Nido et al., 1998; 18. Chudeau,1920; 19. Este trabalho.

Embora as análises baseadas nos padrões de crescimento da madeira sejam problemáticas quando baseadas em um único espécime, o padrão de crescimento da madeira identificado em *Agatoxylon santanensis* sp.nov. procedente da bacia de Araripe, permite algumas especulações.
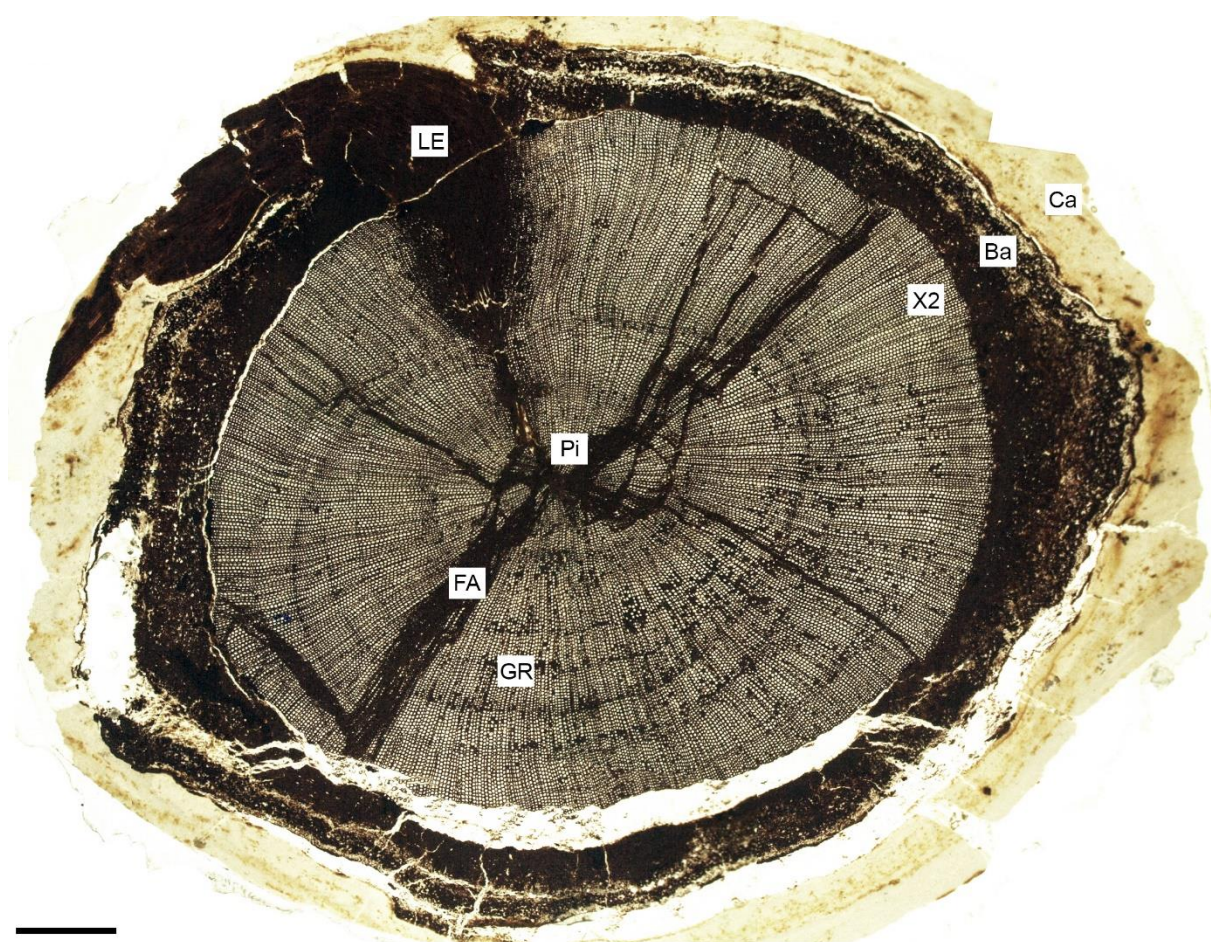
Figura 11. Imagem composta de uma seção tranversal completa sob microscópio estereoscópio mostrando a camada de carbonato (Ca), medula irregular (Pi), xilema secundário maciço e homogêneo (x2), anéis de crescimento uma emergência foliar, casca e o ataque de fungos.

As zonas de interrupção do crescimento do lenho, resultam de uma desaceleração temporal, mas não desativameneto da atividade cambial (Creber & Chaloner, 1984; Schweingruber, 1992, 1996; Wang et al., 2014). Sua origem é atribuída principalmente às secas, inundações, incêndios, ventos ou períodos

incomuns e súbitos de baixa temperatura (Fritts, 1976; Ash, 1983; Dechamps, 1984; Ash &Creber, 1992; Schweingruber, 1992, 1996; Young et al., 1993; Falcon-Lang, 2003; Wang et al., 2014). No caso do material em estudo, essas marcas de interrupção foram interpretadas como assinaturas de abruptos períodos de escassez de água intercalados com intervalos de condições favoráveis de crescimento (Fritts, 1976; Schweingruber, 1992, 1996). Estas assinaturas no lenho indicam que as condições ambientais para o desenvolvimento de coníferas araucarianas eram vigentes em áreas continentais não tão distantes do lago Crato.

6.3 Processos de Fossilização

Os processos de preservação que permitiram a observação das características anatômicas foram distintos nas diferentes bacias.

6.3.1 Lenho procedente do Membro Crato (Formação Santana, Bacia do Araripe).

A composição elementar de paredes celulares e preenchimentos dos lumens celulares foram estabelecidas usando detector de espectroscopia dispersiva de energia (EDS) acoplado ao equipamento F50 FEI SEM.

A análise de EDS elementar indicou, nas paredes celulares, que o processo de petrificação do lenho envolveu degradação parcial de componentes orgânicos e mineralização por minerais dominantes de ferro (Fe), na presença de oxigênio (O), além de carbono (C) que provavelmente compunham a parede originariamente.

A mineralização de vazios anatômicos correspondentes a lumens celulares e cavidades resultantes de fitofagia ocorreu principalmente por precipitação de cálcio em forma de cristal (Ca). Consequentemente, a fossilização do lenho resultou de uma combinação de processos de permineralização de paredes e mineralização de espaços vazios.
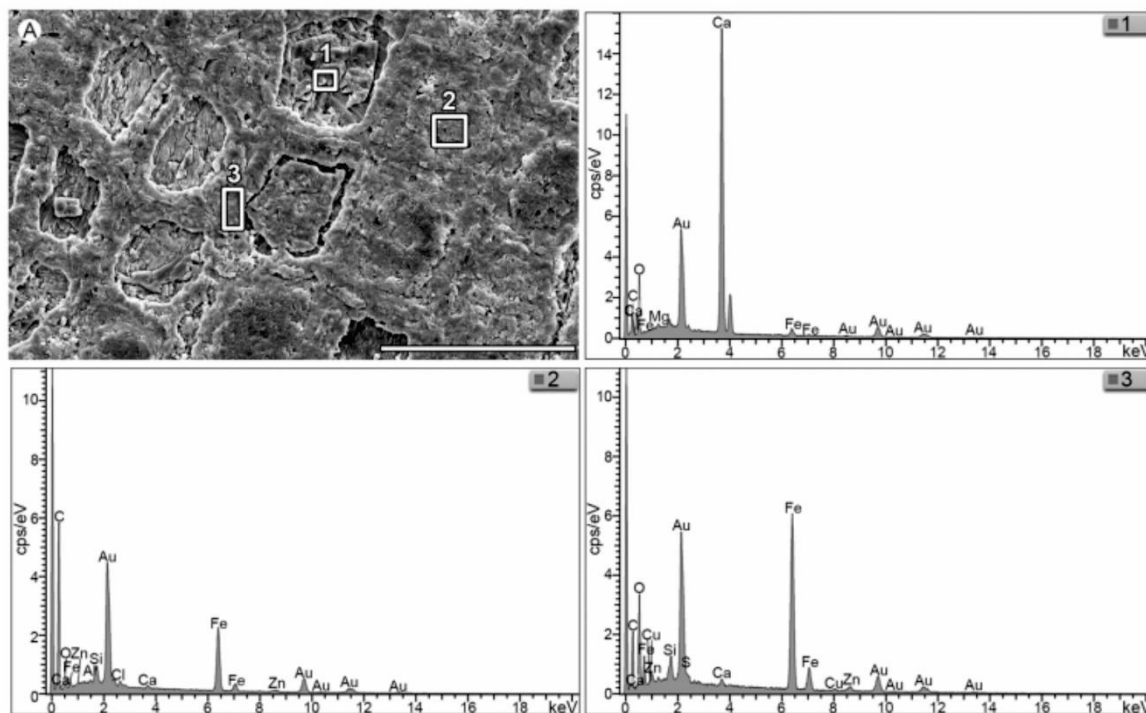
Figura 12- Resultados semiquantitativos de EDS mostrando a composição química das paredes celulares e do lumem celular. (A). Localização das medições realizadas (1 e 3). Barra de escala: 100mm.

6.3.2. Lenho procedente da Formação Maceió (sub-bacia de Alagoas)

O processo de preservação do lenho foi identificado através de análise em blocos polidos sob óleo, usando microscópio de luz incidente equipado com espectrofotômetro e também sob microscopia eletrônica de varredura (MEV) (Fig. 13).

Foram observados diferentes estágios de preservação de tecidos, ocorrendo células com diâmetro original e arquitetura de paredes celulares preservada enquanto que em outras regiões os outros tecidos mostram parede celular parcialmente estruturada atingindo estágios de total obliteração do lumen celular.
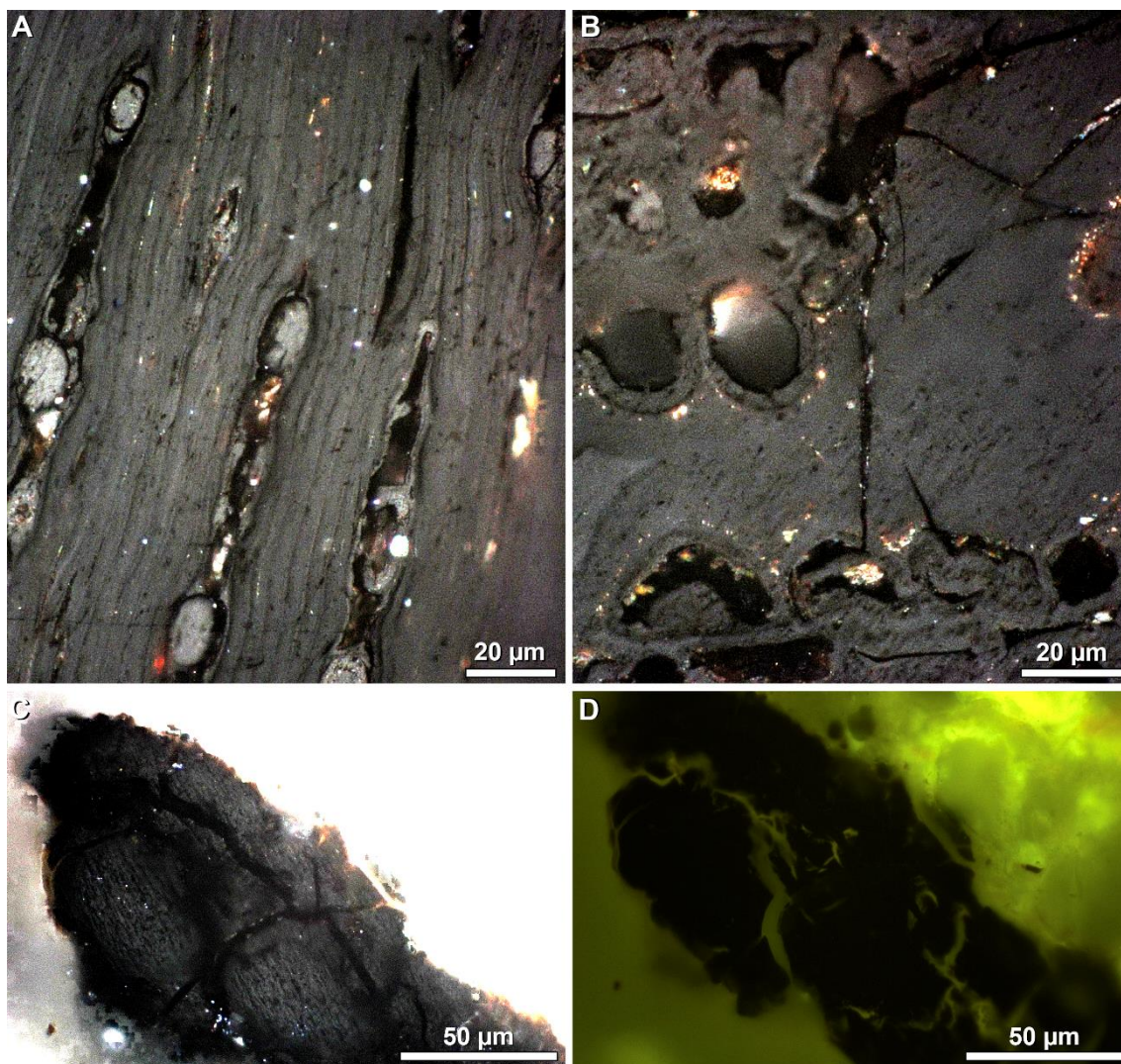
Figura 13. Fotomicrografias de seções polidas de lenho geleificado; (A) Tecido de raio não comprimido; (B) diferentes estágios de xilema comprimido; (C) e (D) lenho altamente comprimido. (A,B,C) iluminação de luz branca incidente; (D) iluminação sob excitação de luz azul incidente (modo fluorescência).

Estas características indicam processo de geleificação do lenho gerando uma transformação bioquímica por ação de microrganismos aeróbicos e anaeróbicos (Bend, 1992).

As análises de petrografia orgânica permitiram identificar macerais e submacerais do Grupo da Huminita no lenho, o que inclui o material em estudo na categoria de lenho geleificado segundo os critérios do ICCP (1971). A refletância média (Ro 0,36%) indica matéria orgânica imatura compatível com estágio de linhito (ICCP, 1971; Alpern & De Souza, 2002; ISO 2005).

A identificação da lamela média distinta nas paredes celulares revelada pela análise em MEV afasta a possibilidade de afinidade com fusinita (charcoal). O

desaparecimento de estrutura da parede celular em algumas áreas do tecido xilemático (Fig. 13) é consequência do processo de geleificação, o que é ratificado pela baixa refletância (Ro = 3,6%).

6.4 Processos de Degradação Fúngica nos Lenhos

No ecossistema terrestre, os fungos estabelecem uma série de interações ecológicas e co-evolutivas com outros organismos como comunidades de saprofíticas, simbiontes, mutualistas, parasitas, e patógenas (Kiers & Denison, 2008; Perotto et al., 2012). As interações planta-fungo ocorrem em vários níveis e afetam as comunidades de plantas e ecossistemas nos quais estão inseridos (Bonfante & Genre, 2008; Krings et al., 2011).

Evidências de interação lenho–fungo foram detectadas em ambos os lenhos estudados procedentes de diferentes bacias sedimentares, no Intervalo Aptiano, e relacionados ao "Cinturão Equatorial Quente e Árido" (Chumakov et al., 1995).

O xilema secundário do lenho procedente da bacia do Araripe apresenta um padrão de degradação celular caracterizado pela dissolução gradativa da lamela média (composta de lignina e pectina) que se intensifica gradativamente, até que traqueídeos adjacentes ocorrem separados uns dos outros. Além disso, algumas paredes celulares aparecem parcialmente deterioradas pela decomposição progressiva de celulose, hemiceluloses e lignina.
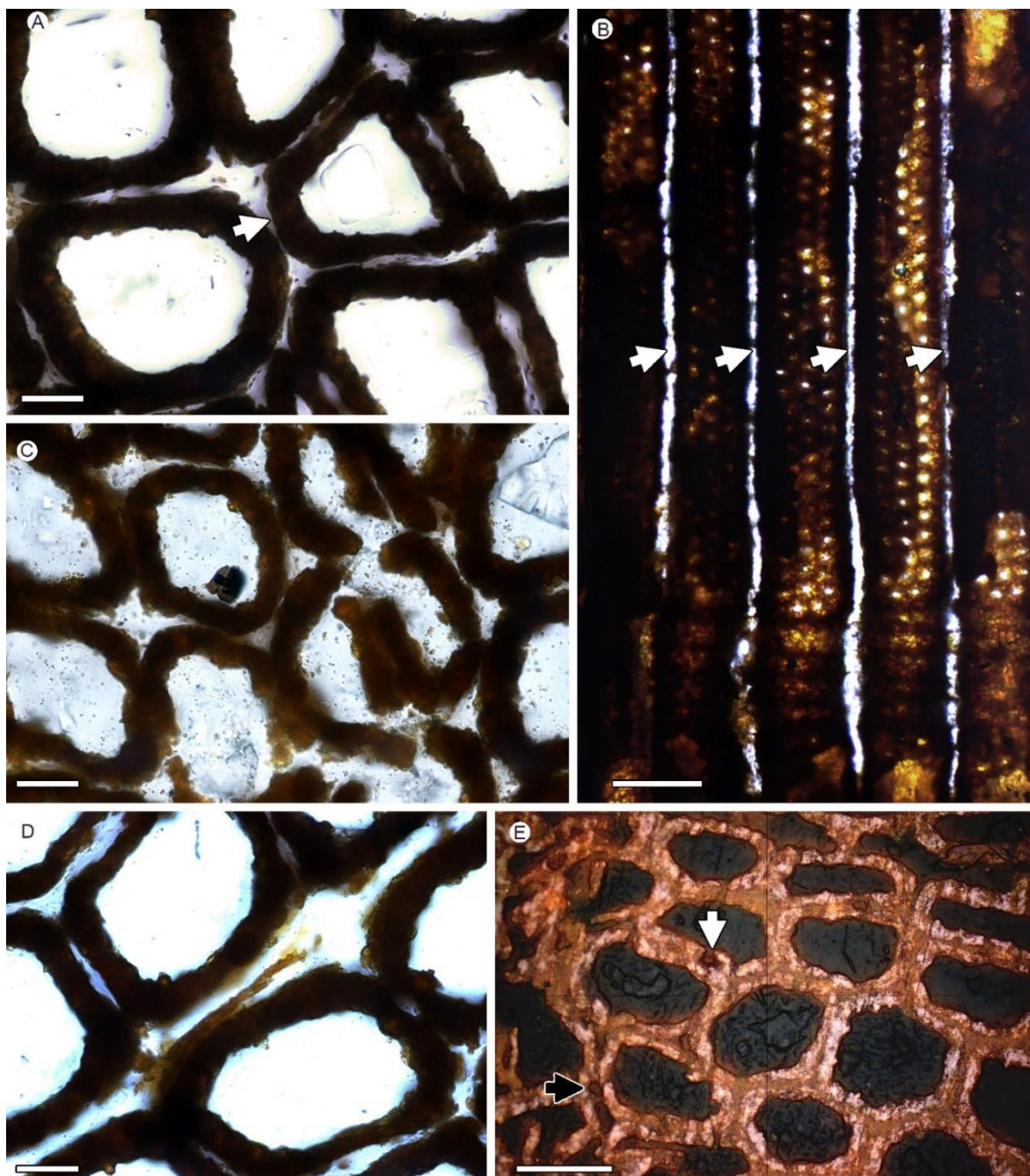
Figura 14. Degradação do xilema secundário em lenho da Formação Santana, Bacia do Araripe. (A) Corte transversal mostrando extensa perda da lamela média entre traqueídeos e deformação celular (setas); (B) Seção radial mostrando a degradação longitudinal contínua da lamela média (setas); (C) Seção transversal mostrando paredes parcialmente degradadas; (D) Células que aparecem como unidades desconectadas; as hifas permanecem no espaço intercelular; (E) Processo de degradação da parede celular secundária (seta branca) lado a lado com evidências de degradação da lamela média (seta preta). Barras de escala: (A, C-D) 20 mm; B, E) 50 mm.
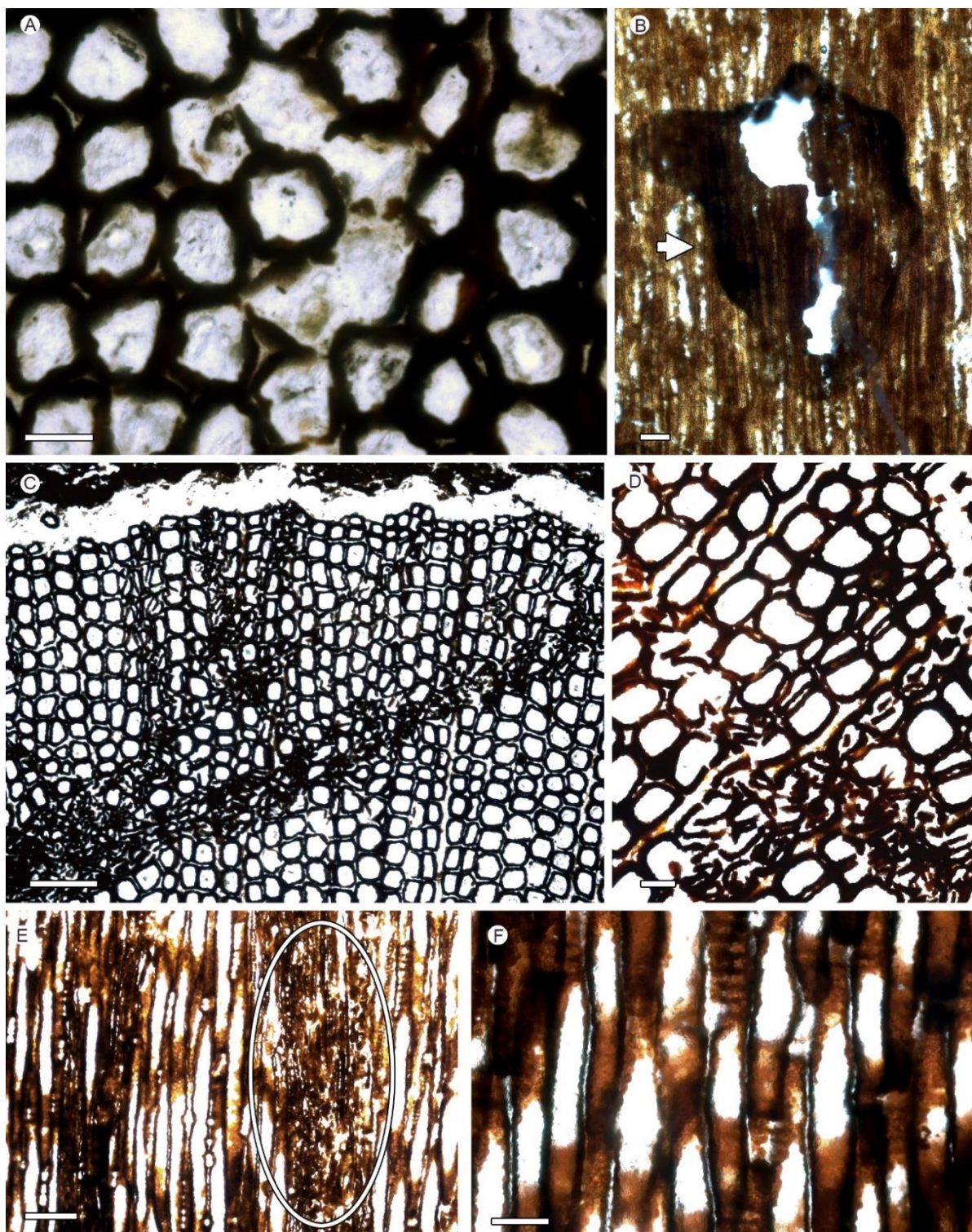
Figura 15. Degradação progressiva no xilema secundário em lenho da Formação Santana, Bacia do Araripe. (A, B) Bolsões pequenos, irregulares, vazios, em seções transversais e longitudinais respectivamente, às vezes circundando por áreas escuras irregulares, provavelmente correspondendo a zona de reação (seta); (C) Faixas degradas alongadas, em seção transversal, com orientação reta e padrão anastomosado. (D-E) Quebra e colapso das paredes celulares dentro das bandas degradadas em seções transversal e tangencial, respectivamente; (F) Células em decomposição em seção longidutinal. Escalas: A,B, D 50mm; C,E 200mm; F)100 mm

Essas características são comuns em padrões de decomposição de lenho causados por Basidiomycophyta, muito raramente Ascomiscophyta e são identificadas como podridão branca de tipo seletiva (Schwarze et al., 1995).

A presença de zonas de reação e zonas de barreira na porção mais externa do xilema indicam que o processo de degradação fúngica iniciou ainda em fase de vida, sendo portanto, ao menos nas fases iniciais do ataque, caracterizado como patogênico.

Restos de fungos são raros, mas presentes nos tecidos do hospedeiro, representados por corpos fúngicos e hifas, não possuíndo características que permitam correlações taxonomicas diagnósticas. Todavia, as evidências indiretas representadas pelo padrão microscópico de ataque levou a definir o envolvimento de Basidiomycophyta como geradores do processo de ataque pelo processo de podridão branca, com base nos critérios de Schwarze et al. (1995).

Já no lenho procedente da Formação Maceió, sub Bacia de Alagoa ocorre a presença de densos micélios de hifas filamentosas, tubulares, septadas. Todavia, não se observa nesse material a intensa degradação da parede celular, típica no lenho da Bacia do Araripe, ocorrendo apenas evidências de degradação insipiente. A ocorrência de caracteristica conexões "clamp" nas hifas (Dennis, 1969, 1970) remete com seguranca para Basidiomycophyta como gupo responsável pela interação. A ausência de zonas de reação e zonas de barreira que fornecem defesa química à invasão fúngica leva a inferir um provável processo de saprofítico como causador da degradação.
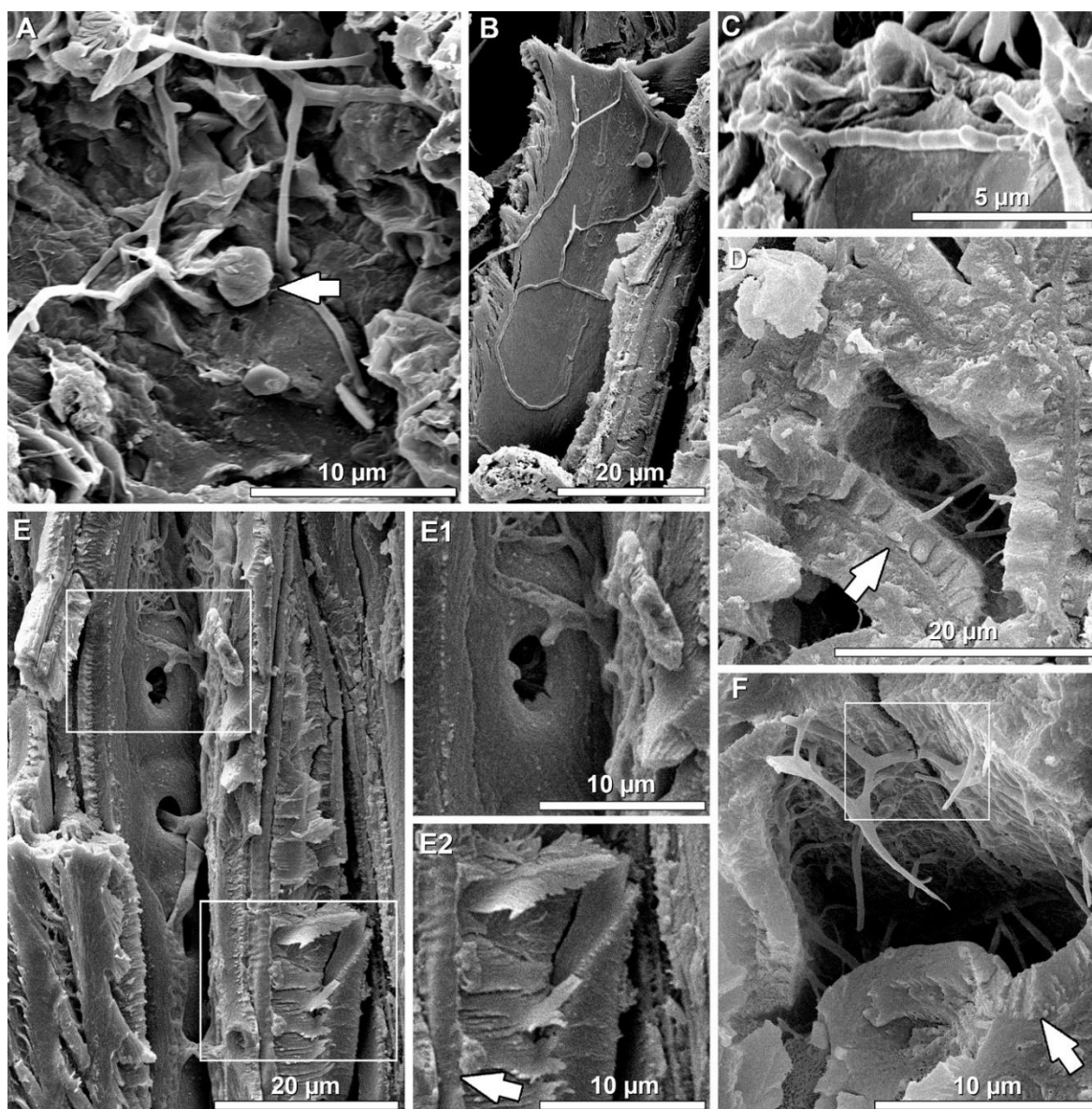
Figura 16. Interação fungo lenho, Formação Maceió, Bacia Sergipe Alagoas. (A) Hifas com formato tubular filamentosas, tridimensionais e não ornamentadas; estruturas esféricas fisicamente conectadas às hifas parentais (seta). (B) Hifas achatadas anexadas diretamente às paredes celulares; (C) Hifas septadas irregularmente; (D), (F) Hifa no lumem do traqueídeo em corte transversal; lamela média (seta); (E), (E1) Penetração da hifa através das pontoações na parede celular (E2) Hifa em parede celular; lamela média (seta).
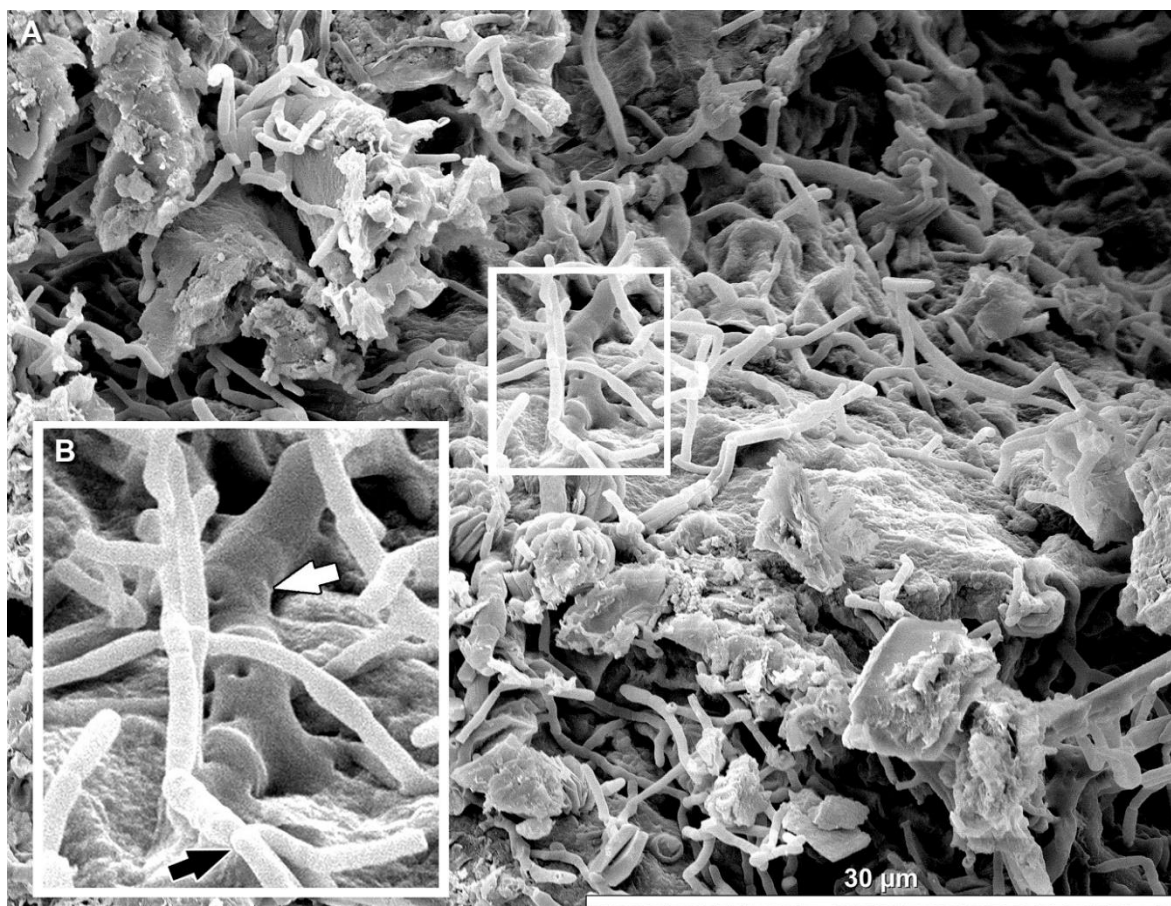
Figura 17. Ataque fúngico em lenho da procedente da Formação Maceió, Bacia Segipe Alagoas. (A) Micélio em bolsões vazios, irregulares no xilema do espécime associados a fragmentos de tecido xilemático deteriorado; (B) Detalhe de A mostrando hifas septadas irregularmente (seta preta) e "conexões de tipo clamp" (seta branca).

Atualmente, os fungos estão amplamente distribuídos em todos os ecossistemas terrestres, mas as relações entre latitude e diversidade indicam que forçantes climáticas impulsionam fortemente processos de degradação fúngica, que é mais marcante em latitudes médias (35° N) (Wang et al., 2019).

O registro de processos de decomposição de lenhos por podridão branca que remontam ao Devoniano, tem sido documentado em diferentes zonas climática desde cinturões tropicais, até temperados e frios (Stubblefield et al., 1985; Krings et al., 2011; Dennis, 1969, 1970; Wan et al., 2017, Barthel, 2010; Wei et al., 2016; Stubblefield & Taylor, 1986; Diéguez & López-Gomez 2005; Wan et al., 2016; Wei et al., 2019; Weaver et al., 1997; Creber & Ash (1992), Gnaedinger et al., 2015; Feng et al., 2015; García-Massini et al., 2012; Sagasti et al., 2019; Tian et al., 2020; Falcon Lang et al., 2001; Pujana et al., 2009).

No presente estudo, ineditamente, os mesmos sintomas de decomposição identificados em paleoclimas com evidência de alguma sazonalidade úmida são

descritos em lenhos incluídos em sistemas deposicionais   incluídos no do "Cinturão Equatorial Quente e Árido" no Aptiano (Chumakov et al., 1995).

Interações fungo–lenho ocorrem, raramente em sistemas áridos atuais (Wicklow, 1981; Zak et al., 1995), onde a baixa umidade e a alta temperatura certamente limitam a atividade fúngica. Todavia, a ocorrência de períodos intermitentes de temperatura e umidade favorável fornece nesses ambientes "janelas de oportunidade" que são cruciais para atividade fúngica (Wicklow, 1981; Zak et al., 1995).

Portanto, as evidências de interação planta-fungo registradas no contexto deposicional das duas bacias analisadas implicam na ocorrência de períodos intermitentes de umidade suficientes para o desenvolvimento dessas interacões durante a vigência do Cinturão Equatorial Quente e Árido no Aptiano, de acordo com Chumakov et al. (1995).

A possibilidade de interação fungo-lenho pós deposicional fica totalmente excluída, dadas características de contemporaneidade entre hifas e estruturas da arquitetura celular. Adicionalmente, os ácidos húmicos gerados no processo de transformação química da lignina e celulose certamente não apresentam especificidade química para se constituírem alimento para os fungos do grupo dos Basidiomycophyta que tem como fonte de energia compostos celulósicos e lignina.

6.5 Análises em sedimentos associados

Além das análises desenvolvidas no próprio lenho, foram efetuadas, também análises geoquímicas nos sedimentos que envolviam o lenho procedente do Afloramento Morro do Camaragibe (Formação Maceió) com objetivo de contextualizar a ocorrência de lenho em alguma das fases do sistema turbidítico definido para esse afloramento (Almeida et al., 2017).

Dessa forma, resultados de análises de palinofácies nos pacotes sedimentares sotopostos e sobrepostos ao lenho revelaram, pela dominância de fitoclastos não opacos e cutículas (25 a 100% da matéria organica particulada) e ausência de elementos aquáticos de água doce ou marinhos indicam sedimentação compatível com depósitos de configurações distais de canal. Essa interpretação está de acordo com a de Almeida et al. (2017) que considerou a

deposição do domínio central do afloramento Morro do Camaragibe (de onde procede o lenho) como parte das porções predominantemente fluvio- deltaicas do sistema, mais próximas da área fonte.
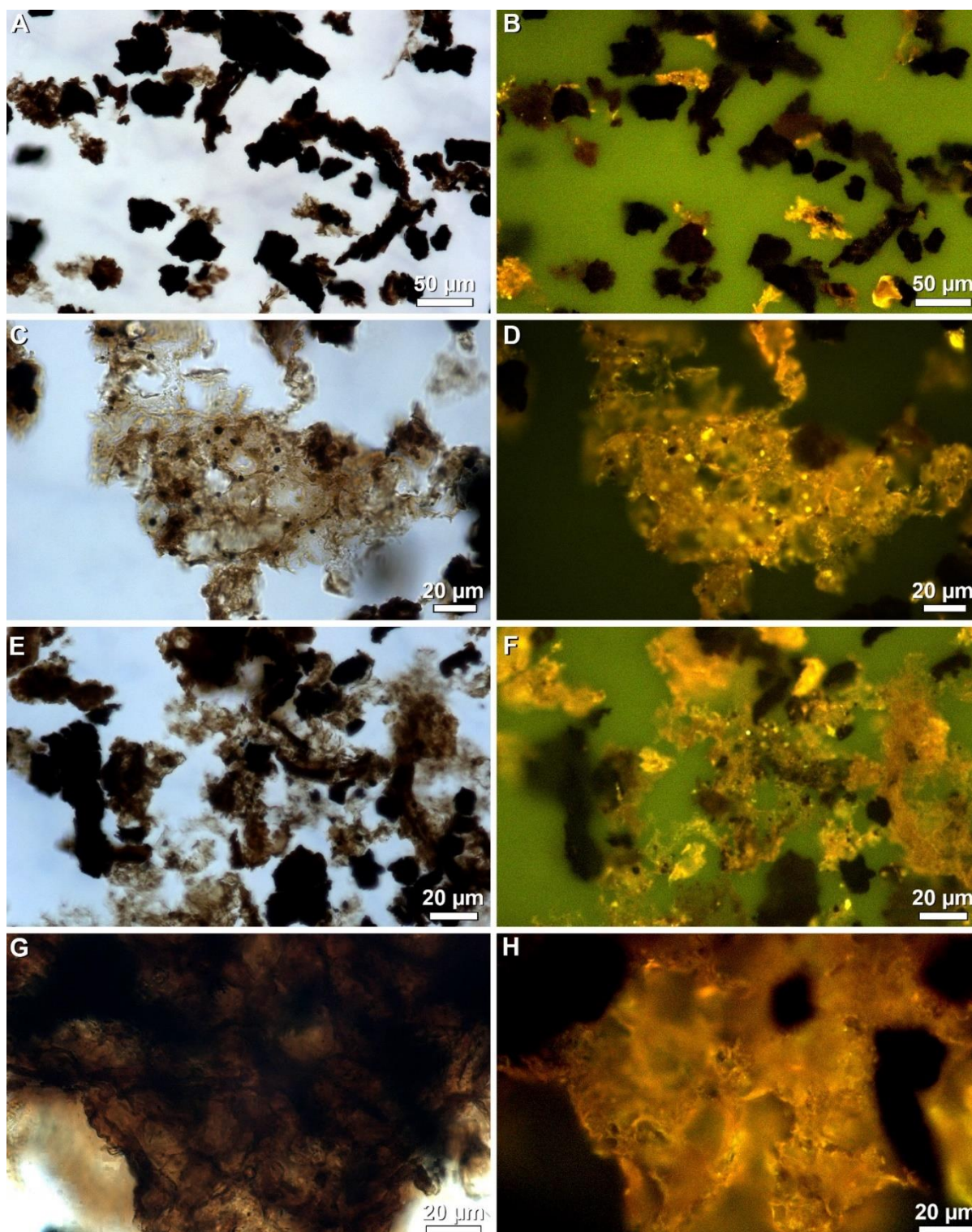
Figura 18. (A), (B) Fitoclastos não opacos. (C), (D) Cutícula. (E), (F) Fitoclastos não opacos e cutícula. (G), (H) Cutícula. (A), (C), (E) e (G) luz branca transmitida; (B), (D), (F) e (H) sob exitação por luz incidente azul (modo fluerecência).

A ocorrência de grãos de pólens do gênero *Cedripites* (Wodehouse) cuja afinidade botânica tem sido relacionada a Pinacea (Grímsson and Zetter, 2011) em sedimentos da Formação Maceió comprova que esse grupo de coníferas era elemento comum nas associações vegetais em áreas continentais marginais no intervalo de sedimentação Aptiano (Fig. 19).
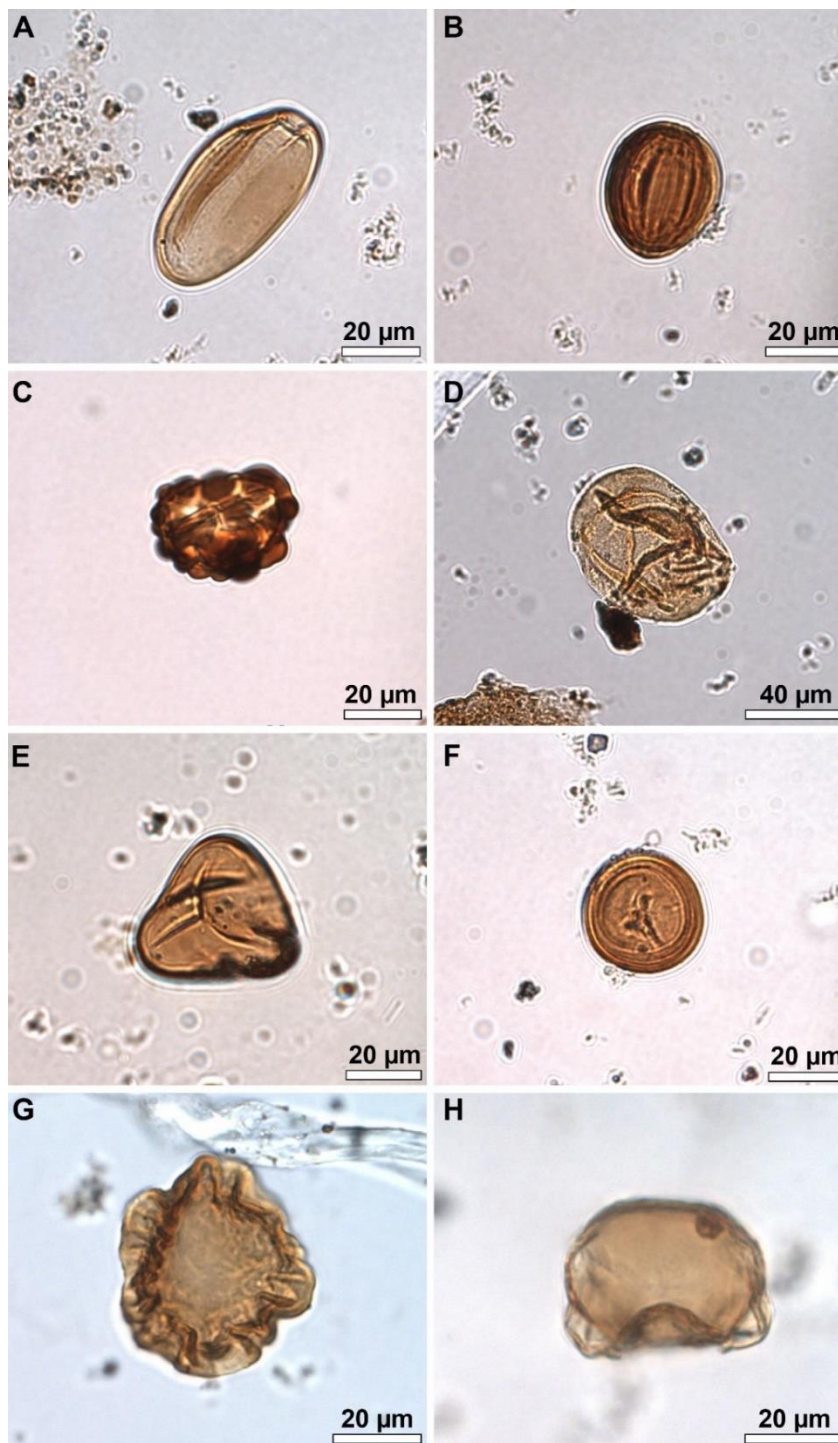
Figura 19. Palinomorfos de fácies da Formação Maceió, Sergipe Alagoas (A) *Cycadopites* sp. (D11); (B) *Equisetosisporites* sp. (M15-3); (C) *Leptolepidites psarosus* (O42); (D) *Araucariacites australis* (K22); (E). *Deltoidospora hallii* (R16-4);

(F). *Classopollis classoides* (R21-2); (G) *Callialasporites segmentatus* (V-4); (H) *Cedripites* sp. (H-5).

Os resultados obtidos em análises de biomarcadores aromáticos no lenho e nos sedimentos associados revelou a presença de perileno. Evidências indiretas de sedimentos e óleos do Holoceno apoiam a hipótese de que há uma forte relação entre esse marcador e a atividade de fungos degradadores de lenho (Suzuki et al., 2010).

Além disso, evidências diretas de sedimentos de lagos modernos indicam que o perileno se origina principalmente do DHPQ *Cenococcumgeophilum,* que corresponde a um esclerócio fúngico (Itoh et al. 2012). Esses resultados contradizem a hipótese anterior de Silimann et al. (1998) que consideraram o perileno como um indicador das condições de deposição, ao invés da fonte de matéria orgânica.

7. CONCLUSÕES

A integração dos resultados do presente estudo, que envolveu análises em lenhos fósseis gimnospérmicos procedentes do intervalo Aptiano em diferentes bacias sedimentares brasileiras, bem como de faciologias sedimentares a e eles relacionadas, leva a concluir que:

- A identificação de padrões anatômicos detalhados em lenhos é indispensável à determinação de afinidades sistemáticas as quais, consequentemente, são fundamentais a estudos que pretendam estabelecer padrões de provincialismo de associações vegetais e consequentes correlações paleobiogeográficas, paleoclimáticas e paleoambientais no Mesozoico, mais especificamente no intervalo Jurássico–Cretáceo, relacionado às fases de pré-ruptura, ruptura e pós-ruptura do continente Gondwana.

- A presença do gênero *Agathoxylon,* definido com base em padrão morfométricos de xilema e a ocorrência de canais axiais no floema colapsado, além de características de uma folha aderida, mostrando um padrão de venação paralela e estômatos orientados longitudinalmente, são

características que remetem para afinidade botânica com a família Araucariaceae

- A ocorrência de *Agathoxylon* com afinidade a padrões araucarianos no Cinturão Equatorial Quente e Árido, gênero também comum nos cinturões subtropicais e temperados frios contemporâneos no Gondwana Ocidental, indica que coníferas com afinidade à araucariaceae não eram climaticamente controladas no Aptiano.

- As assinaturas de padrões de crescimento em *Agathoxylon santanensis* nov sp indicaram zonas de interrupção causadas por estresse hídrico, implicando em períodos intermitentes de seca sob um clima megatérmico.

- O processo de preservação identificado como geleificação no lenho proveniente da Formação Maceió (Bacia de Sergipe-Alagoas), apesar de gerar alterações na arquitetura celular em alguns tecidos, preservou também tecidos não comprimidos que permitiram a caracterização anatômica diagnóstica da família Pinaceae.

- As características anatômicas diagnósticas para inclusão do lenho procedente da Formação Maceió correspondem à ocorrência de pontoações areoladas dominantemente unisseriadas nos traqueídeos, e pontoações piceoides nos campos de cruzamento, associadas à ocorrência de canais fisiológicos intercelulares com orientação axial, isolados ou em grupos de dois canais, e canais com orientação radial inclusos em raios lenhosos unisseriados. Esses canais apresentam como característica comum a presença de bainha formada por células epiteliais.

- O registro de Pinaceae, até agora inédito, proveniente do Aptiano bacia de Sergipe Alagoas, sub bacia Alagoas, e a ocorrência de pólens dispersos atribuídos a Pinaceae em sedimentos associados (*Cedripites sp.*) suportam algumas inferências no contexto de fragmentação do Gondwana. Os novos dados levam a inferência de que esse grupo de coníferas, muito concentrado no Hemisfério Norte, teria se irradiado durante o Cretáceo Inferior de

extensões de terra da Província Ibérica para áreas continentais da região Periequatorial do Gondwana, hoje correspondentes ao norte do continente Africano e nordeste do Brasil.

- Análises de palinofácies em sedimentos da Formação Maceió (Bacia de Sergipe-Alagoas, sub bacia de Alagoas) nos quais o lenho de Pinaceae estava incluído, que definiram a dominância fitoclastos não opacos e cutículas, além da baixa contribuição de esporomorfos terrestres, e ausência de microplâncton aquático, sugerem deposição em fácies distais de canal em um complexo fluviodeltaico, dentro de amplo sistema turbidítico

- As evidências de interação planta-fungo mostram que coníferas afins a Araucariaceae e Pinaceae foram hospedeiras disponíveis para interações lenho-Basidiomycota no Aptiano. Adicionalmente, essas interações comprovam a importância dos fungos em diferentes processos de transformação da matéria orgânica ao longo do tempo geológico. Essas evidências, adicionalmente, implicam na ocorrência de períodos intermitentes de umidade durante a vigência do Cinturão Equatorial Quente e Árido os quais impulsionaram a regulação da disponibilidade hídrica em ambientes aeróbios.

- A preservação de perileno no lenho de Pinaceae procedente da Formação Maceió e também nos sedimentos associados, ratifica inferências de uma asssociação desse marcador químico com a atividade de fungos em processos de degradação do lenho.

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CAPÍTULO II: artigos científicos

CORPO PRINCIPAL DA TESE

Nesta seção são apresentados os artigos científicos publicados e submetidos em periódicos, com os resultados obtidos para a realização da Tese. Este capítulo foi incluído de forma integral, da maneira em que os artigos foram enviados às revistas, seguindo as normas de formatação de cada revista. Portanto, a numeração das figuras e tabelas estão restritas a cada periódico.

Artigo 1

Fungus–plant interactions in Aptian Tropical Equatorial Hot arid belt: White rot in araucarian wood from Crato fossil Lagerstätte (Araripe Basin, Brazil)

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Abstract
For the first time, this study describes the dynamics of white rot fungal decay in a petrified conifer branch with clear araucarian affinity from the late Aptian Crato Lagerstätte (Santana Formation, Araripe Basin, northeastern Brazil). High

resolution optical microscopy was used to identify tridimensional chemical and anatomical evidence in different regions of the bark and xylem tissues of permineralized shoots, and results support the hypothesis that the host responded to disease that may have started when it was still alive. The wood decay pattern was strongly indicative of the selective decay by white rot. The general pattern of interaction is consistent with pathogenic rather than saprophytic fungal activity. Analysis of fungus–plant interactions associated with growth ring patterns imply intermittent periods of favorable temperature-moisture inputs that were crucial for fungal activity during the deposition of the Crato fossil Lagerstätte included in the Tropical Equatorial Hot arid belt.

1. INTRODUCTION

It is currently known that the macroflora of the late Aptian Lagerstätte of the Crato Member (Araripe Basin, northeastern Brazil) consisted of angiosperms (32%), conifers (30%), gnetaleans (19%), and lycophytes, sphenophytes, filicophytes, pteridosperms, bennettitaleans, and gymnosperms *incertae sedis* (19%) (Table 1, updated from Bernardes-de-Oliveira et al., 2014). The conifers described to date from laminated carbonates deposited in the Crato paleolake that lay within the Tropical Equatorial Hot arid belt (Chumakov et al., 1995) belonged to the families Cheirolepidiaceae and Araucariaceae. Many plant taxa from the Crato Lagerstätte adapted to the dry paleoenvironmental conditions and unfavorably dry climate in the Tropical Equatorial Hot arid belt, as evidenced by sunken stomata, increased cuticle and epidermis thicknesses, and the development of papillae and hairs (Dilcher et al., 2005; Feild et al., 2004; Mohr et al., 2006, 2007).

Table 1. Macrofloral biodiversity of the Crato Lagerstätte (updated from Bernardes-de-Oliveira et al., 2014).

Name	References
Lycophytes	
Isoetes	Bernardes-de-Oliveira, et al., 2003
Sphenophytes	
Schizoneura	Dilcher et al., 2000
Filicophytes	
Ruffordia goeppertii	Mohr et al., 2015
Pteridospermales	
Caytoniales	Fanton et al., 2007
Bennettiales	
Ptilophyllum	Duarte, 1985
Coniferales	
Duartenia araripensis	Mohr et al., 2012
Pseudofrenelopsis capillata	Sucerquia et al., 2015
Tomaxellia biforme	Kunzmann, et al., 2006
Araucaria sp.	Kunzmann et al., 2004
Araucarites/Araucaria cartellei e *A. imponens* (Sec. Columbea)	Duarte 1993; Sucerquia, 2006
Araucariostrobus sp.	Kunzmann et al., 2004
Brachyphyllum obesum	Duarte, 1985; Kunzmann et al., 2004; Batista et al., 2017
Lindleycladus sp.	Kunzmann et al., 2004
Gnetales	
Cratonia cotyledon	Rydin et al., 2003
Priscowelwitschia austroamericana	Dilcher et al., 2005
Welwitschiophyllum brasiliense	Dilcher et al., 2005
Welwitschiostrobus murili	Dilcher et al., 2005
Ephedra paleoamericana	Kerkhoff and Dutra, 2007
Cearania heterophylla	Kunzmann et al., 2009
Cariria orbiculiconiformes	Kunzmann et al., 2011
Itajuba yansanae	Ricardi-Branco et al., 2013
Friedsellowia gracilifolia	Löwe et al., 2013
***Incertae sedis* gymnosperms**	
Novaolinda dubia	Kunzmann et al., 2007
Angiosperms	
Jaguariba wiersemana	Coiffard et al., 2013
Pluricarpellatia peltata	Mohr et al., 2008
Klitzschophyllites flabellatus	Mohr and Rydin, 2002; Mohr et al., 2006
Endressinia brasiliana	Mohr and Bernardes-de-Oliveira, 2004
Schenkeriphyllum glanduliferum	Mohr et al., 2013
Araripia florifera	Mohr and Eklund, 2003
Iara iguassu	Fanton et al., 2007
Hexagyne philippiana	Coiffard et al., 2014
Cratolirion bognerianum	Coiffard et al., 2019
Cratosmilax jacksoni	Lima et al., 2014
Spixiarum kipea	Coiffard et al., 2014

The main goal of the present study is to fill gaps in the knowledge of plant–fungus interaction in the late Aptian Tropical Equatorial Hot arid belt. The working hypothesis of the present study is based on a sample of petrified conifer wood that shows evidence of fungal decay. Although it is assumed that the wood was derived from a hot arid environment, the paleoclimatic context of the white rot decay record from the Late Devonian to the Eocene (Table 2) comprised at least sporadic phases of humidity. Anatomical analysis of the well-preserved specimen that was complete with pith, secondary xylem, and bark, enabled taxonomic identification and observations of the three-dimensional development of degradation patterns and chemical and anatomical responses of the host wood to the disease. This provides advantages over previous studies based on gymnosperms woods, where it was not possible to determine the original extent of the fungal infection, mainly due to the incompleteness of the specimens due to fossil fragmentation from taphonomic processes (Falcon-Lang et al., 2001; García-Massini et al., 2012; Gnaedinger et al., 2015; Pujana et al., 2009; Sagasti et al., 2019; Wan et al., 2016).

Table 2. Indirect and direct records of white rot decay in woods from the Devonian to the Eocene.

Interval	Evidence		Climatic zones (Scotese, 2011; 2014)	References
	Direct	Indirect		
Late Devonian	x	x	Warm/arid	Stubblefield et al., 1985
Mississipian	x		Tropical	Krings et al., 2011
Middle Pensilvanian	x		Tropical	Dennis, 1969, 1970
Early Permian	x	x	Tropical	Wan et al., 2017
	x	x	Tropical	Barthel, 2010
Middle – late Permian	x		Cool Temperate	Wei et al., 2016
Late Permian	x	x	Cool Temperate	Stubblefield and Taylor, 1986
		x	Warm	Diéguez and López-Gomez, 2005
	x	x	Cool Temperate	Wan et al., 2016
		x	Cool Temperate	Wei et al., 2019
	x	x	Cold	Weaver et al., 1997
Early Triassic		x	Warm	Stubblefield and Taylor, 1986
Late Triassic		x	Tropical	Creber and Ash, 1990
Early Jurassic	x	x	Warm Temperate	Gnaedinger et al., 2015
Middle Jurassic	x	x	Warm	Feng et al., 2015
	x	x	Warm	García-Massini et al., 2012
Middle/Late Jurassic			Warm	Sagasti et al., 2019
Early Cretaceous	x	x	Boreal Tropical	Tian et al., 2020
Mid-Cretaceous		x	Cool	Falcon Lang et al., 2001
Late Eocene		x	Warm	Pujana et al., 2009
Early Cretaceous	x	x	Arid	This paper

2. GEOLOGICAL SYNTHESIS

The Araripe Basin (Fig. 1) is a hinterland basin covering an area of 12,200 km² that originated during a Berriasian-Hauterivian tectonic phase connected with the first stages of South America and Africa rifting (Carvalho, 2000; Matos, 1992). Situated above a major unconformity representing a significant hiatus, the post-rift stage of the Araripe Basin is represented by deposits of the Araripe Group that cover the late Aptian to the early Albian (Coimbra et al., 2003). According to Assine (2007), low subsidence during this stage resulted in the deposition of deltaic to lacustrine sediments (Rio das Batateiras Formation and Crato Member, Santana Formation), followed by evaporites (Santana Formation, Ipubi Member) and marginal marine shales (Romualdo Member of Santana Formation and Arajara Formation).
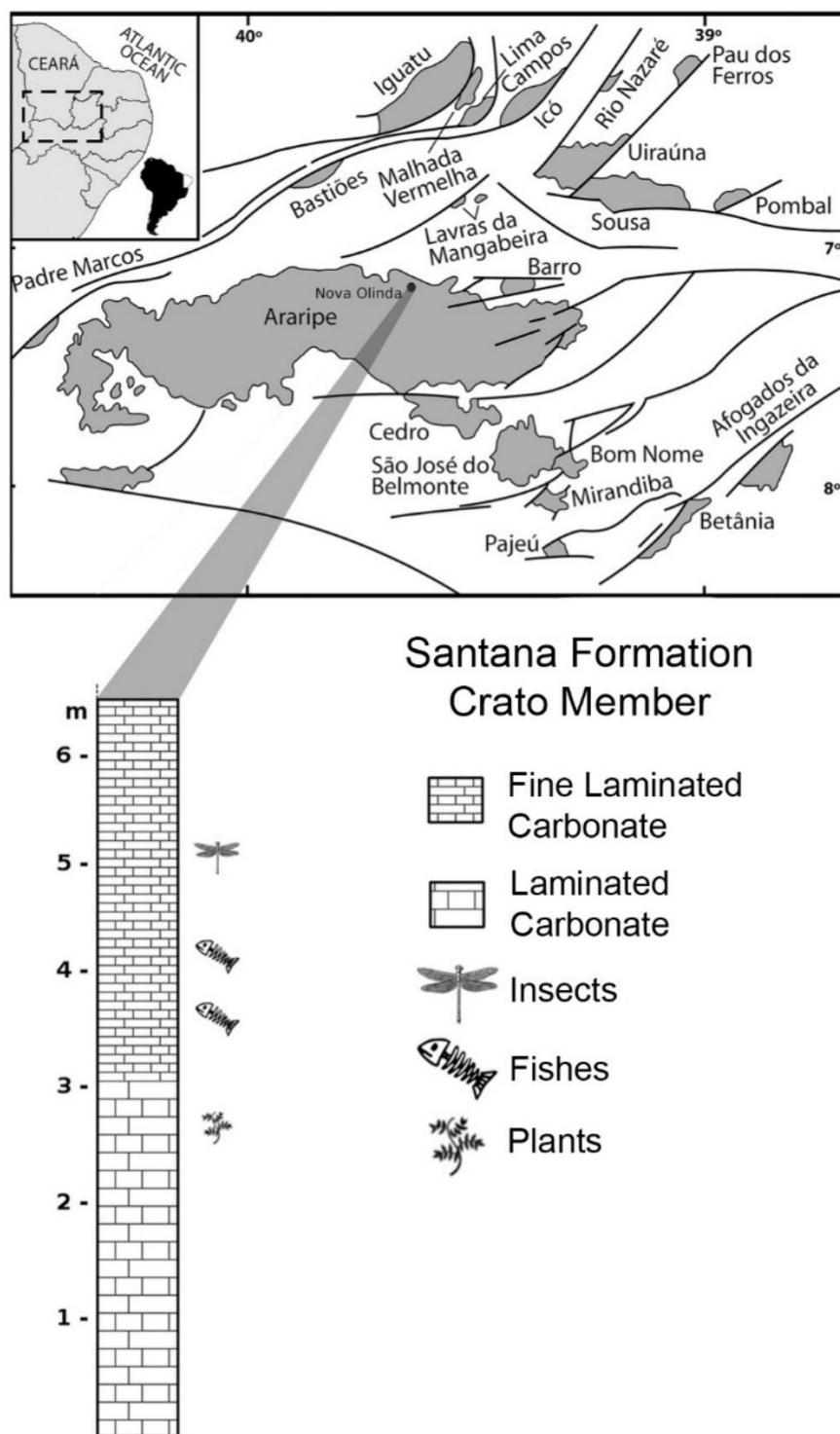
Figure 1. Location map of the Araripe Basin in the context of the Cretaceous Brazilian Northeastern intracratonic basins and stratigraphic profile of the collection site. Pedra Branca Mine, Nova Olinda County, Brazil (Carvalho et al., 2019).

Based on the widespread occurrence of evaporites along the evolving South Atlantic rift system, the absence of coal deposits, and the dominance of drought-resistant, xerophytic vegetation (Mohr et al., 2007; Ziegler et al., 2003), it is assumed that semi-arid to arid climatic conditions predominated during the deposition of the Araripe Basin, which was situated within the Tropical Equatorial Hot arid belt of

Chumakov et al., (1995) in late Early Cretaceous times. Scherer et al. (2015) integrated sedimentological and paleoclimatic data in the Aptian succession of the Araripe Basin that point to the existence of consistently high temperatures, albeit with variable humidity. Sedimentological evidence indicates that, despite variations in the oxygenation degrees of the lakes, the climate was relatively humid or sub humid, and that no major climatic changes occurred during deposition of the basal sequences. Furthermore, Goldberg et al. (2019) determined that the strong marine influence was already established during the deposition of the Ipubi layers (sensu Assine, 2007).

The Santana Formation (sensu Ponte and Appi, 1990) is a 60 m thick succession of fine laminated carbonates interlayered with green shales and fine-to-coarse sandstones. The lowermost Crato Member, which is the focus of this study, hosts the Crato fossil Lagerstätte. Soft tissues, color patterns, and fine details of plants, invertebrates, and vertebrates are preserved within the carbonatic succession (Carvalho, I.S. et al., 2019; Grimaldi, 1990; Martill and Bechly, 2007; Naish, 2007; Pinheiro et al., 2012), and a late Aptian age (119–113 Ma) can be inferred for this interval from palynological data (Rios-Netto et al., 2012).

Heimhofer and Hochuli (2010) inferred that the bulk of limestone from the Crato Member was formed via the authigenic precipitation of calcite. Microfacies analysis (Catto et al., 2016) indicated that the limestones were genetically associated with lacustrine systems in a negative hydric balance. Neumann et al. (2003) and Martill and Bechly (2007) considered that hypersaline lakes with low oxygen concentrations would have developed under low energy and shallow waters that are associated with high evaporation. However, the influence of marine waters (with strongly fluctuating salinities) has clearly been demonstrated for other stratigraphic units of the basin.

3. MATERIAL AND METHODS

The specimen analyzed in this study is petrified wood that is likely a secondary branch (length 395 mm; mean diameter 21 mm). While removing it from the carbonate sediment, it broke into seven fragments. In general, the solidity of the wood is intact, preservation of the wood is generally good, and the anatomical features are clearly observable. The specimen is housed in the paleontological collection of the Departamento de Geologia, Instituto de Geociências, Universidade

Federal do Rio de Janeiro under the acronym 2443Pb, and thin sections are stored under the codes 2443Pb-1 to 35.

3.1 Fossil preparation and observation

Successive transverse (7 slides), radial (14 slides), and tangential sections (14 slides) were taken from seven different fragments of the single branch to observe the anatomical structure and three-dimensional development of degradation. Successive descriptions of the fungus decay spectrum were made along the entire wood sample from the periphery of the bark to the outer, central, and innermost secondary xylem of the sample (Fig. 2). Since the branch was narrow, every single slide comprised all tissues from border to border. The methodology adopted was similar to that used by Harper et al. (2018) for a pteridophyte stem but considering the peculiarities of fungal pathogenic attack in a gymnospermous wood.
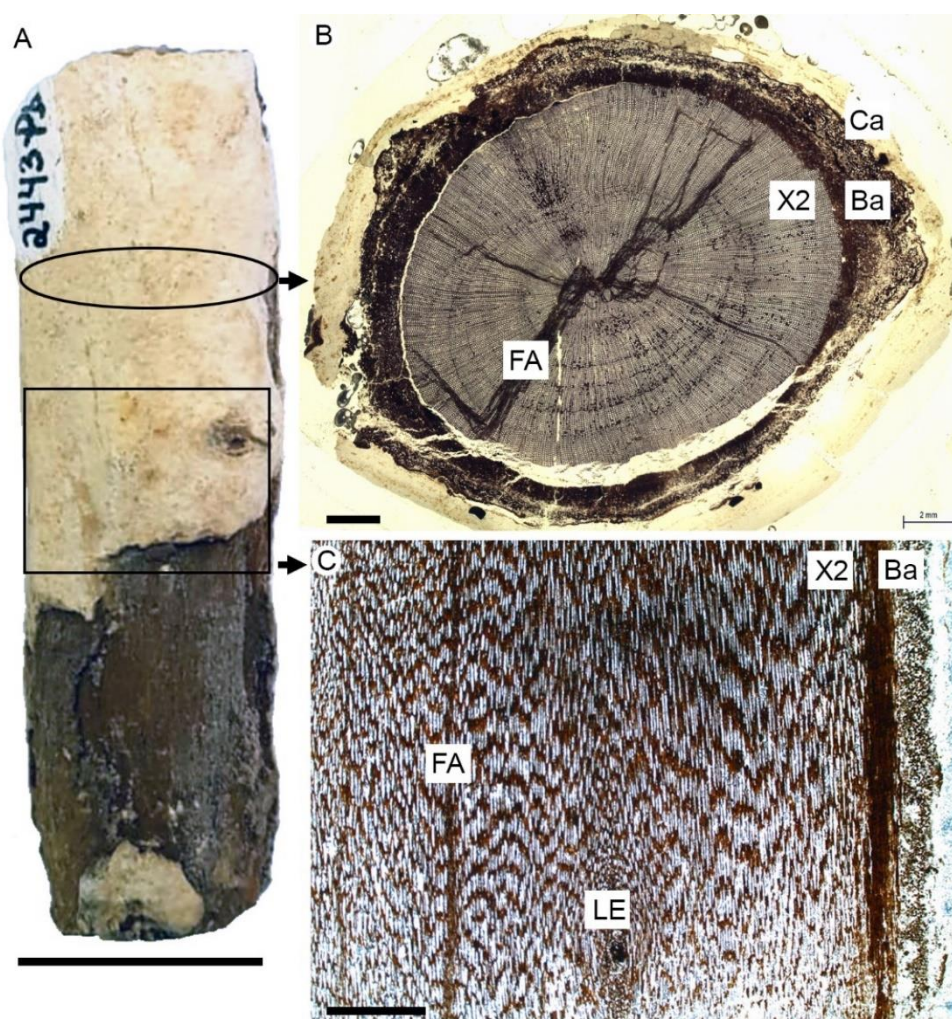
Figure 2. Schematic illustration of the sections made from the seven branch fragments (specimen 2443-Pb). A) Branch fragment; B) cross section; C) longitudinal section. Ba: bark; Ca: carbonate layer; FA: fungal attack; LE: leaf emergence; X2: secondary xylem. Scale bars: A) 2 cm; B, C) 2 mm. For more details see Material and Methods section.

Polished and uncoated thin sections (40 μm thick) were produced from material that was highly mineralized by iron minerals, which frequently impaired observations of anatomical details. Epoxy resin was used as an embedding and mounting medium. The sections were polished using 0.05 mm aluminum oxide powder.

An anatomical analysis was conducted under transmitted and reflected light microscopy. However, attempts were made to observe the anatomy of the wood under scanning electron microscopy (SEM) following standard techniques, but these were unsuccessful.

The thin sections were examined and pictures were taken with a Leica S8 APO stereoscopic microscope with a mounted camera, a Zeiss AxioScope A1 transmitted light microscope with an AxioCam MRc camera (located at UFRGS), and a Zeiss AxioScope 2 Plus reflected light microscope equipped with a spectrophotometer J&M (MSP 200) through a 50x objective lens (located at UFRJ).

The images were analyzed, and measurements were taken using Zeiss Axio Vision4.8.1 software. Plates were composed using Adobe Photoshop CS3 Extended. Transformations were made to the images using cropping, rotation, contrast adjustments, focus stacking, and image composition. The terminology used to provide anatomical details of the wood followed the recommendations of Richter et al. (2004).

The elemental composition of cell walls and infillings of cell lumina were analyzed using an energy dispersive spectroscopy (EDS) detector coupled to an Inspect F50 FEI SEM located at the Centro de Microscopia e Microanálises IDEIA at Pontifícia Universidade Católica do Rio Grande do Sul, and employing the same slides as those used to conduct anatomical analyses (which had been gold-coated to conduct the unsuccessful SEM observations).

4. RESULTS AND DISCUSSION

4.1 Wood petrification process

Elemental EDS analysis indicates that the wood petrifaction process involved partial degradation of organic components and mineralization by dominant iron minerals (Fe), oxygen (O), besides carbon (C) in the cell walls and in massive dark areas of the sample, whereas the mineralization of anatomical voids corresponding to cell lumina mainly occurred with respect to crystal-shaped calcium (Ca) (Fig. 3). Therefore, wood fossilization resulted from a combination of permineralization and replacement processes.
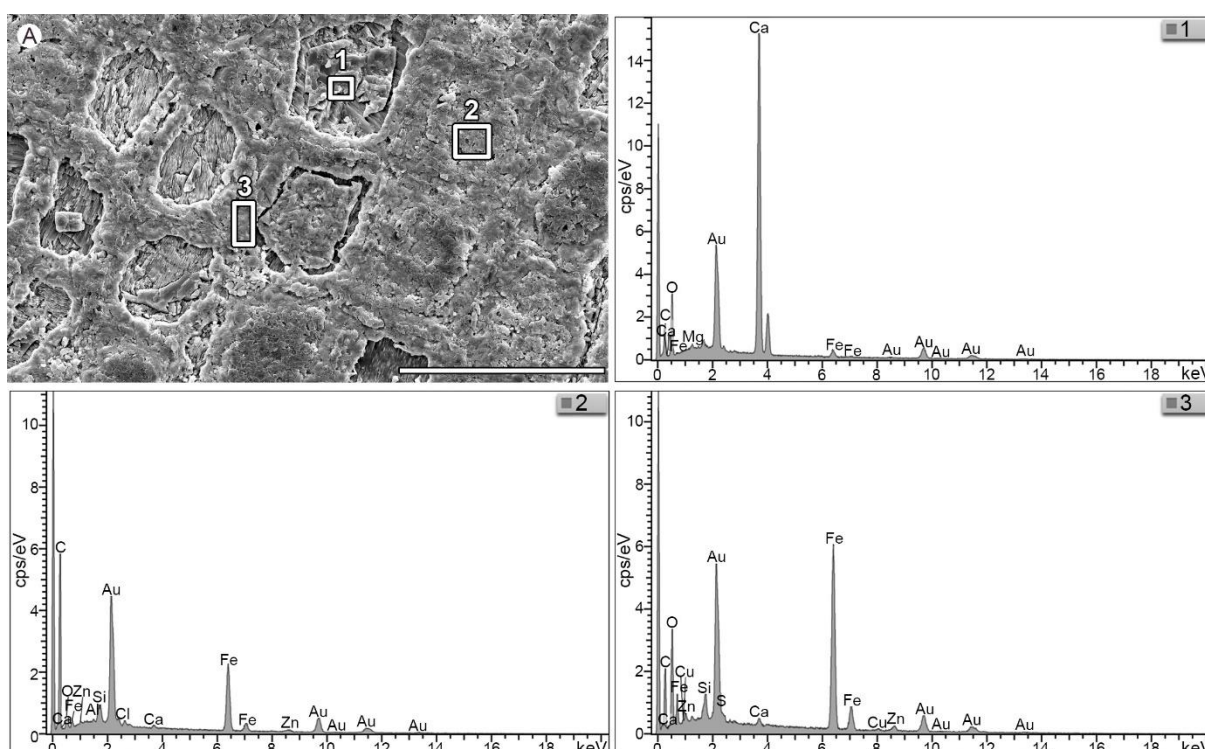
Figure 3. EDS semi-quantitative results showing chemical composition of cell walls and cell lumen (specimen 2443-Pb). A) Location of performed measurements (1 to 3). Scale bar: 100 µm.

4.2 Main anatomical wood patterns: systematic, climatic, and ecological constrains

The specimen is a piece of gymnospermous wood (ca. 21 mm in diameter) composed of a very small pith with irregular boundaries surrounded by a massive homogeneous secondary xylem (up to 16 mm wide). The wood tissue is surrounded by poorly preserved bark (2 mm wide). Given the diagnostic features (the presence

of compression wood, leaf traces, and a leaf organically connected to the axis), the specimen is determined to be a branch (Fig. 4).

The small, heterogeneous pith (ca. 0.5 mm in diameter) is composed of rounded or polygonal parenchymatous cells in cross-section and dispersed sclerenchymatous clusters. The thick zone of the secondary xylem shows a typical gymnospermous pycnoxylic pattern and is composed of elongated tracheids and transverse parenchyma rays. In cross-section, the tracheid outline is square to polygonal and ca. 70 μm in diameter (9 μm mean wall thickness). The tracheids are arranged in regular rows and are limited by elongated, rectangular, parenchymatous ray cells with thin walls (3 μm) that show a uniseriate disposition.

Four to five growth rings with variable widths (680 to 948 μm) are observed in the transversal mesoscopic view of the seven fragments from the single specimen. These are seen to be uneven under higher magnification, and they are characterized by a very low proportion of latewood composed of only one or two tracheids with reduced radial diameters and no significant increases in wall thickness. These factors associated with high ring width variability imply stressful growing conditions (Fig. 4A, B). In addition, the subtle discontinuous ring boundaries of some of the growth rings (Fig. 4B) indicate that they were formed during a short-term reduction in cambial activity.
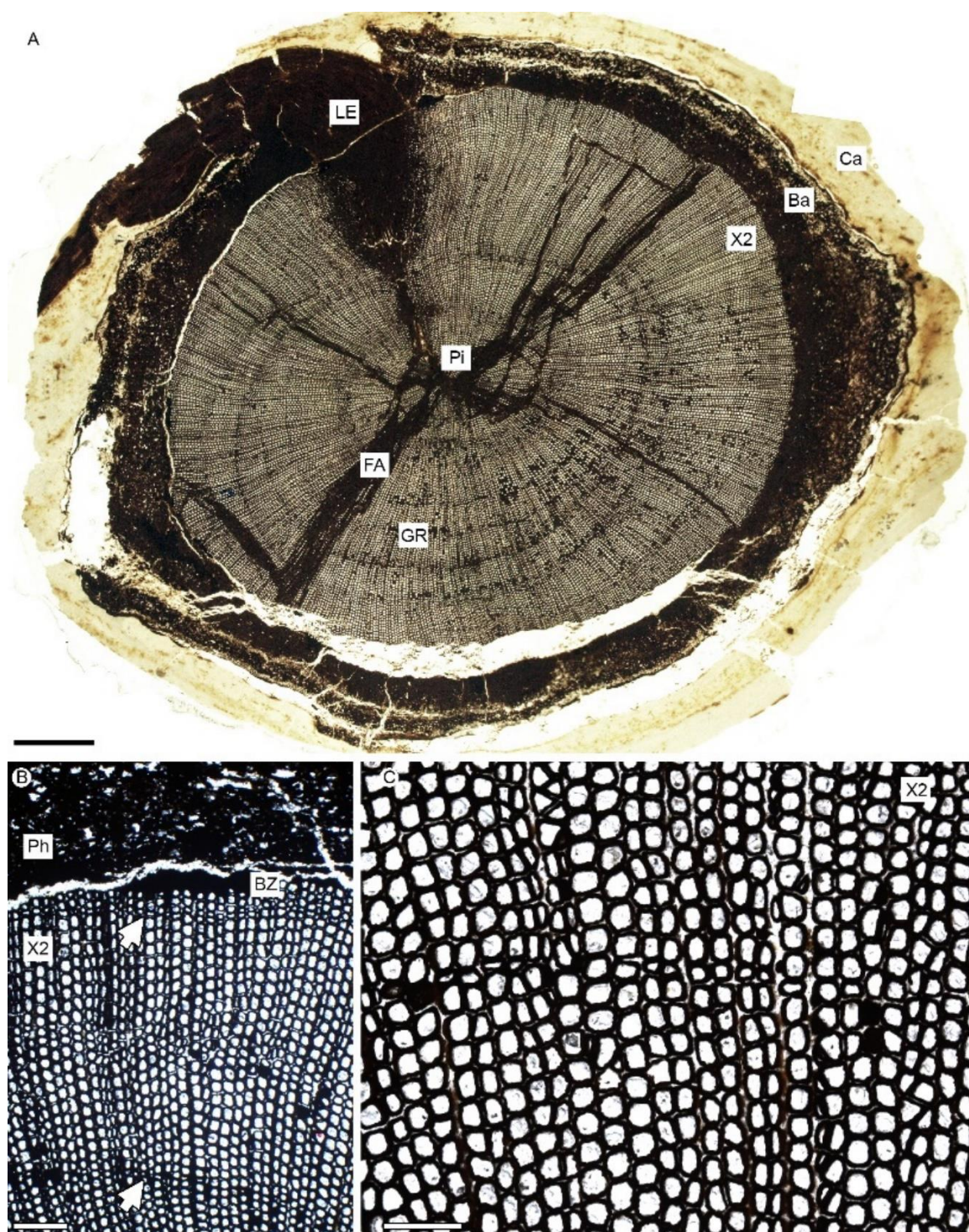
Figure 4. Gross morphology of the secondary branch in cross-section (slide 2443-Pb-1). A) Composite image of a full cross-section under stereoscopic microscope showing the carbonate layer (Ca), irregular pith (Pi), the massive, homogeneous secondary xylem (X2), the growth rings of variable width (GR), a leaf emergence (LE), the bark (Ba) and fungal attack (FA); B) detail of the secondary xylem showing uneven growth rings (arrows); C) growth ring boundary. Scale bars: A) 2 mm; B, C) 200 μm.

In longitudinal radial sections (Fig. 5), the tracheids mainly show crowded triseriate (rarely biseriate), alternate, areolated pitting with flattened borders and

hexagonal boundaries, in addition to rounded or slightly elliptical apertures (Fig 5A). The pit spacing on the tracheid radial walls has a compact arrangement from margin to margin; this is a striking anatomical feature that is present from the initial to the outer rows of the secondary xylem, in both the early and late wood (Fig. 5B). Crossfields are wide, showing typical elongated parenchyma cells with thin walls; in some areas it is possible to observe that crossfield pits are crowded and have an araucarioid pattern, which according to the criteria of IAWA (Richter et al., 2004) consists of numerous, densely arranged pits with cupressoid organization (Fig. 5C, D).
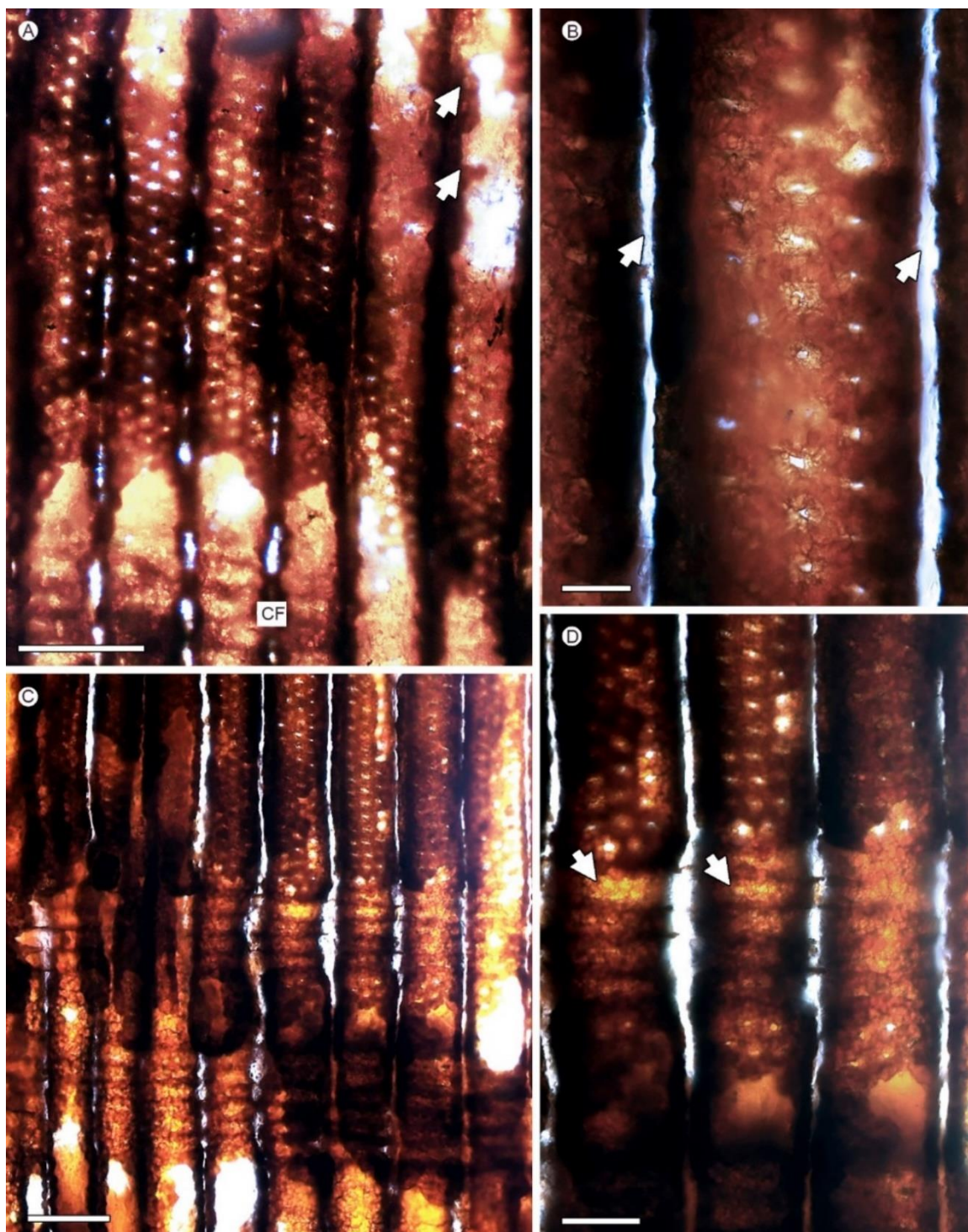
Figure 5. Main anatomical wood pattern in radial section (slide 2443-Pb-8). A) Elongate tracheids, crossfields (CF) and evidence of fungal attack (arrows). B) detail of a tracheid showing crowded triseriate, alternate hexagonal areolated pitting in compact, margin to margin arrangement and decayed middle lamella (arrows); C) tracheids with multiseriate hexagonal areolate pitting and crossfield with araucarioid pitting; D) detail of hexagonal pitting in crossfields (arrows). Scale bars: A, C) 100 µm; B) 20 µm; D) 50 µm.
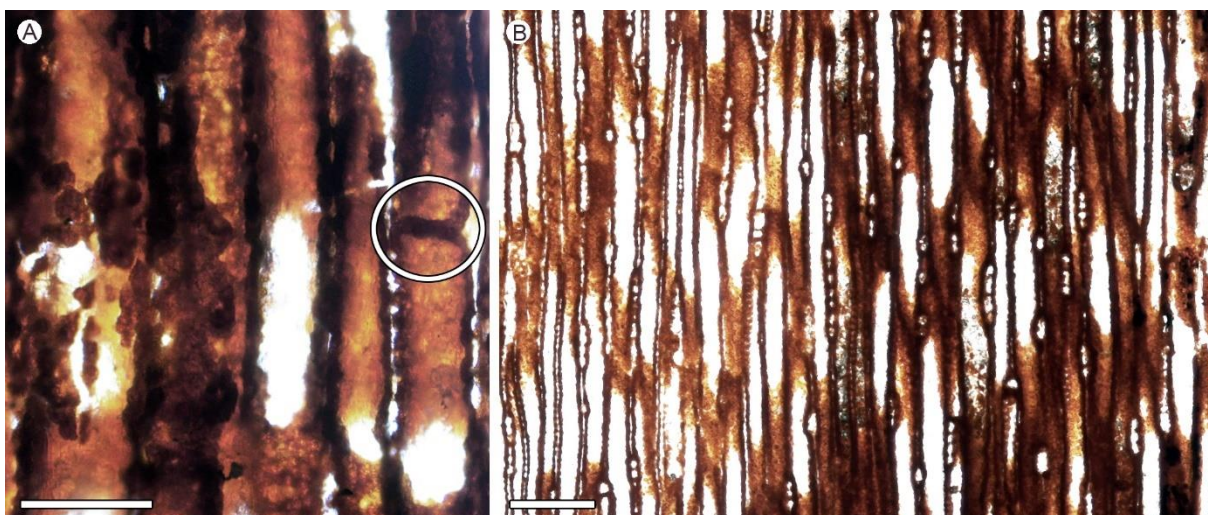
Figure 6. Longitudinal sections. A) Resin plug inside tracheid in radial section (encircled) (slide 2443-Pb-13); B) tangential section showing uniseriate rays (slide 2443-Pb-22). Scale bars: A) 50 µm; B) 200 µm.

The xylem is encircled by a poorly preserved vascular cambium comprising one to two subrectangular cells. The non-collapsed, conducting secondary phloem region (0.95 mm mean thickness) is also poorly preserved, but frequent irregularly shaped lacunae are evident (Fig. 7A). In the region of the collapsed secondary phloem, there was a belt of stone cells and canals (Fig. 7A, B). Tangential lacunae occur in areas originally occupied by the rhytidome, and lenticels occur in the outer surface (Fig. 7C).
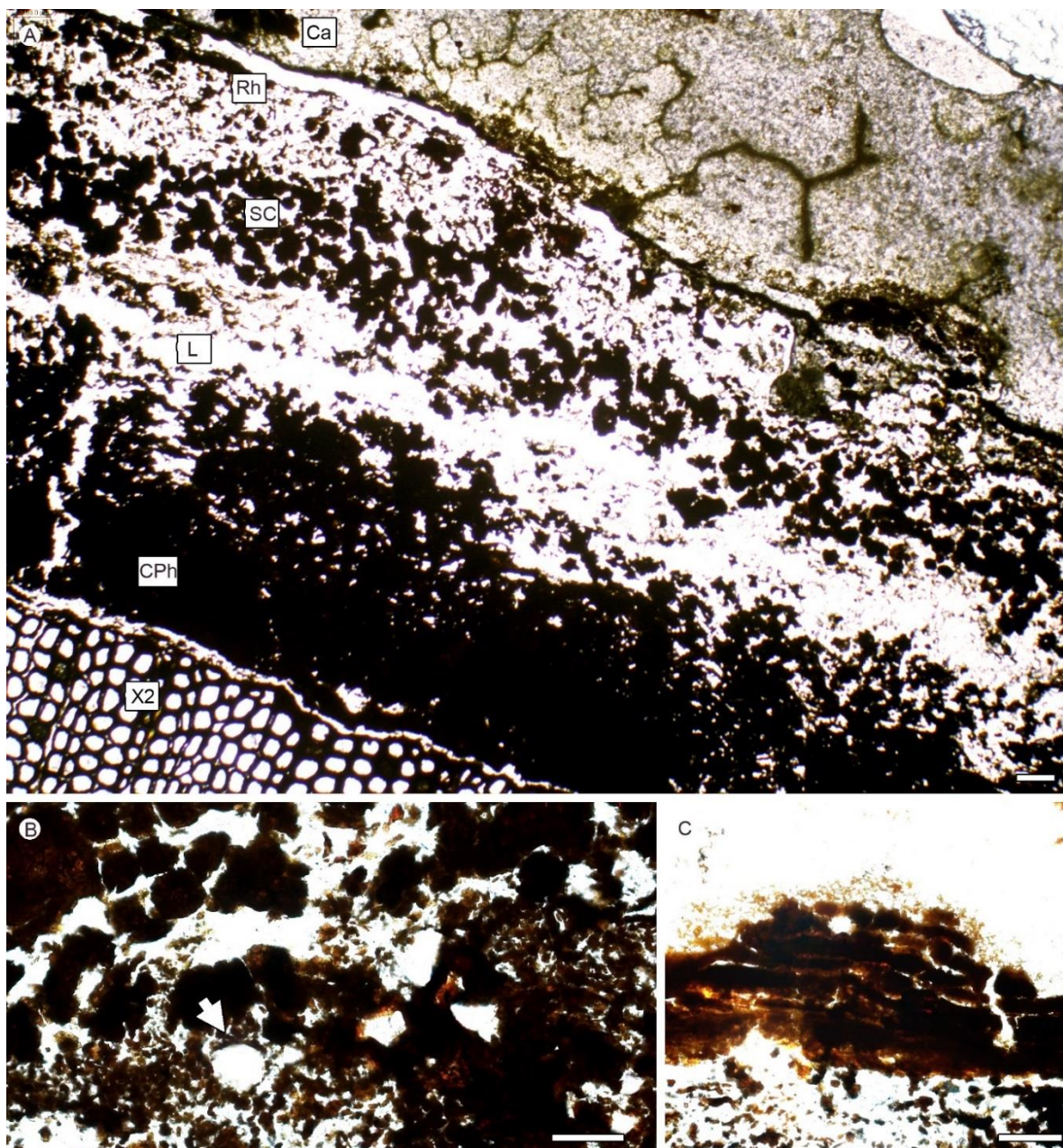
Figure 7. Main anatomical bark pattern (slide 2443-Pb-3). A) Cross-section showing lacuna (L), belt of stone cells (SC), vestigial rhytidome (Rh) and collapsed phloem (CPh); B) canal in cross section (arrow); D) lenticel in cross section. Ca: carbonate layer. Scale bars: A, C) 100 μm; B) 50 μm.

The constancy of the tracheid pitting characteristics (which occur in a compact arrangement from margin to margin all along the wood), coupled with those of the crossfield pitting showing a constant araucarioid organization, and the presence of resin plugs in the tracheids, exceed the morphotype criteria established by Philippe and Bamford (2008) for characterizing *Agathoxylon* Hartig, and suggest that the specimen has a biological affinity with the extant coniferous family, Araucariaceae. In addition to the xylem pattern, the occurrence of canals in the

phloem (Kershaw and Wagstaff, 2001) corroborate this affinity. Furthermore, the anatomical features are more consistent with *Araucaria* (sensu Greguss, 1955) than with other genera in the family.

Previously described fossil remains from the Crato Member also support the hypothesis that our specimen has an araucarian affinity. Such fossils are represented by *Araucaria cartellei* leaves (Duarte, 1993), *Araucariostrobus* sp. cones (Kunzmann et al., 2004), and branches of *Brachyphyllum obesum* (Duarte, 1985; Kunzmann et al., 2004, Batista et al., 2017). The macroscopic occurrences are also supported by palynological data (Heimhofer and Hochuli, 2010; Souza-Lima and Silva, 2018).

Wood patterns of Araucariaceae in the Gondwanan Mesozoic were previously recorded for the Jurassic in Chile by Gnaedinger et al. (2015), and for the Jurassic in Argentina by García-Massini et al. (2012) and Sagasti et al. (2019), and for the Early Cretaceous by Vera and Césari (2012).

In addition, the substantial presence of conifers in the Crato Lagerstätte (Table 2) contradicts the conclusion of Spicer and Skelton (2003) who found no evidence of tropical humidity that was high enough to have supported expressive terrestrial productivity within the Tropical Equatorial Hot arid belt in the early Cretaceous greenhouse climate.

The potential use of araucarians for palaeoenvironmental reconstruction relates to their past and present distributions, and shows that they have a preference for subtropical or mesothermal environments (Kershaw and Wagstaff, 2001). Therefore, available ecological data about Araucariaceae and the growth-ring pattern of the specimen in this study suggest that the plant grew in conditions compatible with the Tropical Equatorial Hot arid belt (Chumakov et al., 1995) with the occurrence of environmental cycles controlled by alternations in water availability (Schweingruber, 1996).

4.3 Fungal remains

Fungal remains are present in the host tissues as scattered fungal bodies and hyphae. Most of them do not possess diagnostic features allowing correlations with extant taxa.

Fungal hyphae (Fig. 8) are present mainly in the xylem tissue and less commonly in the bark. Some propagules are smooth walled (8 μm average diameter) and tubular shaped, non-septate (Fig. 8A, B) or septate (Fig. 8C) and occur in relatively straight (Fig. 8A, B) or curving course (Fig. 8C). They commonly travel intracellulary, either extending parallel to the long axis of the tracheids (Fig. 8A) or can be traced cross-cutting tracheid lumen (Fig. 8C). Terminal ellipsoidal hypha swellings physically connected to a portion of the intercellular parental hypha commonly found within tracheid lumina (Fig. 8D) and bark cells were identified as conidia of ascomycetes (see Harper et al., 2018).

Unbranched hyphae were found in both xylem and phloem tissues displaying straight tubular shape (15.3 μm average diameter) crossing cells (Fig. 8E) with lateral, randomly arranged emergencies from the main axis (Fig. 8F). Septa are irregularly spaced and connected to the hypha walls at right angles (Fig. 8G).
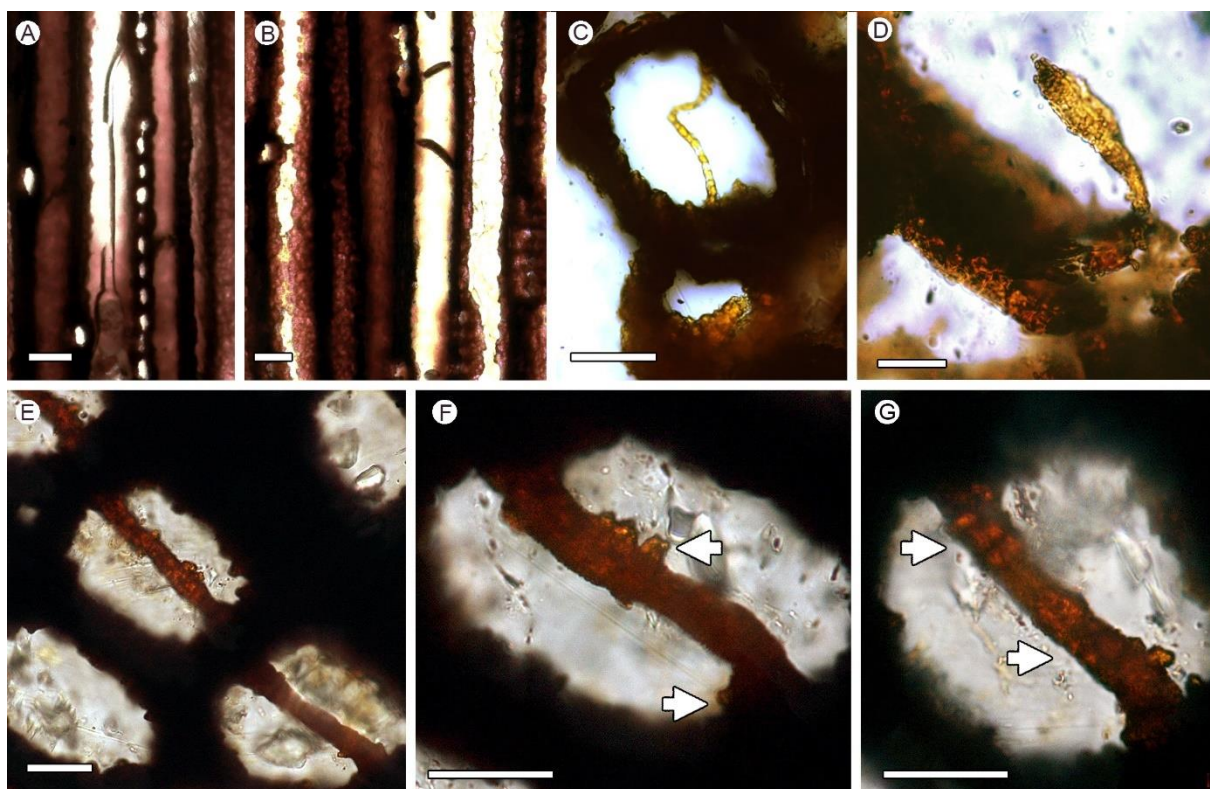
Figure 8. Fungal hyphae in tangential (A-B) and cross-sections (C-G) of the secondary xylem. A, B) Non-septate, relatively straight smooth-walled tubular hyphae extending parallel to the tracheid axis

and cross cutting tracheid walls respectively (slide 2443-Pb-26); C) regularly septate tubular hypha with curved course cross-cutting tracheid walls (slide 2443-Pb-5); D) ellipsoidal terminal hyphal swelling physically connected to a portion of the intercellular parental hypha (slide 2443-Pb-6); E) straight unbranched, clamp-bearing tubular hyphae crossing cells (slide 2443-Pb-7); F) hypha with lateral, randomly arranged emergencies (slide 2443-Pb-7); G) hypha with clamp connection showing transversal septa (encircled) connected to the hypha walls at right angles (slide 2443-Pb-7). Scale bars: A, B) 50 µm; C, E-G) 20 µm; D) 10 µm.

Some structures found within bark cells and in the lumina of peripheral tracheids were presumed to represent terminal microsclerotia connected to the cell wall by hypha strands (Fig. 9A, B). A probable incomplete, apically branched conidiophore bearing radiating short arms (Fig. 9C) was preserved in a void space within the bark. However, organically associated spores were not present. Bullate globose bodies (Fig. 9D) were commonly found within tracheid lumina and were identified as putative oogonia.
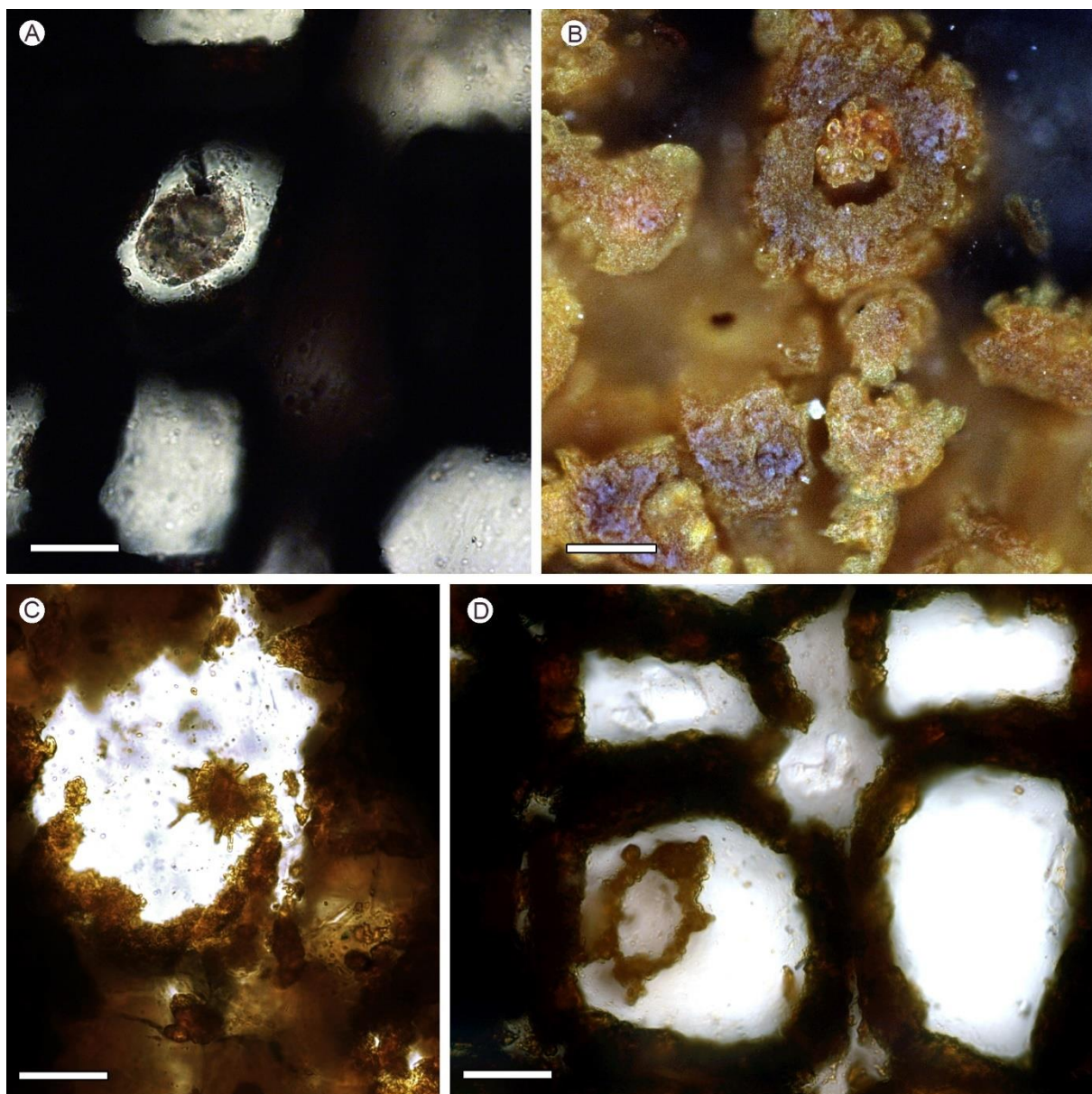
Figure 9. Fungal bodies in the secondary xylem (A, D) and bark (B-C, E) in cross-sections. A, B) Arbuscule-like structures composed of several thick-walled bodies attached to the cell wall by a hypha corresponding to microsclerotia (slide 2443-Pb-2); C) putative incomplete apically branched conidiophore bearing a series of radiating short arms preserved in a void space within the bark (slide 2443-Pb-4); D) bullate globose body identified as putative fungal oogonium commonly found within tracheid lumina (slide 2443-Pb-4). Scale bars: 20 μm.

4.4 Host–fungus interactions

The responses of extant infected plants to fungal invasion involves a range of physical and chemical defenses used to retard further invasion (Bennett and Wallsgrove, 1994; Sadavasian and Thayumanavan, 2003; Schwarze, 2007; Stubblefield and Taylor, 1986). These defenses provide immediate resistance to stem invasion, but they may be overcome by organisms that have become adapted to them (Franceschi et al., 2000).

Interactions between fungi and vascular plants in the fossil record are usually measured based on the existence of microscopic putative plant responses to fungal invasion, such as the occurrence of tyloses, various types of resiniferous deposits originating reaction and barrier zones, abnormal growth rings, and appositions (Falcon-Lang et al., 2001; Gnaedinger et al., 2015; Harper et al., 2012; Krings et al., 2007; McLoughlin and Bomfleur, 2016; Pujana et al., 2009; Sagasti et al., 2019; Stubblefield and Taylor, 1986; Taylor and Krings, 2005; Weaver et al., 1997).

In our material the interaction is documented by microscopic responses developed in both the bark of the infected plant and more expressively in the xylem tissue, being represented by putative reaction zones, barrier zones and wall apposition process.

The physical evidence here interpreted as host response processes to fungal attack could alternatively be linked to resins which occur in the ray cells and axial tracheids as resin plugs in the wood of extant araucarians (Stockey, 1982; Jane, 1970). Their mode of occurrence is distinguished from that of other conifers by the absence of resin canals or resin cells. However, the uncommon abundance of dark content in the branch under study and the similarity with records of both extant conifer woods (Schwarze, 2007) and fossil woods attacked by fungi (Pujana et al., 2009; Feng et al., 2015; Gnaedinger et al., 2015; Sagasti et al., 2019) point to physical evidence of plant-fungus interactions.

4.4.1 Bark

The preservation of the bark, showing diffused, extensively decayed areas (Fig. 7A) rather than precisely delimited attacked zones, made it difficult to identify mutualistic, saprophytic or parasitic relationships between fungi and the host.

However, the comparison of fungal infestation in a conifer wood from the Jurassic of Patagonia with symptoms on extant trees showed that phloem infection can promote hypersensitive responses that lead to the accumulation of resins and other defensive chemicals in the cells surrounding the attack site (Sagasti et al., 2019). In our material, putative reaction zones characterized by dark contents in the non-conducting collapsed phloem point to the existence of a pathogenic pattern of fungal attack (Fig. 10A, B) and indicate that the bark was probably the primary site of invasion (Fig. 10C, D).
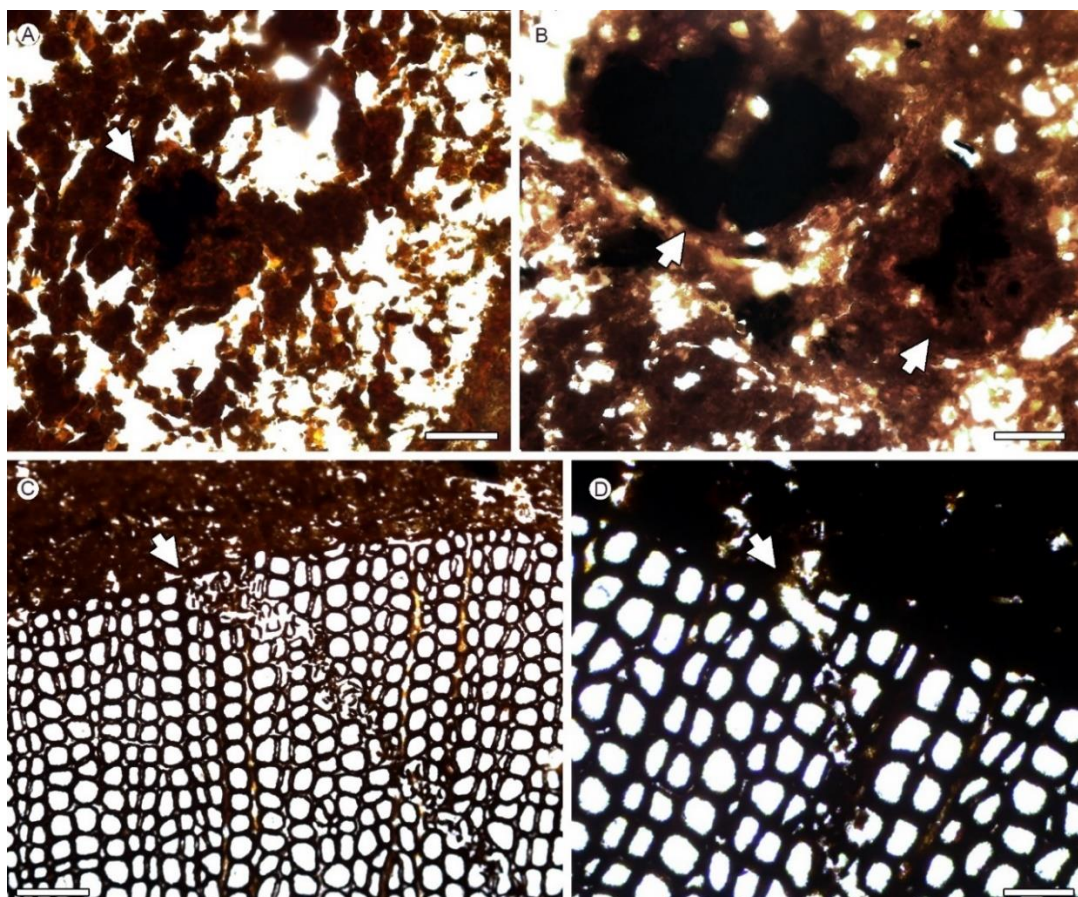
Figure 10. Fungus-host interactions (slide 2443-Pb-1). A, B) Putative reaction zones in the bark in cross-section (arrows); C, D) putative starting decay points at the boundary of the bark with the secondary xylem (arrows). Scale bars: A) 50 µm; B, D) 100 µm; C) 200 µm.

4.4.2 Xylem

The massive, discontinuous, dark bands occurring in the peripheral secondary xylem (Fig. 11A, B) contain a dark substance deposited inside the cell lumina that completely saturates the cell walls; in extant plants, these have been attributed to barrier zones or chemical boundaries (Shain, 1967, 1971, 1979; Shigo and Marx, 1977; Shortle and Smith, 1990; Smith, 2006) and induced chemical reactions to injuries (Bauch, 1984). Evidence of these chemical barriers in fossil wood has also been found by other authors (such as Pujana et al., 2009; Gnaedinger et al., 2015).

The expressively enlarged primary and secondary wall layers found in cells at the margin of the secondary xylem (immediately next to the occurrence of barriers) suggests a host reaction relating to a wall-apposition process (Fig. 11C, D) that partially occludes the cell lumen and may have blocked hyphae growth (Aist, 1976; Shigo and Shortle, 1979). Evidence of apposition walls has previously been registered in Triassic decayed gymnosperms (Stubblefield and Taylor, 1986) and in Jurassic conifers (Feng et al., 2015; Sagasti et al., 2019). In extant plants, the occurrence of fungal bodies and hyphae inside the cell lumina (Fig. 11C, D), which shows evidence of apposition, distinguishes the chemical defenses caused by fungal degradation from those caused by wounds (Schweingruber, 2007).
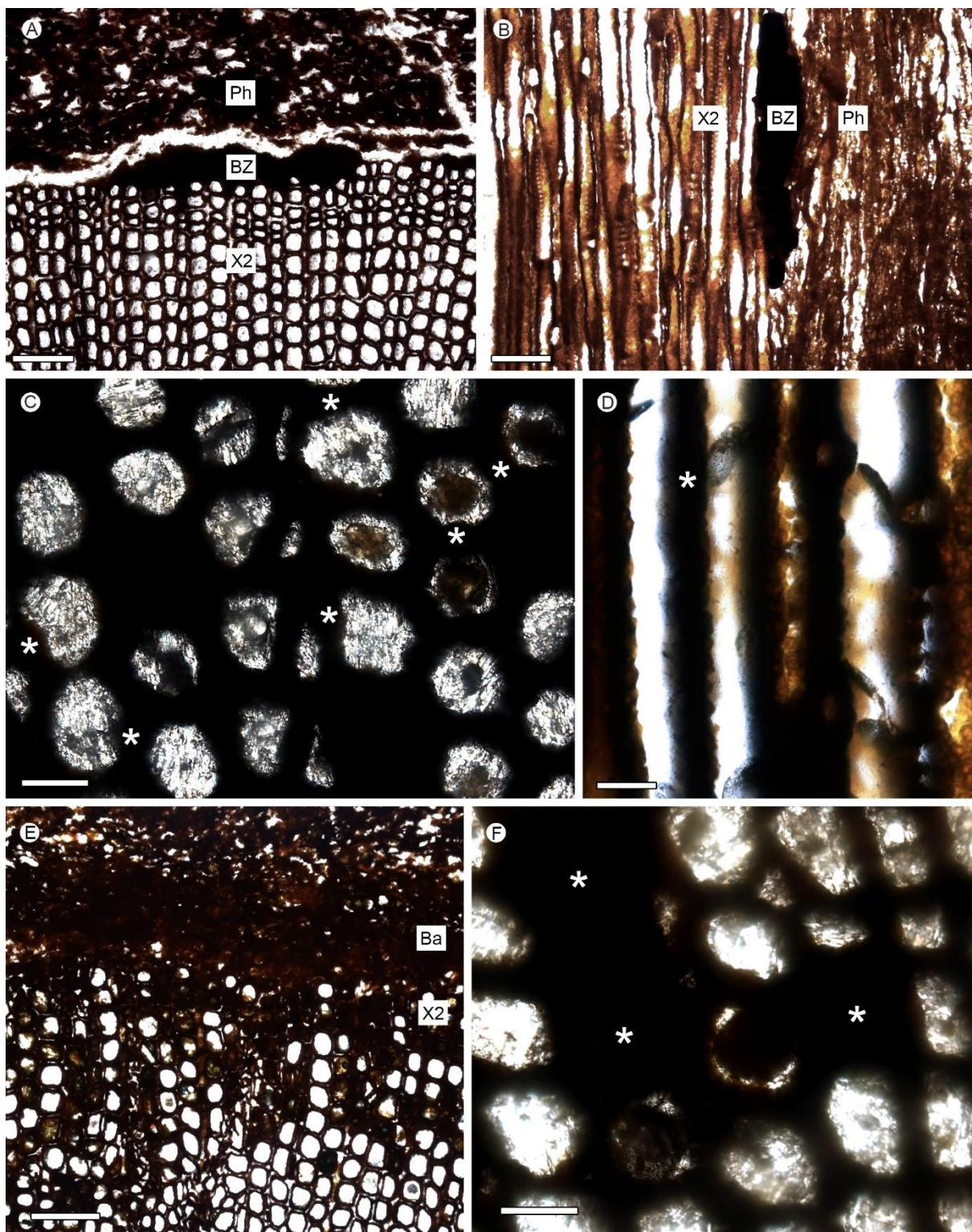
Figure 11. Fungus-host interactions. A, B) Barrier zone at the boundary of the bark with the secondary xylem in cross (slide 2443-Pb-1) and longitudinal sections respectively (slide 2443-Pb-28); C, D) *wall-apposition process (wall thickening) and fungal bodies inside the cell lumina in cross (slide 2443-Pb-6) and longitudinal (slide 2443-Pb-30) sections; E, F) cross-sections showing *tracheids filled with dark content, isolated and in clusters (slide 2443-Pb-4);. Ba: bark; BZ: barrier zone; Ph: phloem; X2: secondary xylem. Scale bars: A, B, E) 200 µm; C, D, F) 50 µm.

In extant trees, the abundance of tracheids filled with a dark content occurring in isolation or clustered in small groups without forming a laterally continuous morphological barrier are recognized as being relicts of reaction zones (Blanchette et al., 1990; Boddy and Rayner, 1983; Pearce and Rutherford, 1981; Shain 1967, 1971, 1979; Smith, 2006). Such anatomical evidence in decayed fossil wood may likely document host cell reactions to fungal attack (Fig. 11E, F) (Feng et al., 2015; Pujana et al, 2009).

The development of these putative defense mechanisms occurring in the secondary xylem are inferred from different chemical and anatomical evidence and through comparisons with modern analogues, and indicate that the fungal attack occurred while the host was still alive.
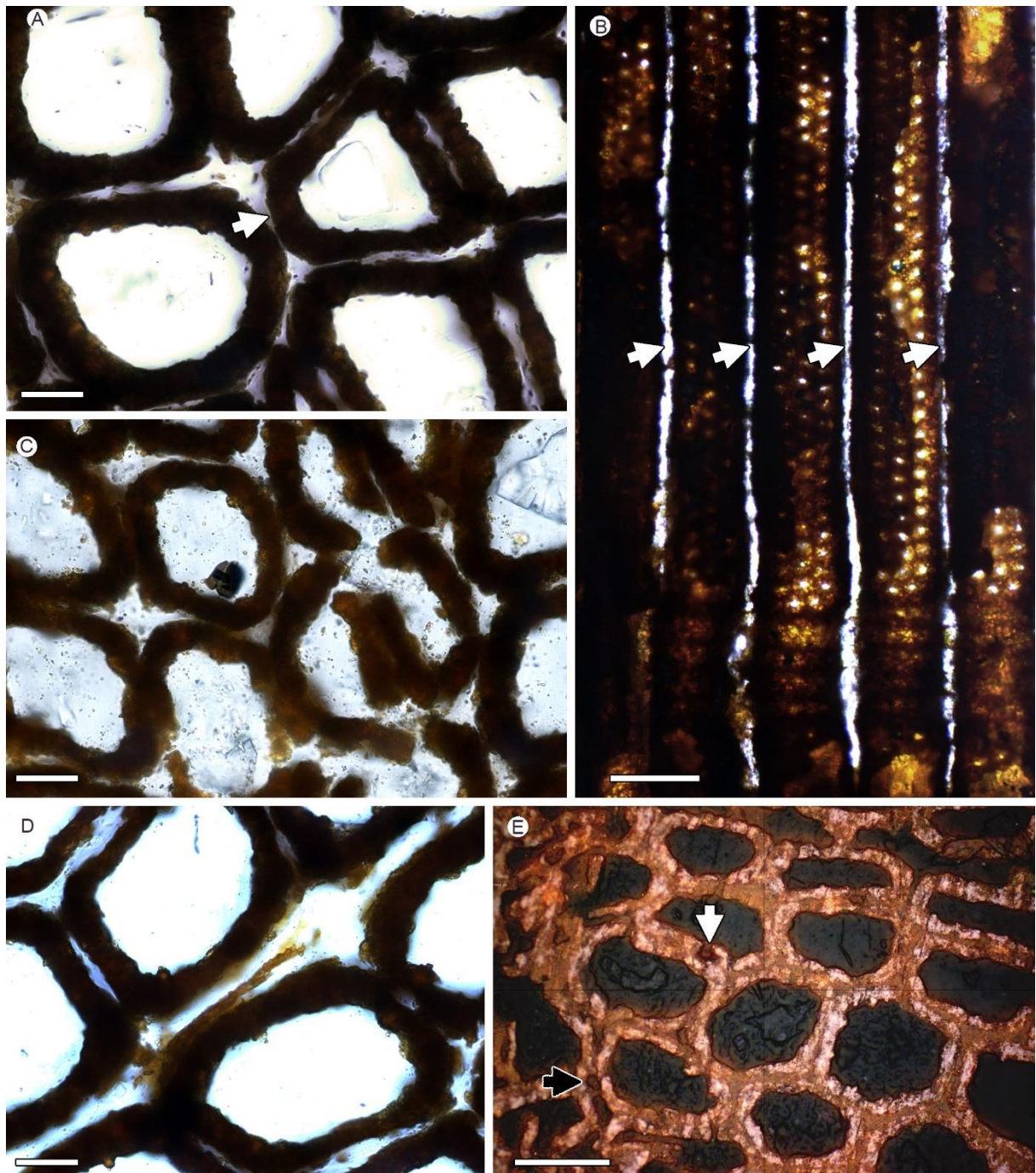
Figure 12. Degradation of the secondary xylem. A) Cross-section showing the extensive loss of middle lamella between tracheids and cell deformation (arrow) (slide 2443-Pb-6); B) radial section showing the longitudinally continuous degradation of the middle lamella (arrows) (slide 2443-Pb-18); C) cross-section showing partially decayed cell walls (slide 2443-Pb-6); D) cells appearing as disconnected units; hypha remain in the intercellular system (slide 2443-Pb-6); E) process of decay of the secondary cell wall (white arrow) side by side with evidence of middle lamella degradation (black arrow) (slide 2443-Pb-6). Scale bars: A, C-D) 20 µm; B, E) 50 µm.

4.5 Degradation pattern in secondary xylem

The secondary xylem has a degradation pattern characterized by the extensive loss of middle lamella, which is composed of lignin and pectin. Tracheids (Fig. 12) are decayed in various degrees under this process. The dissolution of the lamella gradually intensifies, until the adjacent tracheids are eventually separated from each other (Fig. 12A-D). In addition, cell walls are partially decayed and are thinned by the progressive decomposition of cellulose, hemicelluloses, and lignin. However, in the intercellular system, the presence of fungal remains in voids that were previously occupied by the middle lamella (Fig. 12D) is not decisive evidence of decay from a direct fungal attack, because decay of the middle lamella in extant plants occurs through enzymatic degradation (Schwarze, 2007).
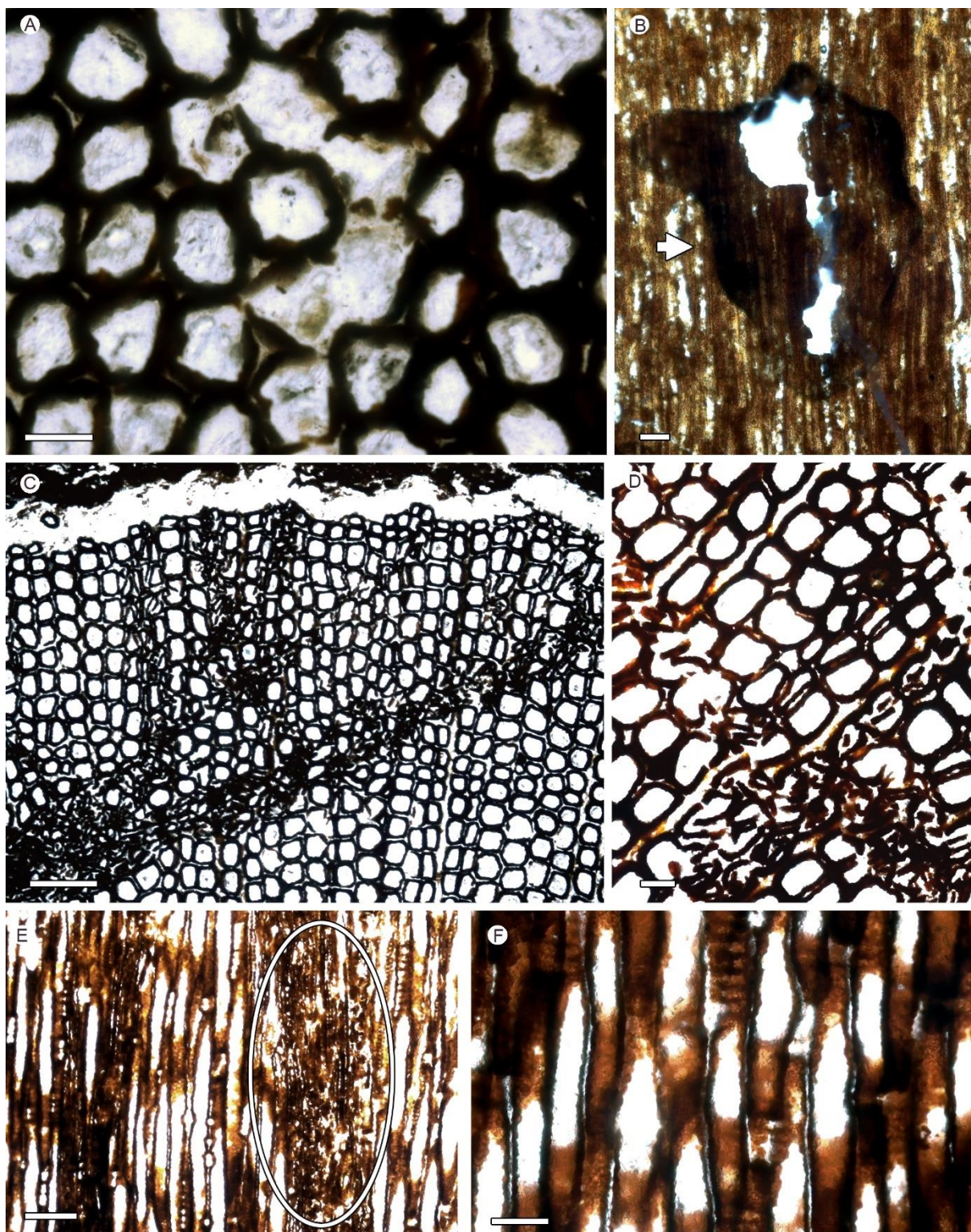
Figure 13. Progressing degradation in the secondary xylem. A, B) small, irregular, empty pockets, in cross (slide 2443-Pb-6) and longitudinal (slide 2443-Pb-27) sections respectively, sometimes surrounded by dark irregular areas probably corresponding to reaction zones (arrow); C) elongate degraded bands, in cross-section, with straight orientation and anastomosed pattern (slide 2443-Pb-7); D, E) breakdown and collapse of the cell walls within the degraded bands in cross (slide 2443-Pb-7) and tangential (slide 2443-Pb-34) sections respectively; F) decayed cells with U-shaped notches or fusiform features and erosion troughs in longitudinal section (slide 2443-Pb-10). Scale bars: A, B, D) 50 μm; C, E) 200 μm; F) 100 μm.

Infrequently in cross section, some tracheids show decay of the secondary wall only and other tracheids show degradation of the middle lamella (Fig. 12E). As it is difficult to establish clear boundaries between the distinct rot decay patterns of delignification that co-occur in the single secondary wood branch, we agree with Eaton (2000), who stated that rigid boundaries between different types of fungal decay are not currently appropriate.

The progressive degradation has formed small, irregular, empty pockets within the wood that are mainly observable in cross and longitudinal sections (Fig. 13A, B), sometimes surrounded by dark irregular rings probably corresponding to reaction zones (Fig. 13B). However, the most conspicuous type of degradation is that of long and continuous bands showing straight orientation and anastomosed pattern (Fig 13 C, D, E), sometimes reaching the pith, in which the parenchymatous and sclerenchymatous tissues show no clear direct or indirect evidence of fungal attack.

The loss of wood integrity is evident within the continuous bands, and this ultimately resulted in the breakdown and collapse of cell walls (Fig. 13D, E). Despite the dense occurrence of cell wall fragments within these bands, there is no development of damaged pockets that are devoid of cells inside the bands. However, the damage pattern points to parasitic rather than saprophytic decay, which would show a more diffuse pattern of attack (Creber and Ash, 1990).

In longitudinal section, the secondary wood also displays decayed cells with U-shaped notches or fusiform features and erosion troughs; almost all of these are restricted to the lumen of single cells (Fig. 13F) and do not coalesce into longer or wider pockets. The honeycomb-like degradation pattern occurring in extant plants, however, is the result of the coalescence of cellular degradation processes (Schwarze, 2007).

The absence of expressive damage pockets in the wood as a consequence of progressive decay validates the hypothesis that after the initial reaction from the host, decay was inhibited early by sedimentary entombment, and mineralization ensued very rapidly from the quick burial of the branch.

The microscopic features of the decayed wood in the araucarian branch investigated here correspond with those caused by extant wood rot fungi (Schmidt, 2006); they are consistent with white rot decay patterns caused by basidiomycetes

and certain ascomycetes, being similar to the selective white rot decay defined by Schwarze et al. (1995) and Schwarze (2007).

The selective delignification described in our material occurs in both extant broad-leafed trees and conifers; however, the simultaneous rot, which is absent in the araucarian branch under study, occurs mainly in broad-leafed trees and seldom in conifers (Schwarze and Baum, 2000).

It has been determined that the higher lignin content of gymnosperms (composed of guaiacyl monomers) compared to angiosperms (composed of guaiacyl and syringyl monomers) is the main factor involved in the pattern of white rot, being the dominant decay type in extant angiosperm trees from the Cretaceous to the present (Floudas et al., 2012; Ryvarden and Gilbertson, 1993; Whetten and Sederoff, 1995).

A model of host evolution suggested by Krah et al. (2018) shows that brown fungi in extant floras are generalists or gymnosperm specialists, whereas most white rot fungi are angiosperm specialists. It is considered that angiosperms were a new mega niche, and white rot fungi exploited them well, which led to the high specialization rate.

The effectiveness of white rot attack on extant Araucariaceae was tested by Modes et al. (2012) by evaluating the natural resistance of the wood of different angiosperm and gymnosperm specimens after incubation with fungal colonies of Basidiomycetes, which cause white rot decay. Angiosperm forms were classified as being very resistant to resistant, whereas the gymnosperm *Araucaria angustifolia* was classified as being moderately resistant, which corresponds to the greatest loss of mass and lower mass specific apparent.

Martínez et al. (2005) indicated that the ability to degrade or modify lignin is an enzymatic process that originated in the Upper Devonian in parallel with the evolution of vascular plants, whereas Nelsen et al. (2016) concluded that genomic data are directly consistent with the evolution of lignin in the Devonian. These studies agree with the oldest known indirect evidence of the involvement of basidiomycetes in cell alteration in the progymnosperm *Callyxylon* reported by Stubblefield et al. (1985) from the Upper Devonian (USA). However, records of Basidiomycete fungal bodies associated with late Paleozoic stems are scarce, and the oldest records are those of Krings et al. (2011) for the Mississipian of France and of Dennis (1969, 1970) for the middle Pennsylvanian of North America.

Reports of wood decay by white rot documented in Table 2 are from tropical, warm, cool, and cold climatic zones from the late Devonian to the Eocene. The growing number of studies in the last decades reporting symptoms of decay by basidiomycetes during the Jurassic and Cretaceous ratify the claims of Taylor and Taylor (1997), who stated that Mesozoic greenhouse conditions favored the decay process.

The same decay symptoms identified in paleoclimates with evidence of some humid seasonality are described here in an Araucariaceae branch from a thermophilous equatorial flora (Mohr et al., 2007) under greenhouse climate in the late Aptian within the Tropical Equatorial Hot arid belt (Chumakov et al., 1995; Hay and Floegel, 2012).

Currently, fungi are widely distributed in all terrestrial ecosystems, but relationships between latitude and diversity of possible plant pathogenic fungi indicate that climatic forces strongly drive those processes, with marked changes in diversity around middle latitudes (35°N) (Wang et al., 2019).

Extant arid ecosystems are highly sensitive to global patterns of environmental change, but models from mesic ecosystems do not apply to these environments when high temperatures and erratic moisture inputs impose a pulsed pattern on biological activities (Collins et al., 2008 and citations therein). While low moisture and high temperature certainly limit fungal activity in hot arid environments, intermittent periods of favorable temperature–moisture combination provide "windows of opportunity" that are crucial for fungal activity (Wicklow, 1981; Zak et al., 1995).

The evidence provided by the analysis of modern arid ecosystems support the inferences made here that not only was moisture important within the Aptian Tropical Equatorial Hot arid belt, but also its temporal and spatial patterning made the development of fungus–plant interactions possible. This is also in agreement with our climatic inferences based on the wood growth pattern suggesting cycles of water availability alternated with intervals of dryness in stressful growing conditions.

In addition, the presence of resting structures like microsclerotia in both bark and xylem tissues points to some exposure to adverse conditions during the period of infestation, probably as an answer to intermittent periods of dryness (Powell, 2007; Schwarze, 2007). The presence of superficial lenticels is linked to the direct exchange of oxygen, carbon dioxide, and water vapor between the internal tissues and the atmosphere; these processes occur through bark, which is otherwise

impermeable (Lendzian, 2006). Some extant conifers produce lenticels in the bark of their aerial parts during summer under peak temperatures to regulate transpiration more effectively (Rosner and Kartusch, 2003).

5. CONCLUSIONS

This is the first study to investigate plant-fungus interactions in a complete Araucariaceae wood sample collected in the Crato Fossil Lagerstätte. Observations of three-dimensional reaction and decay patterns along the whole stem were made, and the results provide evidence of the paleoecology and climatic cycles of Aptian terrestrial ecosystems in the Tropical Equatorial Hot arid belt.

The available ecological data relating to Araucariaceae, and the growth ring patterns of the host, imply that plant growth was controlled by cyclic alternations in water availability under frequent stressing conditions. Cyclical dryness was probably related to precipitation restrictions.

The occurrence of conifers in the Crato Lagerstätte, including Araucariaceae, shows evidence that tropical humidity was high enough to support trees under greenhouse climate conditions of the early Cretaceous.

The compartmentalization process, which was detected by chemical and anatomical criteria along the phloem and mainly in the xylem tissue, indicates host-fungus interactions that are comparable with cell reactions to fungal pathogens that occur in extant living conifers, which indicates that the fungal attack begun while the plant was still alive.

The wood decay was strongly indicative of the selective pattern of white rot, which is caused by basidiomycetes and certain ascomycetes, and provided evidence that Araucariaceae had already developed defense mechanisms under the general progress of the Cretaceous greenhouse climate.

Evidence of fungus–plant interactions associated with growth ring patterns imply intermittent periods of favorable temperature-moisture inputs that were crucial for the fungal activity during the deposition interval of the Crato fossil Lagerstätte included in the Tropical Equatorial Hot arid belt.

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Contributions:

A.C.S.S, M.G.S., I.D.S., and A.M.S. conducted the analyses under TLM and SEM and wrote the introduction, material and methods, results, discussion and conclusions; I.S.C. wrote the geological synthesis and collected the fossil; J.G.M.F. and J.O.M. conducted the analysis under incident light.

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Agathoxylon santanensis sp. nov. from the Aptian Crato fossil Lagerstätte, Santana Formation, Araripe Basin, Brazil

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Highlights

- *Agathoxylon santanensis sp nov* shows araucarian affinities
- *Agathoxylon* was not climatically controled in the Aptian

- *Agatoxylon* was found in hot and arid biome

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ABSTRACT- The study of a petrified twig from the late Aptian Crato Member (Santana Formation, Araripe Basin, northeastern Brazil) under high-resolution optical microscopy allowed for the first formal record of the morphogenus *Agathoxylon* and the description of a new species, *Agathoxylon santanensis*. The wood is characterized almost exclusively by araucarian triseriate alternate bordered pits with hexagonal boundaries in a compact arrangement, and crossfield pits with araucarioid organization. In addition to *Agathoxyon*-type of xylem, the preservation of axial canals in the non-functional phloem and the parallel venation associated to longitudinally disposed stomata in an attached leaf point to a probable araucariacean affinity for the species. The presence of *Agathoxylon* in the Tropical-Equatorial Hot Arid belt, in addition to its common presence in contemporaneous Warm to Cool- Temperate belts indicate that the genus was not climatically controlled. The general growth pattern indicates growth interruptions zones caused by water stress, implying intermittent periods of drought under a general megathermal climate.

Key words: Araucariceae, wood anatomy, bark, wood growth pattern.

Introduction

The macroflora of the late Aptian Lagerstätte of the Crato Member of the Santana Formation, northeastern Brazil is abundant and diversified, according to different authors (Santos *et al.* 2020 and citations therein). The Araucariaceae and Cheirolepidiaceae conifers represent about 30% and angiosperms are the dominant forms the fossil plant assemblage (32%), whereas gnetaleans (19%) and lycophytes, sphenophytes, filicophytes, pteridosperms, bennettitaleans, and *incertae sedis* gymnosperms (19%) are complementary elements of the fossil plants association (Bernardes de Oliveira et al., 2014, Souza-Lima and Silva 2018). Palynological data (Heimhofer and Hochuli 2010) support the macroscopic occurrences.

Fossil plants occur mainly as authigenic preservation and more rarely as coalified compressions (Schopf, 1975). Petrified woods have not been described for the Crato Lagerstätte so far, however, given the characteristics of the paleobotanical assemblage, largely composed of fragments of potential arborescent trees, the representativeness of petrified woods must be attributed to taphonomic bias rather than to scarcity of the parent plants in the source environment.

The anatomical analysis presented here was performed on a petrified twig from the lowest portion of the late Aptian Crato Member (Santana Formation) and allowed for the identification of an araucarian type of xylem corresponding to *Agathoxylon* Hartig. This morphogenus, with wide temporal and spatial distribution, has records dating back to the Paleozoic and extending into the Mesozoic (Philippe et al., 2004; Philippe, 2011; Panti et al., 2012; Peralta-Medina and Falcon-Lang 2012, Rößler et al., 2014, Del Fueyo et al., 2021).

Among extant conifers only the Araucariaceae have wood of the *Agathoxylon* type, but in the Jurassic – early Cretaceous other plant groups may have had wood of this

type, e.g., Pteridospermales and Cheirolepidiaceae (Philippe et al., 2004). However, different authors have pointed to systematic relationships of Mesozoic *Agathoxylon* woods from western Gondwana with Araucariaceae (e.g. Zamuner and Falaschi, 2005; Panti et al. 2012; Vera and Césari, 2012; Garcia Massini et al., 2012; Gnaedinger et al., 2015; Greppi et al., 2020; Sagasti et al., 2019; Del Fueyo et al., 2021).

The main goal of the present study was to propose a new taxon, *Agathoxylon santanensis*, based on distinct characteristics from other species of the genus *Agathoxylon.* Anatomical patterns identified in bark fragments organically associated to the secondary xylem, and general morphological features from a connected leaf were evidence of probable systematic affinities. In addition, the wood growing pattern offered some speculations about the climate conditions during the deposition of the basal portion of the Crato Member of the Santana Formation.

Geological Synthesis

The Araripe Basin (Fig. 1a) is a hinterland basin covering an area of 12,200 km² that originated during the Berriasian-Hauterivian times (early Cretaceous), related to the first rifting stages between South America and Africa (Carvalho, 2000; Matos, 1992).

The Santana Formation (Ponte and Appi 1990) included in the post-rift stage is a 60 m thick succession of finely laminated carbonates interlayered with green shales and fine-to-coarse sandstones. The lowermost Crato Member, from where the wood material studied here comes from, hosts the Crato fossil Lagerstätte, with exquisite preservation of plants, invertebrates, and vertebrates within a carbonate succession (Grimaldi et al., 1990; Martill, 1993; Martill and Bechly, 2007; Naish,

2007; Pinheiro et al. 2012; Barling et al. 2015; Carvalho et al., 2019). The age of the Santana formation has been largely discussed (e.g. Martill, 2007), and a late Aptian age (113-119 Ma) was inferred based on the recognition of the palynological subzone P-270-2 (Regali and Santos, 1999; Heimhofer and Hochuli, 2010; Rios-Netto et al., 2012). The laminated carbonate layer (Fig.1b) was interpreted as a shallow meromictic lacustrine environment (Heimhofer and Martill 2007; Heimhofer et al., 2010) with episodic freshwater influx (Selden and Nudds, 2012).

The widespread occurrence of evaporites along the evolving South Atlantic rift system, in addition to the absence of coal deposits, and the dominance of drought-resistant, xerophytic vegetation (Ziegler et al., 2003; Mohr et al., 2007), elicted inferences about the paleoclimate. Semi-arid to arid climatic conditions were suggested for the Aptian deposition interval of the Araripe Basin included in the Tropical-Equatorial Hot Arid belt (Chumakov et al., 1995).
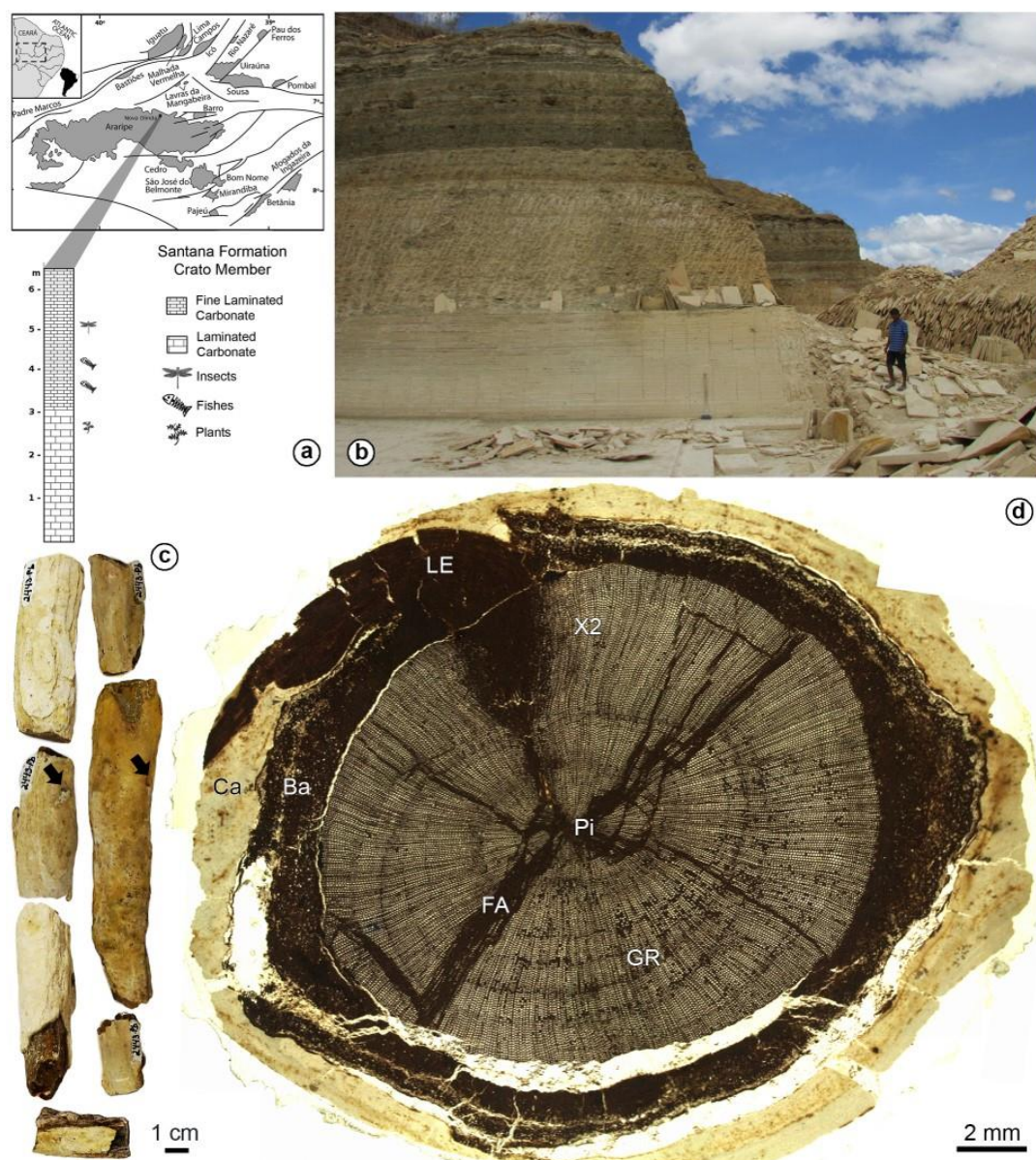
Fig 1. Location map, collection site and gross morphology of the type specimen. a. Map of the Araripe Basin in the context of the Cretaceous Northeastern Brazilian intracratonic basins and stratigraphic profile of the collection site Pedra Branca Mine, Nova Olinda County, Brazil (Carvalho et al., 2010). b. Fossiliferous outcrop of the Crato Member (Santana Formation) at Nova Olinda County. The studied fossil comes from the lower laminated carbonate succession. c. Seven branch fragments (2443Pb) showing inconspicuous leaf emergences (arrows) d. composite image of a full cross-section under stereoscopic microscope showing the carbonate layer (Ca), irregular pith (Pi), the massive, homogeneous secondary xylem (X2), growth interruptions of variable width (GR), a leaf emergence (LE), the bark (Ba) and fungal attack (FA) (slide 2443Pb-1).

Material and Methods

The fossil specimen is likely a secondary branch measuring 395 mm long and 21 mm in diameter containing petrified wood and bark. The studied material was previously analyzed by Santos et al. (2020) aiming to characterize white rot fungal decay in the secondary wood. Elemental EDS analysis indicated a dominant mineralization by iron (Fe) in the cell walls (Santos *et al.* 2020). Oxygen (O), in addition to carbon (C) are probable remains of the original organic matter of the cell walls. The mineralization of cell lumina occurred mainly with respect to crystal-shaped calcium (Ca).

The single fossil specimen broke into seven fragments when the fragment was mechanically removed from the carbonate sediment (Fig. 1c). The macroscopic type-specimen is housed in the paleontological collection of the Departamento de Geologia, Instituto de Geociências, Universidade Federal do Rio de Janeiro under the acronym 2443Pb. Thin sections are stored under the codes 2443Pb-1 to 2443Pb-35.

Different fragments of the single branch were sectioned in transverse, radial and tangential sections and polished, uncoated thin sections (40 µm thick) were produced. Epoxy resin was used as an embedding and mounting medium. The sections were polished using 0.05 mm aluminum oxide powder. The anatomical analysis was conducted under transmitted and reflected light microscopy.

The thin sections were analyzed and photographed with a Leica S8 APO stereoscopic microscope and a Zeiss AxioScope transmitted light microscope with mounted cameras at the Universidade Federal do Rio Grande do Sul (UFRGS).

Zeiss Axio Vision 4.8.1 software was used to make measurements and the plates were composed with Adobe Photoshop CS3 Extended. Transformations

done to the images were cropping, rotation, contrast adjustments, focus stacking, and image composition. The terminology used to provide the anatomical details of the wood followed the recommendations of IAWA Committee (2004), Decombeix et al. (2019), Schweingruber (1992, 1996) and Falcon-Lang (2003).

Systematic Paleobotany

Genus *Agathoxylon* Hartig 1848

Type species: *Agathoxylon cordaianum* Hartig, 1848; Triassic, Coburg, Germany.

Agathoxylon santanesis sp. nov.

Figs: Fig. 1c, d to Fig 5

Etymology: The specific epithet is named after the stratigraphic horizon of the specimen, the Santana Formation from the Araripe Basin (Brazil).

Holotype: 2443Pb (petrified wood fragment).

Type locality: Mina Pedra Branca, 7º5`40" / 39º42`6"

Type horizon: laminated carbonate layer at lowest portion of the late Aptian Crato Member, Santana Formation, Araripe Basin.

Diagnosis: Wood growth interruptions distinguishable; tracheid quadrangular in cross-section. Secondary wood homoxylic, pycnoxylic; tracheid pitting in radial section with araucarian arrangement, bordered pits alternate, exclusively triseriate, in compact arrangement, with the pits completely packing the tracheid radial walls.

Resin-filled tracheids present; rays parenchymatic, homogeneous, uniseriate. Crossfield pitting araucarioid, with 4–8 pits per crossfield. Resin plugs common.

Morphological Description

The specimen corresponds to a homoxylous wood (IAWA Committee 2004; Decombeix et al., 2019) composed of tracheids as conducting cells, measuring 21 mm in mean diameter and 395 mm of preserved length (Fig. 1c), showing a very small pith (393,65 µm) with irregular boundaries (Fig. 2a), surrounded by a massive secondary xylem (up to 16 mm wide) and a 2 mm wide bark. The presence of a leaf organically connected to the axis confirmed the identification of the specimen as a branch (Fig. 1d).

Transversal Section

The very small pith has irregular boundaries (Fig. 2a) which indicate proximity with branch abscission zone (Schweingruber, 2007). It is characterized by rounded to square parenchyma cells and clusters of sclerenchyma cells 30 to 43 µm (34 µm) wide (Fig 2a), with cell walls up to 13 µm thick, 29 to 34 µm (average 30 µm) in diameter. Primary xylem bundles are inconspicuous, showing endarch and centrifugal wedge-shaped bundles lying outside the periphery (Fig. 2a). The secondary xylem shows a typical pycnoxylic pattern (Decombeix et al., 2019) composed of tracheids in dense arrangement and uniseriate parenchyma rays. In cross-section, the tracheids are square, arranged in regular rows, limited by elongated, rectangular parenchyma ray cells with thin walls (3 µm). Tracheids with dark fillings, probable relicts of resins, are a common feature within the secondary xylem and are randomly dispersed or in clusters (Fig. 2b).

Cell-by-cell measurements in cross-section have detected 5 rings 680 to 948 mm wide (Fig. 1d). In each ring, the tracheids of the initial wood are 60 to 95 μm (average 75 μm) in radial diameter and have cell walls are 6 to 13μm (average 9 μm) thick. In the latewood, 1 to 3 rows of tracheid are flattened, each tracheid measuring 29 to 50 μm (average 36 μm) in radial diameter and cell walls are 6 to 13 μm (average 9 μm) thick. These rings are distinguished from growth rings (IAWA Committee, 2004) by the absence of thickened cell walls in the latewood in relation to the earlywood tracheids (Fig. 2b, c, d). In addition to the absence of thickened walls, rings show abrupt decline followed by a rapid rise back up in the tracheid diameter (Fig. 2c). Some rings are inconspicuous or subtle, and the boundaries cannot be completely traced laterally (Fig.2d). The vascular cambium is indistinct.
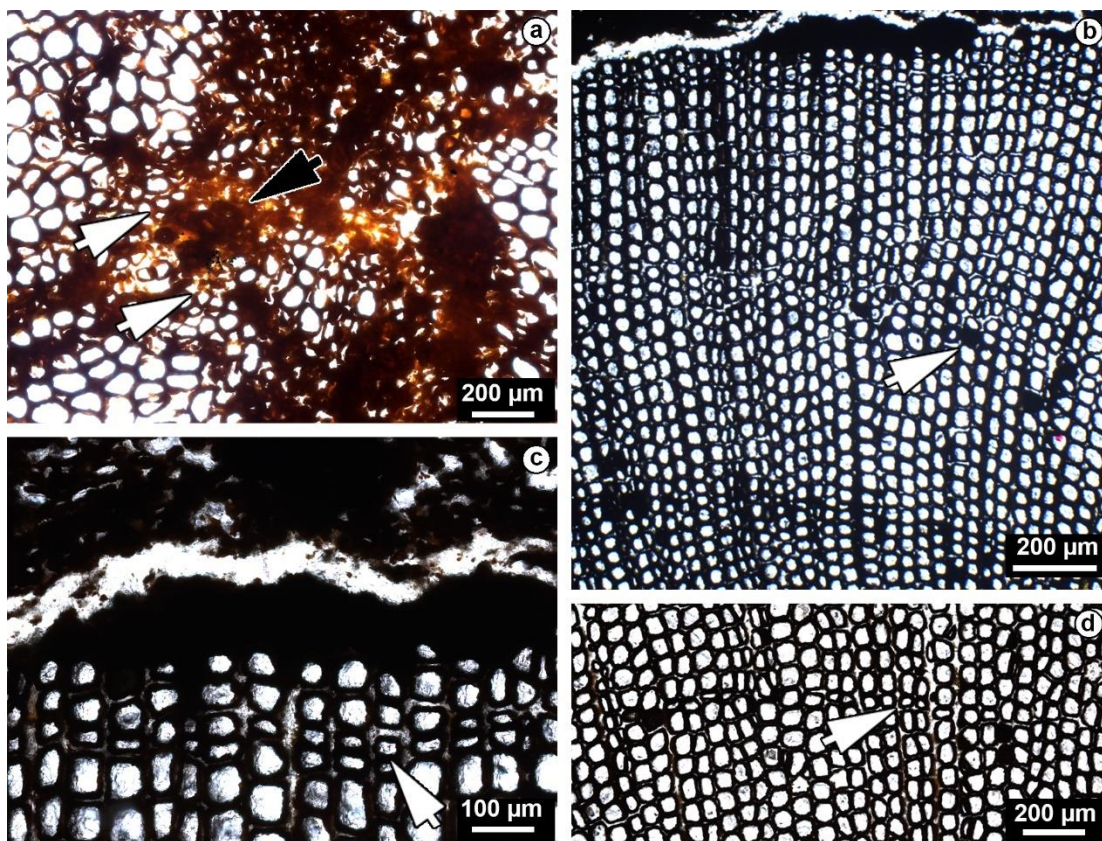
Fig. 2. Anatomical features in cross-section (slide 2443Pb-7). a. Pith with very irregular boundaries and clusters of sclerenchyma cells (black arrow); primary xylem inconspicuous, endarch, centrifugal (white arrows). b. Secondary xylem with growth interruptions and resin-filled tracheids (arrow). c.

Detail of growth interruption boundary. d. Subtle growth interruption zone with boundaries that cannot be traced laterally.

Radial Longitudinal Section

The tracheids of the secondary xylem show hexagonal bordered pitting and crossfields with araucarioid pits (Fig. 3a). The intertracheary pits are crowded, ranging from 14 to 16 μm diameter, and are mostly triseriate (95%), rarely biseriate alternate (5%), with flattened borders, with rounded or elliptical apertures (Fig. 3b,c). Sanyo bars, secondary spiral thickening, and trabeculae are absent. The compact arrangement of the pits (Fig. 3b, c) is a striking anatomical feature that is present from the initial to the outer rows of the secondary xylem.

Crossfield pits are crowded and half-bordered (oculipores) and have an araucarioid pattern (Barefoot and Hankins 1982; Vogel, 1995) with densely arranged pits (4 to 8), smaller (13 μm diameter) than the tracheid pitting (Fig. 3d).

It is important to emphasize that the araucarioid crossfield pattern, in spite of showing predominantly cupressoid individual pits (i.e., pits have elliptical apertures definitely narrower than the border), shows pits arranged in three or more alternate rows, with a tendency to crowding.

Plate-like resin plugs approximately 38.9 μm in width extend fully across the tracheid (Fig. 4a). The rays are wide, showing exclusively typically elongated parenchyma cells, with straight horizontal and perpendicular end walls.

and 13 to 30 µm (average 20 µm) wide. The tangential surfaces of the ray cells are not pitted.

Ellipsoid branch traces, up to 823µm long, occurr in the marginal part of the tangential sections, crosscutting the wood, (Fig. 4c, d). The traces show anatomical organization similar to that of the twig and are composed of a central mass of poorly preserved parenchyma cells and dispersed sclerenchyma cells with irregular boundaries. The central mass (pith) is surrounded by a massive homogeneous secondary xylem composed of tracheids with small lumens, 5 to 13 µm wide (average 9 µm) (Fig. 4c).
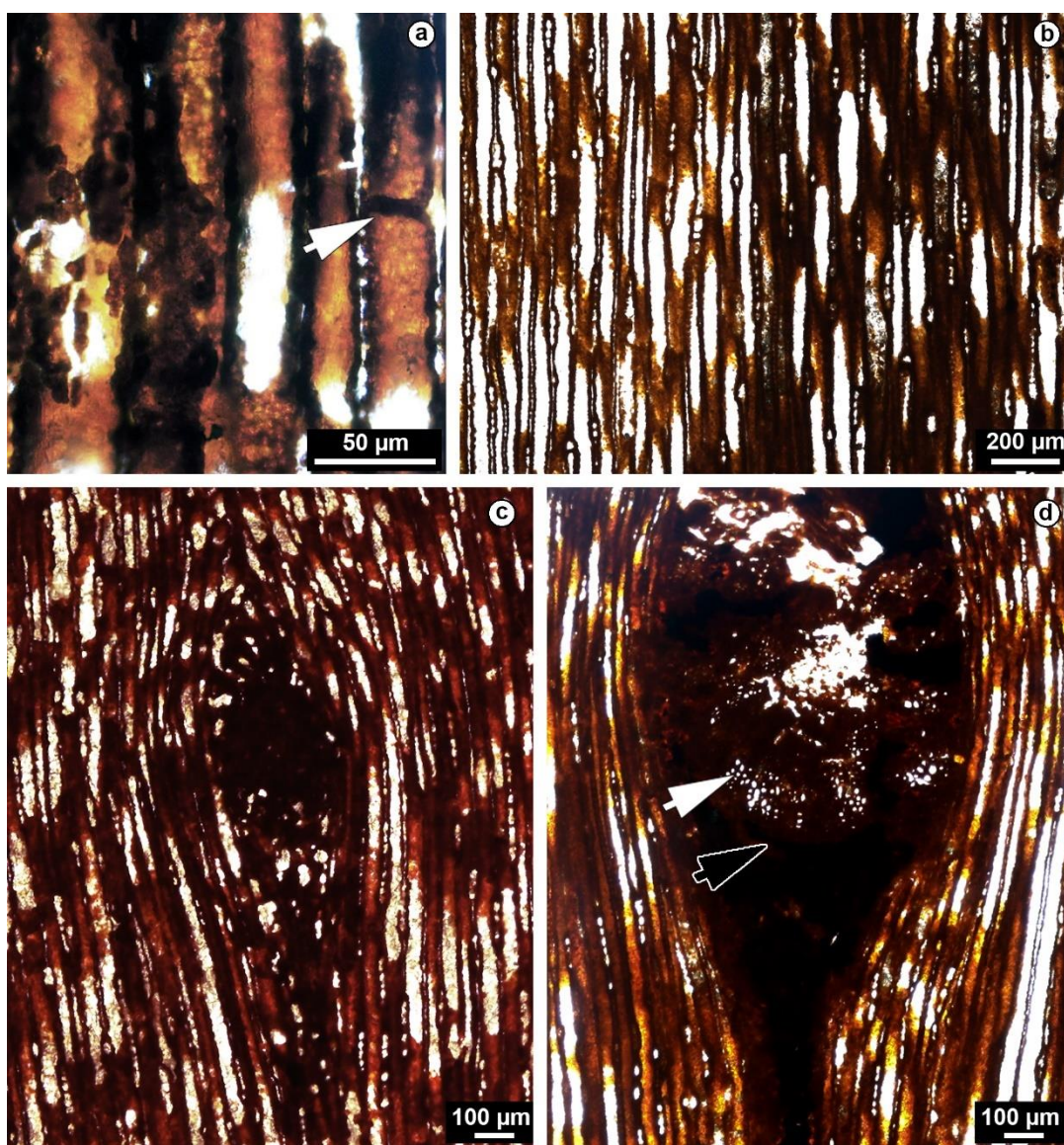
Fig. 4. Main anatomical wood pattern in radial and tangential sections. a. Resin plug in tracheid in radial section (arrow). b. Uniseriate, homogenous rays (slide 2443Pb-22). c. Ellipsoid branch trace cross-cutting the xylem tissue (slide 2443Pb-01). d. Detail of a branch trace (slide 2443Pb-08) showing a central parenchyma mass (pith) encircled by xylem tissue (white arrow) and concentration of dark material (black arrow).

Bark

The secondary phloem is poorly preserved, probably due to taphonomic bias, given that this tissue is originally composed of living cells with thin walls, which promptly collapse upon tree death. The secondary phloem tissue (641 μm mean width) is collapsed, obstructing the identification of different cells types and the distinction between functional and nonfunctional phloem zones. An irregular lacune (465 μm mean width) separates the phloem from the outer bark which consists of a ring of stone cells (sclereids) and randomly-dispersed physiological axial resin canals. The canals are round to ellipsoidal , measuring from 37 to 85 μm across. The stone cells are polygonal to semi-square and occur in groups (Fig. 5b, c).

An occasional, discontinuous small amount of flattened, stacked thickened cells can be observed at the branch periphery. They are interspersed with anticlinal and periclinal intercellular pore-like spaces (diameter ranging from 6 μm at their outer, narrowest point to 28 μm). The number of stacked closing layers ranges from 5 – 8 (Fig. 5e).
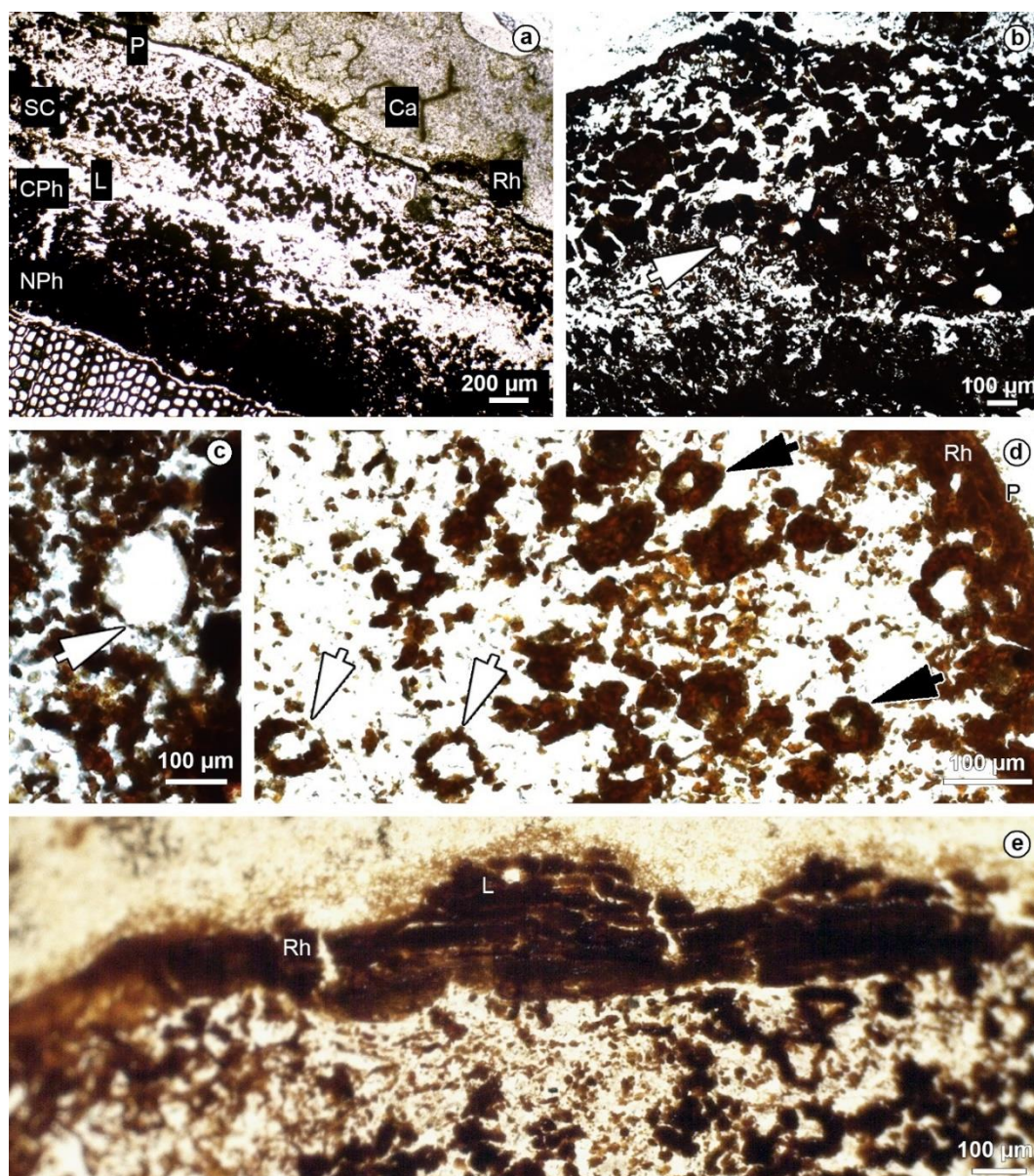
Fig. 5. Bark anatomy in cross-section (slide 2443Pb-3). a. Phloem (Ph), lacuna (L), belt of stone cells (SC), surrounding carbonate layer (Ca). b. Canal within the belt of stone cells (arrow). c. Detail of canal showing remnants of thin-walled epithelial cells (arrow). d. Stone cells with thick walls (black arrows) and canals (white arrows). e. Outermost layer of flattened, stacked thickened cells interspersed with anticlinal and periclinal intercellular pore-like spaces.

Branch Surface Structures

The branch is mostly naked presenting inconspicuous leaf scars, which are likely helically arranged (Fig. 1c). One attached leaf can be observed in cross-section (Fig. 1d). The leaf is sessile with acute apex. Its visible length is 10.6 mm and it is 3.11 mm wide at the insertion point. Assuming that it is folded at the midrib, a total width of 4.94 mm can be projected at its widest point. The width/length ratio is 0.47 and the distance between the leaf base and the maximum width represents a 55% of the leaf length.

The venation is parallel, maintaining the same caliber along the leaf with 32 ridges per mm (Fig. 6a). The stomata are arranged in longitudinal rows between the ridges. The stomatal pore is 25 – 42.5 µm long and 13 – 23.5 µm wide and oriented parallel to the ridge (Fig.6b). The stomata are partially covered by 4 papillae, 2 lateral and 2 polar, consistently 14 µm long and 10 µm wide (Fig 6, b). The outline of the epidermal cells was obscured by the permineralization with iron.
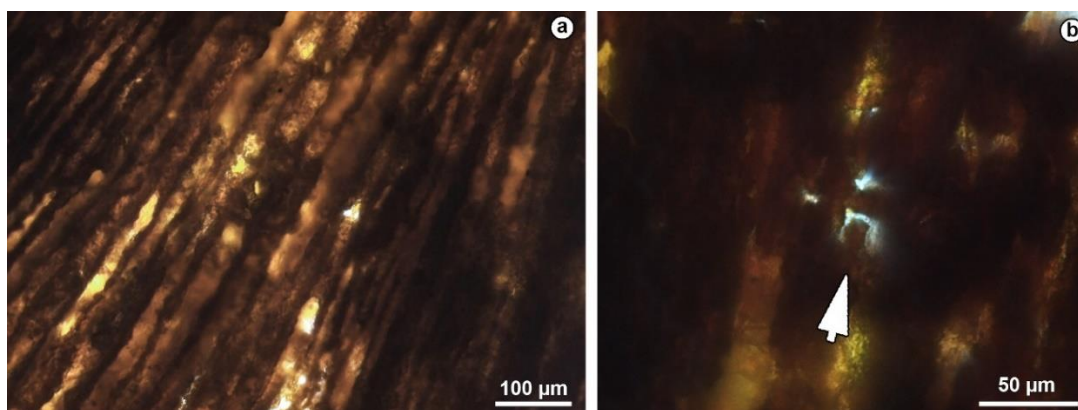
Fig. 6. Leaf surface (slide 2443Pb-12). a. Parallel venation. B. Stoma showing two lateral and one of the two polar papillae (arrow).

Discussion

The homoxylic, pycnoxylic wood specimen with araucarian tracheid pitting in the radial walls of the tracheids, homogeneous, uniseriate parenchymatic rays and araucarioid crossfield pitting point to the morphogenus *Agathoxylon* Hartig according to the criteria of Philippe and Bamford (2008) for Mesozoic gymnosperms based on tracheidoxyl parataxonomy. This systematic approach rests in descriptive terms, and it is not based on hypothetical systematic relationships.

However, distinct systematic affiliations have been attributed to the morphogenus *Agathoxylon,* surpassing the morphometric criteria of Philippe and Bamford (2008). In addition to probable affiliation with Araucariaceae, isolated wood remains of *Agathoxylon* have numerous homoplastic features that have been related to other plant groups such Cordaitales, Pentoxylales, Glossopteridales, Cheirolepidiaceae and Pteridospermermales (Philippe et al., 2004; Philippe, 2011; Peralta-Medina and Falcon-Lang 2012; Rößler et al., 2014).

For Panti et al. (2012), different species of *Agathoxylon* (*Araucarioxylon)* from the Jurassic – late Cretaceous of Argentina, Chile and Antarctica were potentially considered as Araucariaceae.

The affinity of *Agathoxylon* wood-types from the Western Gondwana in the Mesozoic with Araucariacea has also been strongly ratified by different authors (Zamuner and Falaschi, 2005; Vera and Césari 2012; Garcia Massini et al., 2012; Gnaedinger et al., 2015, Kloster and Gnaedinger, 2018, Greppi et al., 2020). Recently, Del Fueyo et al. (2021) based the identity of *Agathoxylon mendezii* (early Cretaceous of Patagonia, Argentina) with Araucariaceae on different parameters such as wood anatomy, fossil records (Leslie et al.*,* 2018), time-calibrated molecular

phylogeny of conifers, and combined phylogenetic analyses on extant and fossil Araucariaceae (Escapa and Catalano, 2013).

The great amount of *Agathoxylon*-type woods described for Warm to Cool Temperate climatic zones (Scotese et al., 2014) of South American Mesozoic revealed poorly diversified wood assemblages (see Del Fueyo et al., 2021), suggesting links with a single group of plants. However, the presence of *Agathoxylon santanensis in* the Aptian Equatorial Hot Arid belt of Chumakov et al. (1995) ratifies the inference of Phillipe et al. (2004) that the parent plants survived in different climatic zones in the early Cretaceous and their occurrence were not climatically controlled.

Since radial pits of the tracheids and of the crossfields are the most important characteristics in the definition of morphogeneric status (Philipe and Bamford 2008) the comparison of the wood from the Araripe Basin with the vast records of *Agathoxylon* species(see Del Fueyo et al. 2021) from the Mesozoic of South America was based on these characteristics. The triseriate alternate, hexagonal radial pitting is shared with *Agathoxylon agathiodes* Torres and Biro-Bagoczky 1986 (Middle Jurassic), *A.* (*Araucarioxylon*) *arayaii* Torres, Valenzuela and Gonzalez, 1982 (Jurassic) *A.* (*Araucarioxylon*) *resinosum* Torres and Biro-Bagoczky, 1986 (late Cretaceous), *A.* (*Araucarioxylon*) *pluriresinosum* Torres and Biro-Bagoczky, 1986 (late Cretaceous), *A.* (*Araucarioxylon*) *kellerense* Lucas and Lacey, 1981 (late Cretaceous), *A.* (*Araucarioxylon*) *chapmanae* Poole and Cantrill, 2001 (late Cretaceous), *A. santacruzense* Kloster and Gnaedinger, 2018 (Middle Jurassic), *A. santalense,* Kloster and Gnaedinger 2018 (Middle Jurassic), *A. termieri* Gnaedinger and Herbst, 2009 (Middle Jurassic). However, the uniseriate, biseriate, and triseriate alternate pit disposition found in these species, contrast with the exclusively

triseriate, alternate, compact arrangement found in *Agathoxylon santanensis* nov. sp. (Fig 3a-d) which is unique and distinguishes the species from the other taxa.

Half-bordered crossfield pitting showing exclusively araucarioid pattern (Fig 3c, d) according to the criteria of IAWA (2004) are shared only with three species, *Agathoxylon santacruzense, A*. *santalense* and *A*. *termieri*. This kind of pitting differs from the cupressoid arrangement present in the remaining taxa and is similar to the alternate intertracheary pitting in extant Araucariaceae (Barefoot and Hankins, 1982; Vogel, 1995). Additionally, the occurrence of a restricted number of pits (4 to 8) in the crossfields, associated with the presence of resin plugs in tracheids in those species are also shared with *A. santanensis*.

In addition to the xylem organization, the presence of axial canals and a belt of sclereids in the secondary phloem point to the extant Araucariaceaceae phloem pattern (Chan 1986; Castro et al.*,* 2006; Castro, 2009).

For Sagasti et al. (2019), the well-preserved secondary phloem identified in a petrified sample of *Agathoxylon* wood from the Jurassic of Argentina, characterized by quadrangular sieve cells with thin and unlignified cell walls, radial parenchyma, sclereids, and uniseriate phloem rays, is comparable to those of extant *Araucaria* species of Argentina (Castro, 2009). Nevertheless, Sagasti et al. (2019) did not register the occurrence of axial canals within the bark, which are typical in the species from the Araripe Basin.

The preservation process obscured most epidermal characters, but there are similarities with the araucarian leaves belonging to most Araucariaceae sections – except for section Eutacta – namely the sessile insertion, stomata with four subsidiary cells and parallel with the leaf axis (Andruchow-Colombo et al., 2018).

Reliable records of fossil plants from the Crato Member also support the affiliation of *Agatoxylon santsanensis* with the family Araucariaceae. Different fossil

taxa, such as *Araucaria cartellei* leaves (Duarte, 1993), *Araucariostrobus* sp. cones (Kunzmann and Bernardes de Oliveira, 2004), branches of *Brachyphyllum obesum* (Duarte, 1985; Kunzmann and Bernardes de Oliveira, 2004; Batista et al., 2017) and *Brachyphyllum sattlerae* (Batista et al., 2017) are common in the plant assemblage. The macroscopic occurrences are also supported by palynological data (Heimhofer and Hochuli, 2010; Souza-Lima and Silva, 2018).

To date, formal systematic identification of *Agathoxylon* for the Mesozoic in Brazilian basins is restricted to the record of *A. africanum* Crisafulli, Dutra and Herbst, 2016 and *A. canoasense* Crisafulli, Herbst and Dutra, 2018, for the Triassic of the southernmost Paraná Basin.

Batista et al. (2017) suggested the occurrence of araucariacean wood in the Aptian Crato Lagerstätte by linking external surface patterns of a *Brachyphyllum obesum* branch and internal anatomical patterns of *Agathoxylon*-type of wood. Nevertheless, formal analysis was not proposed and the poor preservation of the xylem precluded any taxonomic or systematic approach.

The present analyses is the first formal register of the genus *Agathoxylon* from Brazilian Cretaceous periequatorial basins, and amplify the previous global paleobiogeographic distribution of araucarian-like woods for the Aptian-Albian defined by Peralta –Medina and Falcon -Lang (2012). Thus, the occurrence of *Agathoxylon* type of wood with araucarian affinities in periequatorial latitude show that Northern and Soutern biogeographic zones in Western Gondwana were not completely isolated in the Aptian.

Although analysis based on wood growth patterns is problematic when based on a single specimen, the wood growth pattern identified in *Agathoxylon santanensis* allows for speculation on a paleoclimatic signature. The "wood growth interruption zones", identified in the material on study, result from a temporal slowing

down, but not switching off, of cambial activity (Creber and Chaloner, 1984; Schweingruber, 1992, 1996; Wang et al., 2014). Their origin has been mainly attributed to drought, flood, fire, wind damage or unusual low temperature (Fritts, 1976; Ash, 1983; Dechamps, 1984; Ash and Creber, 1992; Schweingruber, 1992, 1996; Young et al., 1993; Falcon-Lang 2003; Wang et al., 2014). The growth interruption zones in the wood seem to be a signal of short abrupt cycles of water shortage interspaced with intervals of favorable growing conditions (Fritts, 1976; Schweingruber, 1992, 1996). This wood signature probably indicates that environmental conditions for the development of araucariacean trees were available in areas not so distant from the Crato paleolake.

Conclusion

The present study provided the taxonomic identification of a gymnospermous wood for late Aptian lacustrine Crato Member of the Santana Formation (Araripe Basin, Brazil) with anatomical characteristics that are certainly compatible with *Agathoxylon*-type wood and led to the delimitation of the new species *Agathoxylon santanensis.*

In addition to the xylem pattern, the presence of axial canals in the non-functional phloem, and the characteristics of an attached leaf showing parallel venation and stomata longitudinally oriented between ridges suggest an affiliation to Araucariceae.

The presence of *Agathoxylon* in the Tropical-Equatorial Hot Arid belt, in addition to its common presence in contemporaneous Warm- and Cool-Temperate belts in the Lower Cretaceous of Western Gondwana, indicate that the genus was not climatically controlled. The growth interruption zones as wood signatures were

probably induced by short water fluctuations during the deposition of the basal interval of the fossil Crato Lagerstätte.

AUTOR CONTRIBUITIONS

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Prof. Dr. Anelise Siegloch: formal analysis, investigation, writing - original draft.

Prof. Dr. Margot Guerra-Sommer: conceptualization, methodology, validation, writing - original draft, supervision.

Dr. Isabela Degani-Schmidt: formal analysis, investigation, writing - original draft.

Prof. Dr. Ismar S. Carvalho: resources, writing – original draft.

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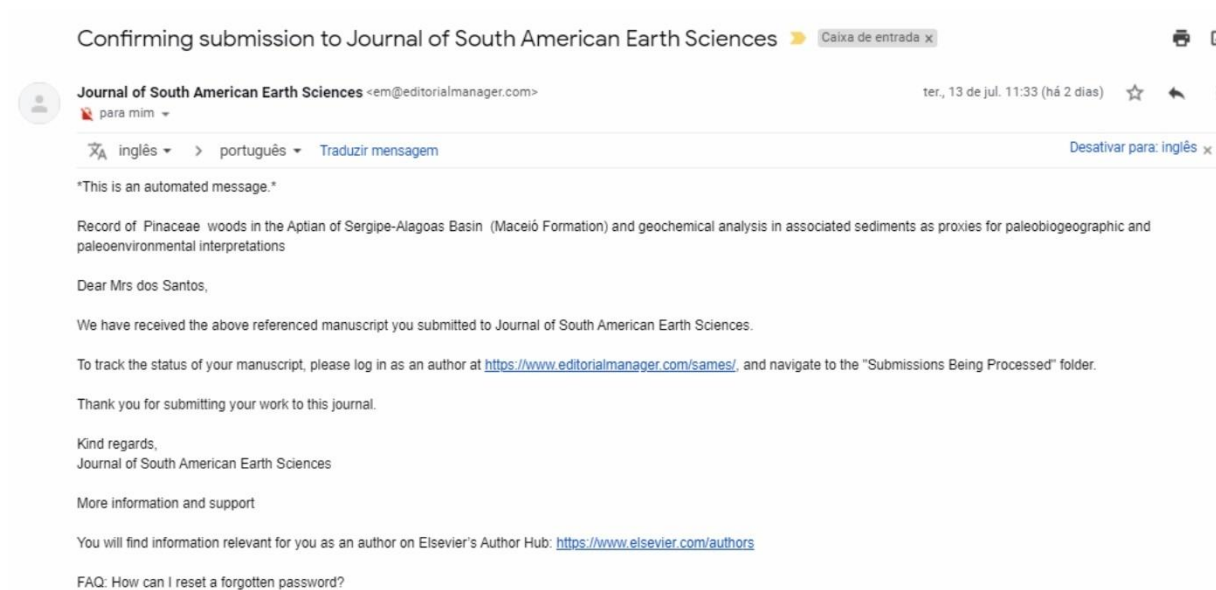
Record of Pinaceae woods in the Aptian of Sergipe-Alagoas Basin (Maceió Formation) and geochemical analysis in associated sediments as proxies for paleobiogeographic and paleoenvironmental interpretations

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Highlights

- First record of Pinaceae wood in the Aptian of Westwern Gondwana.

- Pinaceae radiation from Southern Laurasia through northern Gondwana

- Pinaceae wood details in uncompressed gelified tissues

- Perylene as biomarker of the activity of wood degrading fungi.

Abstract

The first record of Pinaceae wood in South American Gondwana, from the Maceio Formation (Sergipe Alagoas basin), supports implications in the paleogeography of Early Cretaceous of Western Gondwana and led to the inference of Pinaceae radiation from the land masses from Southern Laurasia through Gondwanan African and Brazilian land masses during the Aptian. Wood gelification preserved highly compressed cells, as well as uncompressed tissues that allowed for the identification of intertracheary bordered uniseriate pitting and piceoid crossfield pitting, in addition to physiological axial and radial canals, indicating systematic affinities with Pinaceae. Evidence of decay showed that Pinaceae were available hosts for Basidiomycophyta interactions during the Aptian arid and hot equatorial belt. This implies some environmental forces, represented by windows of opportunity that boosted water regulation in aerobic environments. The organic matter spectrum of the enclosing sediments, dominated by non-opaque phytoclasts and plant cuticles, under the low contribution of terrestrial sporomorphs and absence of aquatic microplankton, suggested deposition in channel distal setting deposits, as part of a river-deltaic interval in a turbiditc system. The identification of perylene in the wood and in the enclosing sediments, ratified relationships of this aromatic biomarker to the activity of wood-degrading fungi.

Key words: Wood anatomy,   Early Cretaceous,   Hot Arid Belt, Palynofacies, Perylene

1. Introduction

The Maceio Formation included in the basin of Alagoas (part of the Sergipe-Alagoas basin) (Fig. 1) signifies the end of the rift tectonossequence and represents the definitive break-up of Africa and South America. The first evaporitic deposits occurred during the evolution of a rift in the drifting basin (Faria de Almeida et al., 2016).
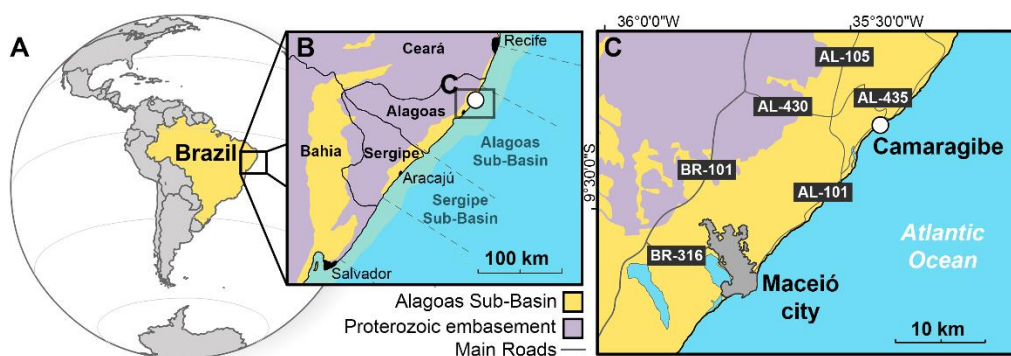
Figure 1. Location map. (A, B) Sergipe-Alagoas Basin; (C) Camaragibe outcrop (modified from Carvalho et al., 2006).

Faciological analyses of the Morro do Camaragibe main outcrop of the Maceio Formation have pointed to a set of facies related to the deposition of gravitational flows into a rift lake (Nascimento and Silva Filho, 2005; Arienti, 2006; Almeida et al., 2017). This process generates intense faults at the basin edge, conditioning large accommodation spaces that are filled by sediments from nearby sources, commonly carried by catastrophic flows.

Abundant dark-gray wood fragments randomly dispersed in the Morro do Camaragibe's main outcrop have often been called "coaly fragments" (Feijó, 1994; Nascimento and Lima Filho, 2005; Arienti, 2006; Almeida et al., 2017). However, their taxonomic affinity and identification as charred (burned) or coalified (compressed) wood has never been established.

The goal of the present study was to establish the botanical affinity of a fossil wood fragment included in the sedimentary packet of the Camaragibe outcrop and identify the mechanism of its preservation using MEV and organic petrographic analyses. In addition, geochemical analyses (palynofacies, total organic carbon (TOC), and aromatic biomarkers) were conducted to study the underlying and

overlying sediments to identify the probable source of organic material in the context of turbiditic deposition.

2. Geological and Paleontological Synthesis

The Sergipe-Alagoas basin, located in the northeast of Brazil, covers a total area of 44,370 km^2 and has the most complete stratigraphic sequence of the eastern Brazilian continental margin (Fig. 1). It is bound by the Alto de Maragogi in the north. The emerged part of the basin is bound by the Estância platform in the south, and in the ocean, it is bound by the Vaza-Barris fault system (Faria de Almeida et al., 2006).

The entire basin presents five tectonic sequences: syneclise, pre-rift, rift, transgressive drift, and regressive drift (Feijó, 1994; Mohriak et al., 1997, 1998; Azambuja Filho et al., 1998; Souza-Lima et al., 2002).

The Maceio Formation, composed of sandstones, shales, evaporites, and calcilutites, is a 3rd order sequence with a subsurface thickness ranging from a few meters to 3000 m, and a thickness of approximately 600 m in the emerged area (Abreu and Potter, 1990).

Galm (1997) identified non-marine ostracods in highly reworked sediments. In addition, Carvalho and Arai (2001) described cizidian concheostraceans under arid climatic conditions, with a negative water balance. Distinct species of actinoptherygian fishes from continental or marine waters were described by Jordan (1910) and Santos (1985), whereas clupeomorph species (Malabarba et al., 2002) pointed to a probable continental environment. The presence of vertebrate coprolites, probably originating from carnivorous fishes of continental to brackish waters, was reported by Souto and Schwanke (2010).

The occurrence of *Sergipea tenuiverrucata* pollen grains (Carvalho, 2004; Heimhofer et al., 2010; Arai et al., 2013), included in the *Dejaxpollenites microfoveolatus* zone (Regali et al., 1974), suggested a deposition in the upper Aptian (115.80 and 111.30 Ma) according to the International Stratigraphic Chart (2020). Plant fossils are not described in this unit.

The Morro do Camaragibe (09°20'06.43"S, 35°26'25.97"W) is an anticline with an approximate length of 800 m. The deposition is linked to the distal part of a turbidite system representing the deposition of gravitational flows into a rift lake (Nascimento and Silva Filho, 2005; Arienti, 2006; Almeida et al., 2017).

The north and central geographical domains of the outcrop are considered a part of the predominantly river-deltaic portions of the system and are closer to the source area, and the southern domain corresponds to the sedimentation in the fringe deposits of the turbiditic system (Almeida et al., 2017).

In the present study, different anatomical and geochemical analyses were performed on a wood fragment and sedimentary facies. The specimen was obtained from the basal horizon of the central domain of the Morro do Camaragibe outcrop (Fig. 2), as defined by Almeida et al. (2017).

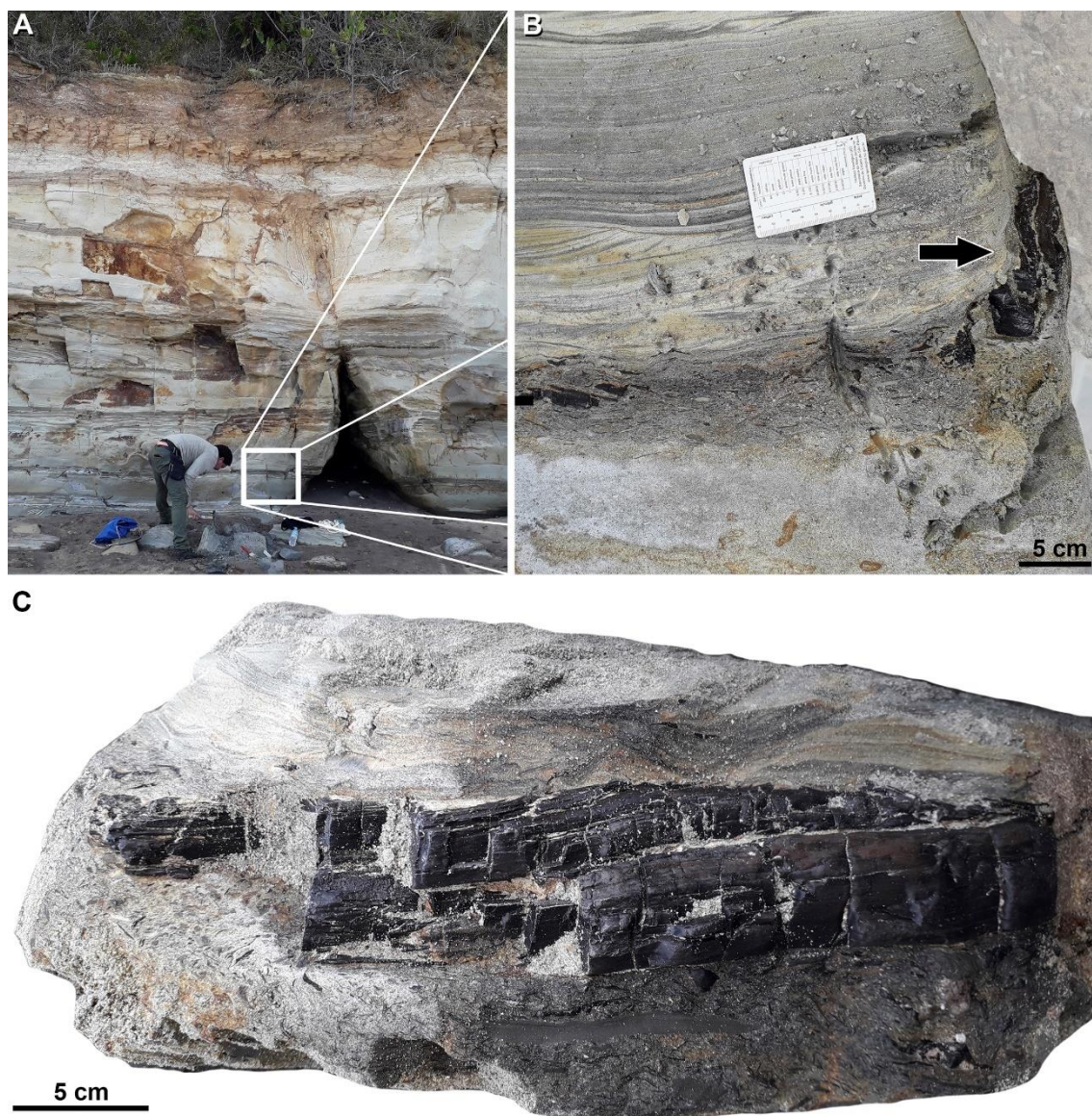Figure 2. Wood sample and enclosing facies in the basal horizon of the central domain of the Morro do Camaragibe outcrop. (A) General view of the studied level and collection point of the sample; (B) detail from (A) showing the wood sample (arrow) between underlying medium grained sandstones with abundant dark wood clasts and overlying medium sandstone with fining upward cycles; (C) close-up of the wood specimen.

3. Material and Methods

3.1 Fossil wood specimen and enclosing sediments

The specimen was an elongated wood fragment (length 20.6 cm × width 3.10 cm), displaying black color and a lustrous sheen. It was found in horizontal disposition, interspersed between underlying medium-grained sandstones with a high amount of darkish wood clasts and overlying medium sandstone forming fining-upward cycles.

3.2 Methods

The following methods were employed to analyze both the wood fragments and the enclosing sediments.

3.2.1 Anatomical Analysis of wood: MEV/ FEG

Anatomical analysis was conducted using scanning electron microscopy (SEM) and an Inspect F50 FEI scanning electron microscope located at the Centro de Microscopia e Microanálises IDEIA at Pontifícia Universidade Católica do Rio Grande do Sul, Brazil, was used for the analyses. The same slides were used for anatomical analyses, which were gold-coated for SEM observation.

3.2.2 Organic petrography

Petrographic analysis was performed on polished blocks covered with oil (Immersol 518 F) using an Axioskop 2 Plus Zeiss microscope equipped with a spectrophotometer J&M Microsystem (MSP 200) and a 50 × objective. The microscope was calibrated using a sapphire standard (0.595 %Ro). The same blocks were analyzed to obtain reflectance data as a proxy for estimating charring temperature (e.g., McParland et al., 2009).

3.3. Palynofacies

The samples were prepared using a non-oxidative procedure for sedimentary organic matter, as described by Mendonça Filho et al. (2010). Samples were fragmented and first treated with HCl and HF, followed by heavy liquid (ZnCl$_2$) to concentrate the organic matter, which was then mounted on slides.

Particulate organic matter was qualitatively examined using microscopy techniques to characterize organic matter. A total of 300 to 500 particles were counted for each sample and normalized in percentiles according to the criteria used by Mendonça Filho et al. (2010).

3.4 Total Organic Carbon (TOC)

The total organic carbon and sulfur in the sediment samples were determined using the LECO SC 144 apparatus. The methods adopted were NCEA-C-1282 (United States Environmental Protection Agency, US EPA, 2002) and ASTM D 4239 (American Society for Testing and Materials, ASTM, 2008).

3.5 Biomarkers

Aromatic hydrocarbons were analyzed using a gas chromatograph coupled to a mass spectrometer (GC/MS). The soluble organic matter (50 g) was extracted with dichloromethane, and subsequently fractionated using an open column liquid chromatography of activated silica. The injector temperature was set to 280 °C. For saturated hydrocarbons, the GC oven temperature program was set at 80 °C (3 min) to 150 °C at a rate of 35 °C/min and to 310 °C at a rate of 3 °C/min. For the identification of the aromatic fractions, the GC oven temperature program was as follows: 40 °C for 5 min and then 4 °C/min to 290 °C for 30 min. MS was operated in electron impact ionization mode at 70 eV with an ionic temperature of 290 °C, interface temperature of 300 °C, and quadrupole temperature of 150 °C. Compounds were identified using MS library comparisons and the data available in the literature.

4. Results and Discussion

4.1. Wood preservation process

4.1.1. Macroscopic analysis

The elongated wood hand specimen (length 20.6 cm × width 3.10 cm) showed black color and a lustrous sheen. It did not soil hands when rubbed and exhibited a vitreous fracture (Fig. 2C), similar to that of vitrain in bituminous coal.

4.1.2. Microscopic analysis

Incident white light illumination and incident blue light excitation analyses on different regions of the single wood showed different stages of preservation, consisting of original cell shapes and cell wall architecture in some tissues (Fig. 2A). However, other tissues showed partially and fully compressed cell wall tissue (Fig. 2B), lacking detailed cell wall structures due to cell wall thickening (Fig. 2C and D).

This result agrees with the gradual morphological change observed in the original cellular structure through gelification, as defined by Spackman and Barghoon (1964), Cohen (1968), Stach et al. (1982), and Bend (1992). In this process, the tissue structure is lost or preserved by a series of biochemical processes that cause swelling, degradation, and infilling of cell lumina and the destruction of recognizable plant cellular structure.

Stach et al. (1982) and Teichmüller (1989) defined the gelification process as the biological and chemical breakdown of carbon molecules in the lignite stage. These processes were part of the broader phases of diagenesis and eodiagenesis during coalification.

The almost uncompressed parenchymatic tissue of rays presented in Fig. 3A (Ro= 0.38–0.40%) exhibited similar reflectance values to the highly compressed ones, presented in Fig. 3B (Ro= 0.33%), in which swelling of the cell walls results in the disappearance of the original detailed cell wall structures and gradual reduction of the cellular lumen. Similar reflectance indices (Ro= 0.36-0.4%) were obtained in regions showing total obliteration of any original cell wall structure (Fig. 3C and D). None of the sections exhibited autofluorescence under incident blue light excitation (i.e. Fig. 3D).
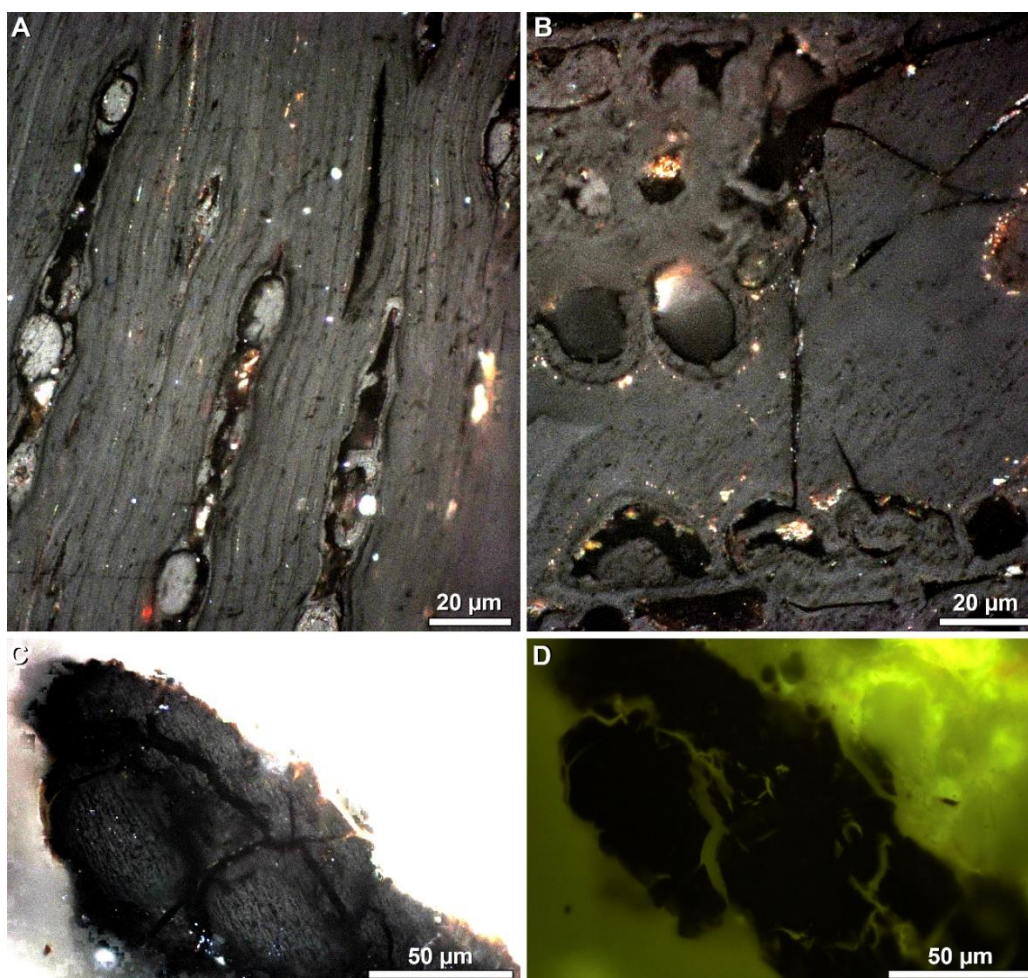
Figure 3. Photomicrographs of polished sections of the gelified wood; (A) uncompressed ray tissue; (B) different stages of compressed xylem; (C) and (D)higly compressed wood. (A), (B), (C) incident white light illumination; (D) incident blue light excitation (Fluorescence Mode).

The general characteristics of the material led to the adoption of the terminology proposed by Stach et al. (1982) for the description of gelification processes when the precursor of vitrinite is included in the huminite group. Different maceral names were used because they exhibited only minor resemblances to their coalification products.

Maceral analyses revealed the dominant presence of maceral/sub-macerals of the huminite maceral group, classifying the material under study into the category of gelified wood, according to the criteria defined by Stach (1971). The average reflectance analyses (Ro = 0.36%) indicated that, in general, the material was considered immature (Ro between 0.2% and 0.4%) and belonged to the category of lignites, according to different classification systems (UN-ECE, 1998; Stach et al., 1971; Alpern and De Souza, 2002; ISO, 2005).

The results from the Early Cretaceous wood sample show a higher degree of gelification as compared to the data obtained from an assemblage of wood samples from Victorian (Australian) Miocene soft brown coal (Russel, 1984).

b. Eletronic Microscophy Analysis (SEM)

The presence of a distinctive middle lamella in cell walls revealed by SEM analyses (Fig. 4A) in several regions of the wood prevents the identification of cell wall homogenization, which is a typical morphological change occurring during the process of origin of charcoal. (Scott and Jones, 1991a; Jones, 1999, Scott, 2010; McGinnes et al., 1971).   The lack of detailed cell wall structure in some areas of the wood (Fig. 4B). is attributed to the gelification process.
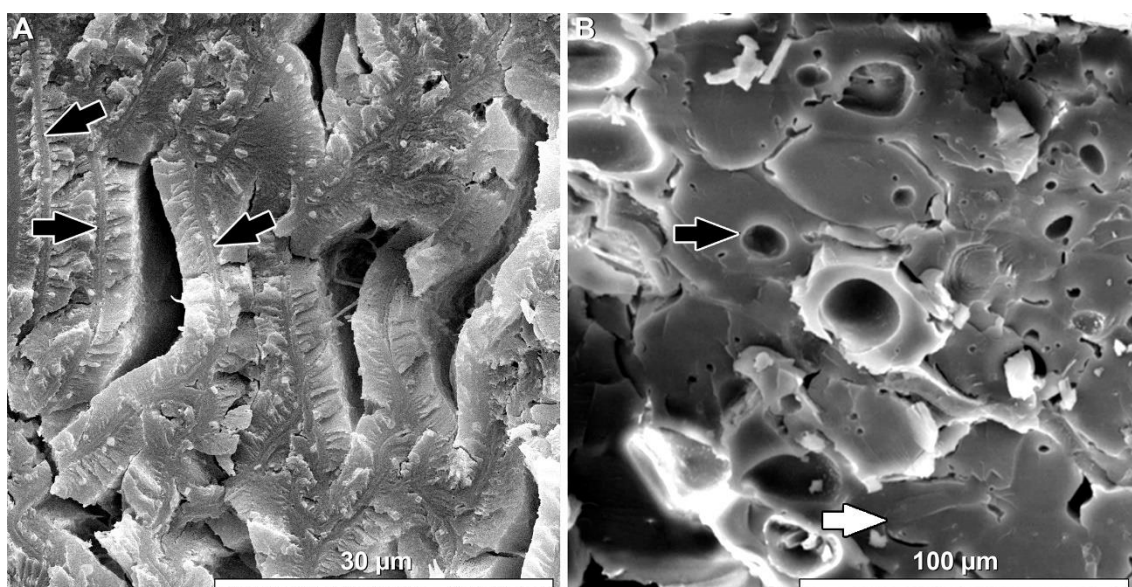
Figure 4. Tissue preservation in transversal section under SEM. (A) Preservation of distinctive middle lamella (arrows) between the cell walls of compressed tracheids; (B) progressive reduction of cell lumen (black arrow), and destruction of recognizable plant cellular structure and homogenization of cell walls (white arrow).

4.2 Wood Anatomical Analyses

Anatomical analyses showed primary and secondary xylem with a typical gymnospermous pycnoxylic pattern. In the cross-section (TS), tracheids were frequently deformed and flattened, showing broken cell walls (Fig. 5A) in some cases curved (Fig. 5B). When uncompressed, the tracheid is oval in shape (Fig. 5C) and rarely polygonal (16 × 16.6 μm). Cell walls with a thickness of 1.3–1.7 μm show a middle lamella with approximate dimensions of 2.7 × 3.3 μm, and intercellular spaces around the cell corners (Fig. 5B and C).
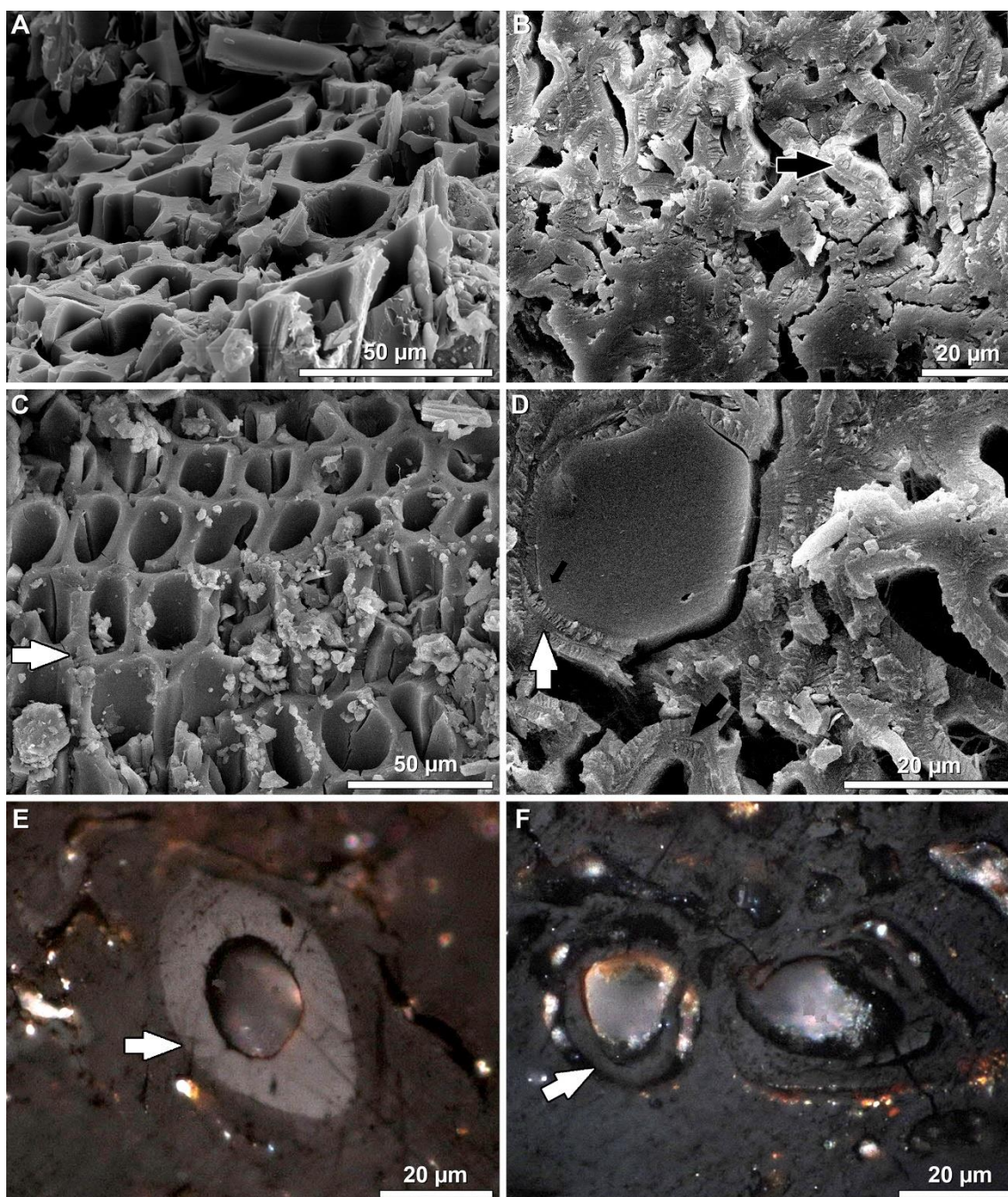
Figure 5. Xylem tissue in transversal view. (A) Partially compressed tracheids with broken cell walls; (B) highly compressed tracheids with curved walls and preserved middle lamella (black arrow) (C) uncompressed oval tracheids and preserved intercellular spaces (white arrow); (D-F) intercellular axial canals with circular lumen lined by epithelial cells (white arrow).

Randomly dispersed intercellular axial canals were oriented longitudinally among tracheary elements, either in solitary arrangements or, more often, in a group of two canals, with circular, weakly compressed lumen (17.1 × 26 µm on average), internally lined by thick epithelial cells (Fig. 5D, E and F).

Spiral-shaped secondary wall microfibrils (Fig. 6A) and intertracheid spiral fissures (Fig. 6B) with a spiral angle between 60° and 70º (Fig. 6A and B) were

observed in the radial sections (RD). Jefferson (1987) attributed the preservation of distorted microfibrils in petrified conifer wood from the Lower Cretaceous of Antarctica to early cell-wall impregnation during the fungi-influenced decay process.
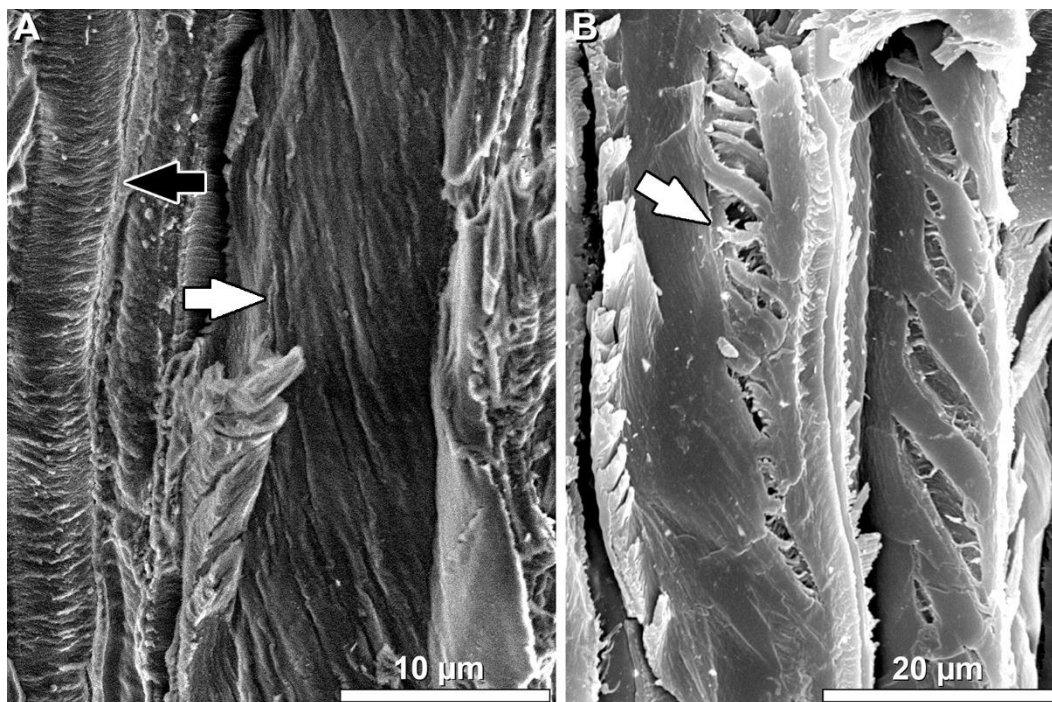
Figure 6. Xylem in radial section. (A) Spiral microfibrils in the secondary wall (white arrow); spiral to reticulate thickening of primary xylem (black arrow); (B) spiral tears in tracheid walls (arrow).

In contrast, Bodnar et al. (2013) reported that spiral fissures in silicified conifer wood from the Jurassic of Argentina are typical of compression wood, rather than being caused by decay. In the present study, the evidence of high compression in both transverse and longitudinal sections along all the wood extensions seems to result from torsions during the process of gelification.

Axial parenchyma was absent in radial sections, and elements of the primary xylem were characterized by spiral or reticulate thickening (Fig. 7A). The intertracheary pitting of the secondary xylem was characterized by uniseriate circular bordered pitting (14–15 µm in diameter), isolated (Fig. 7B), contiguous (Fig. 7C), and in some cases, partially biseriate (Fig. 8B).

Parenchymatic cells of rays are elongated, thin-walled (2.6 µm), with perpendicular or inclined terminal walls. Cross-field pits show a piceoid organization, with an average of two to four pits per field (Fig. 7D and E). Crossfields showing bordered pits were observed in the marginal rows of rays (Fig. 7F). Longitudinal views of axial canals are also seen in radial sections sowing the lumen and the enclosing epithelial cells (Fig. 7G). Radial canals (Fig. 7H) are also

observed, running parallel to the orientation of parenchymatic cells within rays (10,6 x 5,7 µm diameter).
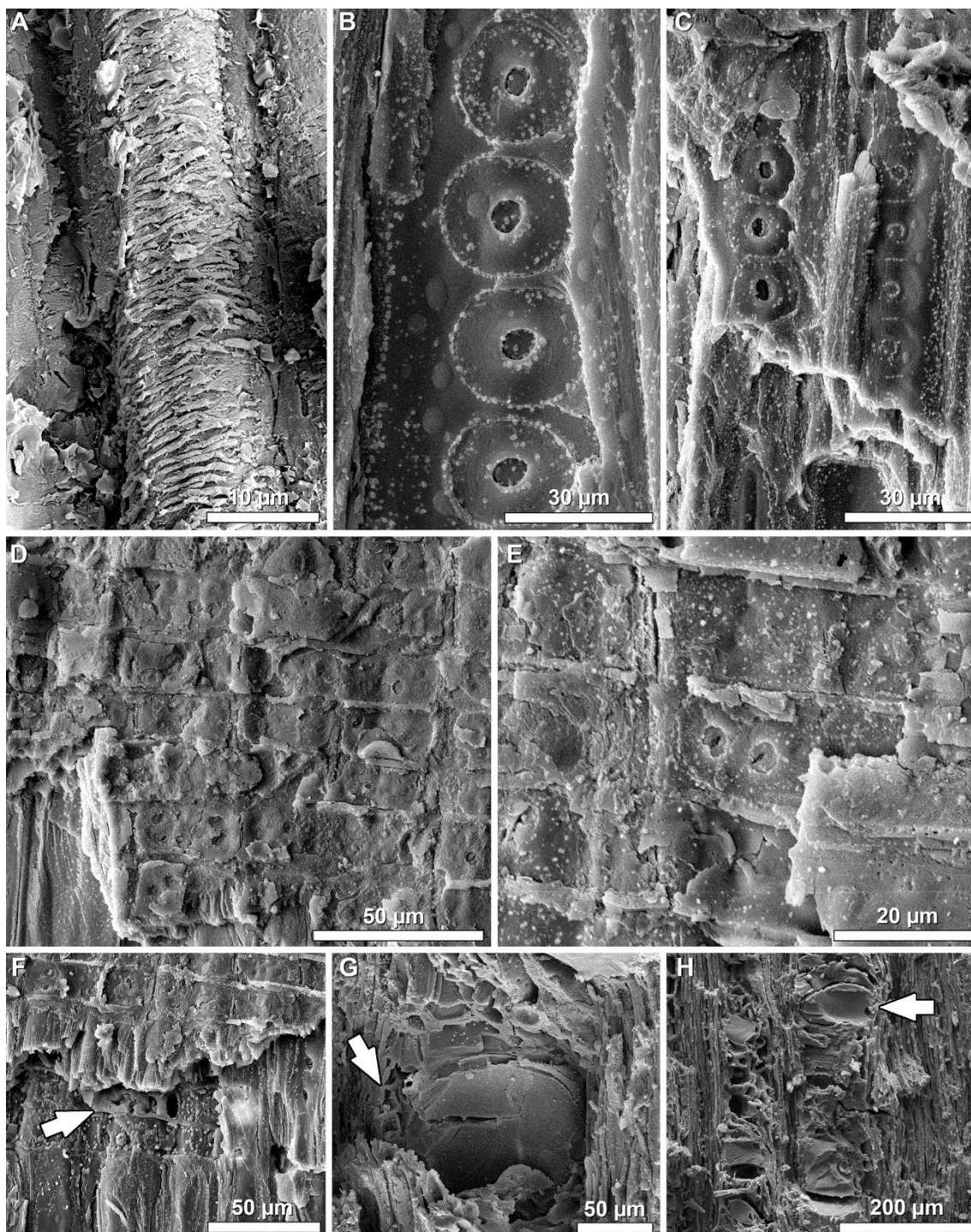
Figure 7. Primary and secondary xylem in radial section. (A) Spiral to reticulate thickening of primary xylem; (B) uniseriate, isolated circular bordered pitting; (C) uniseriate, contiguous circular bordered pitting; (D, E) piceoid crossfield pitting; (F) crossfield bordered pits in marginal ray rows (arrow); (G) longitudinal view of an axial canal showing epithelial cells (arrow) and lumen; (H) radial canals running parallel to the parenchymatic cells in rays (arrow).

Details of tracheid radial pitting were obtained in different preservation stages, from simple circular perforations that demarcated the aperture of the pit (2.9 × 3 μm in diameter) (Fig. 8A) from external convex, circular surface structures showing a circular hollow at the center representing the pit aperture (Fig. 8B). Sometimes, the torus is preserved as a disc-shaped body at the center of the pit aperture (Fig. 8C). In some cases, the margin could not be identified clearly and was approximated (Fig. 8C).
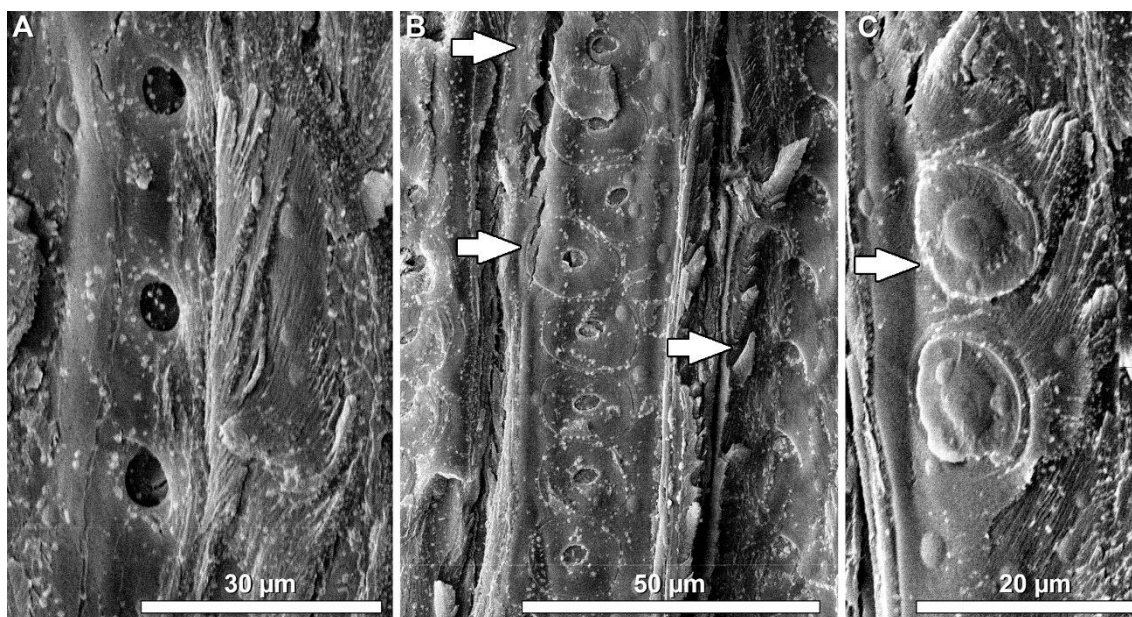
Figure 8. Xylem in radial section and pitting preservation (A) Pit apertures as circular perforations; (B) partially biseriate intertracheary pitting showing outer circular surface (arrows) and circular pit aperture; (C) disk-shaped torus in the center of the pit aperture and margo (arrow).

The torus-margo pitting structure in modern conifers prevents air from spreading between tracheids, avoiding cavitation (Petty, 1972; Domec et al., 2006; Konrad and Roth-Nebelsick, 2005; Evert, 2006). For the Mesozoic, a well-defined torus-margo complex was reported from the Triassic (i.e., Bodnar et al., 2015), Early Jurassic (i.e., Moreau et al., 2019) and Cetaceous (i.e., Schmid, 1967).

Longitudinal tangential sections (LTS) showed uniseriate rays, 2–12 cells high (6 cells on average) (Fig. 9A, B and C). It is also possible to observe the radial canals included in the parenchymatic rays, with circular to elliptical lumens (6.3–12.1 μm in diameter) (Fig. 9D) surrounded by epithelial cells.
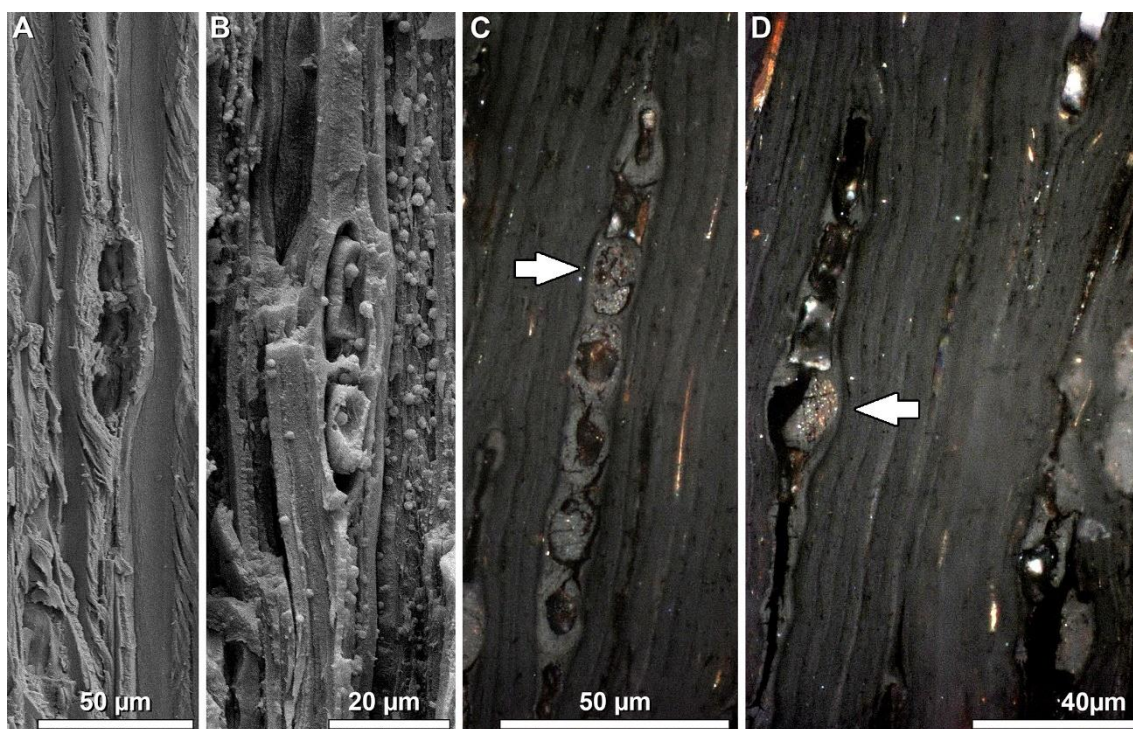
Figure 9. Xylem rays and canals in tangential section. (A, B) Uniseriate parenchyma rays; (C, D) radial canal included in the parenchyma ray with circular lumen (arrows).

Considering the morphogenera with pinoid affinitiy selected by Peralta-Medina and Falcon-Lang (2012) for the Mesozoic *Abiocaulis* (Suzuki), *Cedroxylon* (Kraus), *Keteleerioxylon* (Shilkina), *Laricioxylon* (Greguss)*, Palaeopiceoxylon* (Krause)*, Piceoxylon* (Gothan)*, Pinoxylon* (Knowlton)*, Pityoxylon* (Kraus)*, Protocedroxylon* (Gothan), *Protopiceoxylon* (Gothan), *Protopinuxylon* (Ecklold), the general anatomical pattern of the wood in this study showed similarities with *Laricioxylon* (Greguss) and *Piceoxylon* (Gothan). Both taxa are characterized by the presence of axial and radial canals, in addition to the abietinean disposition of intertracheary-bordered pits (Philippe and Bamford 2008).

Nevertheless, the presence of the intertracheary uniseriate bordered pitting and piceoid cross-field pitting, in addition to physiological axial and radial canals in secondary xylem, exceeds the morphotype criteria established by Philippe and Bamford (2008). The anatomical characteristics points to a biological affinity with the extant coniferous family Pinaceae according to the criteria developed by Greguss (1955), Esteban et al. (2004), and Siegloch and Marchiori (2018). However, the anatomic patterns, although definitive at the family level, are not sufficient for a formal generic designation.

Wood patterns with Pinaceae affinity were recorded for the Lower Cretaceous Botucatu Formation in the Parana Basin (Pires et al., 2011). The affinity was based

on the original description of the genus *Paleopinuxylon* (Mussa, 1974), which was previously described for the same lithostratigraphic unit. The genus was included in the family Protopinaceae defined by Krausel (1917), whose hypothesis was that the Protopinaceae had great phylogenetic significance, being an evolutionary link between Palaeozoic and modern conifers. However, according to Bamford et al., (2016), Protopinaceae is an artificial grouping, and therefore, does not deserve any botanical name sensu ICBN. This is because the taxonomic status is dubious, and it is also no longer tenable that it represents a phylogenetically significant group.

4.3 Wood -fungus interaction

Fungal remains were observed in the xylem tissue in longitudinal and anatomical cross-sections. Walls of fungal hyphae, which are originally composed of polysaccharides (approximately 60% of chitin) and lipids (13%) (Decon, 1984; Isaac, 1992), were colorless, smooth-walled, unornamented (1.9–2.9 µm average diameter), filamentous, mainly tridimensional, and tubular in shape. They occurred in a relatively straight or curved course, showing angle branching (Fig. 10A).

Occasionally, spherical structures were physically connected to a portion of the parental hyphae (Fig. 10A and B), suggesting some relationships with basidiospores produced by extant Basidiomycophyta (Scheureret et al., 2008).

These structures are also similar to the ampule-like hollow structure described by Atfy et al. (2017) from the Late Cretaceous (Bahariya Oasis, Egypt), relatively comparable to an ascus of certain ascomycophytas.

The presence of irregularly septate hyphae (Fig. 10C) indicates a probable relationship with Ascomicophyta, Deuteromycophyta, or Basidiomycophyta (Isaac, 1992). However, a definite affiliation to Basidiomycophyta is indicated by the presence of clamp connections (Dennis, 1969, 1970). (Fig. 11A and B).

Hyphae are commonly flattened when attached directly to the cell walls (Fig. 10B). Tridimensional hyphae were observed penetrating the cell through pit apertures (Fig. 10E and E1), mainly travelling intracellular and can be traced cross-cutting tracheid lumen (Fig. 10D and F), sometimes cross-cutting the cell walls (Fig. 10E2). In certain regions of the wood tissue it was observed a dense concentration of mycelia in irregular void pockets associated to fragments of decayed xylematic tissue (Fig. 11A and B).

In spite that the absence of expressive damage in cell walls of tracheids preclude clear relationships with-the dymanics of white rot decay, the ocurence of clamp conexions in hyphae (Fig. 11A and B), and the progressive degradation that formed, irregular, empty pockets whitin the wood (Fig. 11A and B) validates the hypothesis of Basidiomycophyta wood decaying process.

The broad paleoclimatic context Basidiomycophyta wood-decay record from the late Devonian to the Eocene (see Santos et al., 2020 and citations herein) include warm to tropical and temperate climatic zones (Scotese, 2014).

The present results agrees with Santos et al (2020) that defined fungus-plant interactions in a petrified araucariacean wood during the deposition interval of the Aptian Crato fossil Lagerstätte (Araripe basin) wich imply intermittent periods of favorable temperature/moisture inputs that were crucial for the fungal activity the Equatorial Hot Arid Belt.
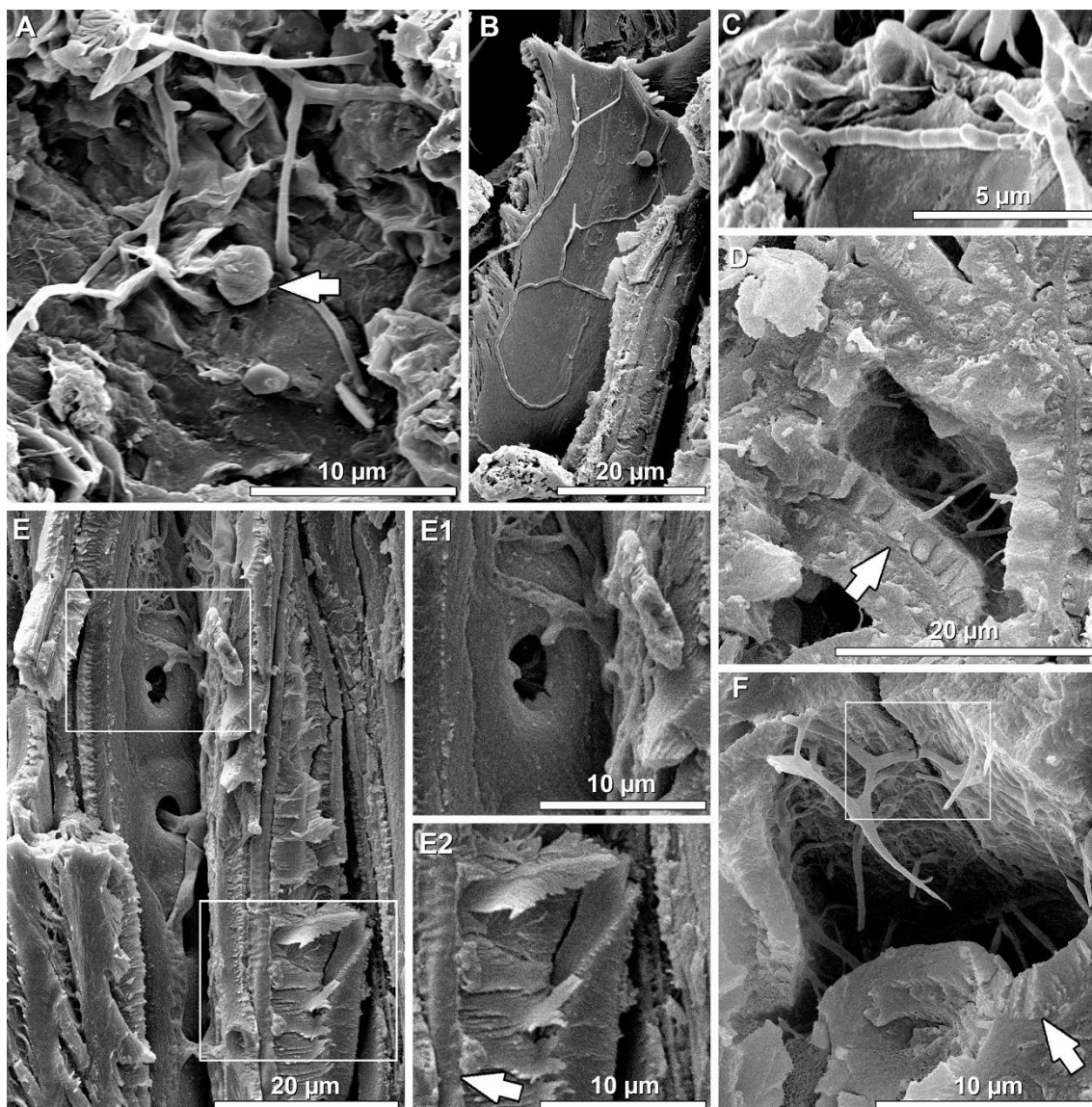
Figure 10. Wood-fungus interactions. (A) Filamentous, tridimensional, unornamented tubular shaped hyphae and spherical structures physically connected to the parental hyphae (arrow); (B) flattened hyphae attached directly to the cell walls; (C) irregularly septate hyphae; (D, F) hypha cross-cutting tracheid lumen and preserved middle lamella (arrows); square outline highlights cracks on the cell wall and broken filamentous hyphae; (E) hyphae penetrating cell through pit apertures and cross cutting cell wall highlighted by square outlines; (E1, E2) details of (E).
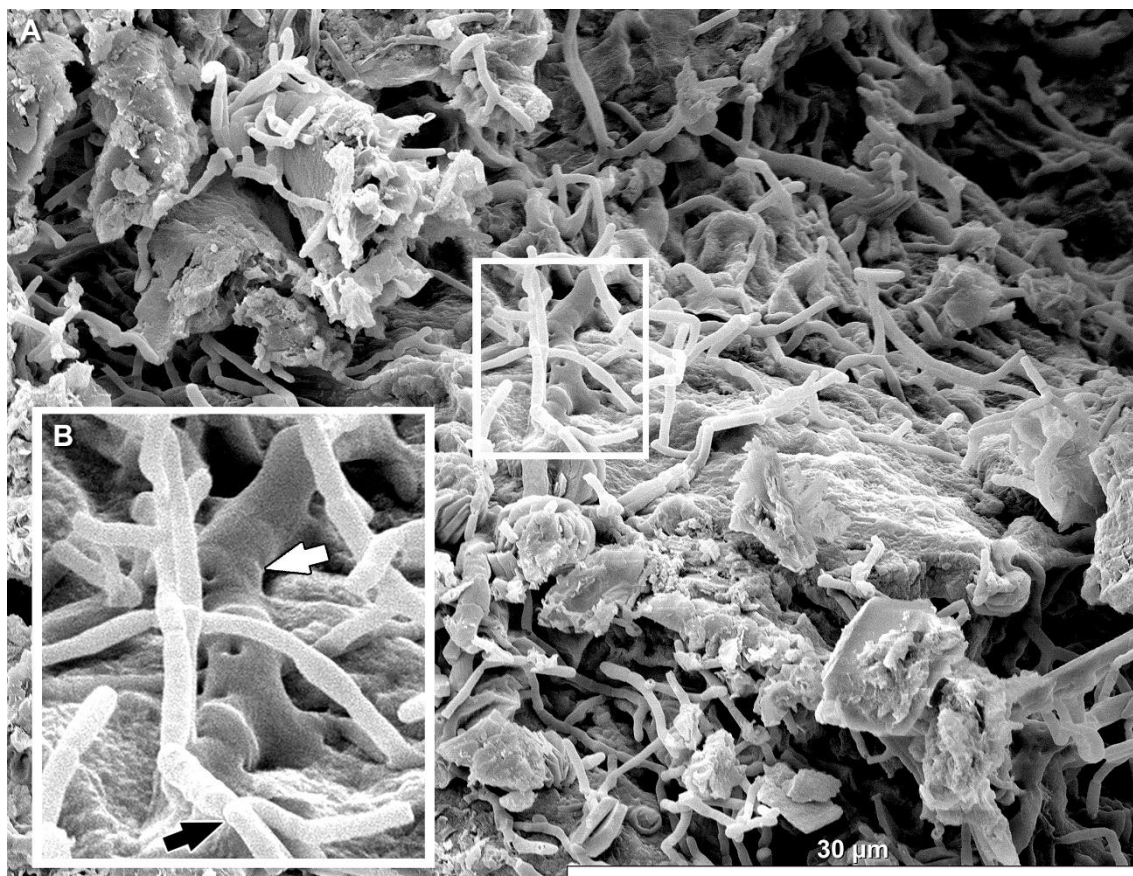
Figure 11. Decay process in wood pockets. (A) General view of mycelia and decayed tracheid fragments; (B) detail of (A) showing irregularly septate hypha (black arrow) and clamp connection (white arrow).

As reaction zones and barrier zones are absent along the infected wood, it is possible to speculate on a likely saprophytic process as the cause of degradation. The possibility of post-depositional fungus-wood interaction was excluded based on distinct evidence, as detailed below. Cracks on the cell wall were commonly accompanied by broken and collapsed filamentous hyphae (Fig. 10F), implying that the same compression process simultaneously damaged the colonizing fungi and the wood anatomy. Additionally, the humic acids that result from chemical transformation processes of lignin and cellulose during gelification make their use unfeasible as a food source for Basidiomycophyta fungi.

4.4 Paleobiogeographical considerations

The differences in the distribution of oceans and landmasses in the Northern and Southern Hemispheres are a consequence of the changing paleocontinental configuration in the Cretaceous (Meyen, 1987; Vakhrameev, 1991; Chumakov et al., 1995, Scotese et al., 2021) and the continental break-up modified paleopositions and shoreline configurations of the landmasses (Holz, 2015). The division of the Earth into isolated landmasses potentially impacted patterns of coniferous biological diversity in the two hemispheres (Philippe et al., 2004; Peralta-Medina and Falcon-Lang, 2012).

According to Hochuli (1981), the Southern Laurasian and Northern Gondwana provinces on the Tethys region during the Early and Middle Cretaceous, in addition to the common presence of conifers represented by *Classopolis* (linked to Cheirolepidiaceae) and *Araucaricites* (linked to Araucariaceae), show major differences in the quantitative distribution of bissacate pollen of pinaceous and podocarpaceus origin, being highly diversified and relatively abundant in Southern Laurasian.

Pinaceae dates to the early Mesozoic, perhaps mid-Jurassic (Axelrod 1986; Millar, 1998; Rothwell et al., 2012; Gerhardt et al., 2018) in the circumpolar continent of Beringia, expanding across lower latitudes around the late Mesozoic and early Cenozoic (Mirov, 1967). However, they remained broadly confined to the Northern Hemisphere (Leslie et al., 2012).

The global distribution of Cretaceous conifers as defined by Peralta-Medina and Falcon-Lang (2012), which provide support for inferences of global patterns of Cretaceous forest composition and productivity, was centered on araucarioid, podocarpoid, pinoid, and cupressoid secondary xylem patterns (reflecting extant Araucariaceae, Podocarpaceae, and Pinaceae).

Wood anatomic data from four intervals (Berriasian–Hauterivian, Aptian–Albian, Cenomanian–Santonian, and Campanian–Maastrichtian) indicated that pinoid conifers were mostly confined to mid- to high paleolatitudes (mostly 40°–65°, mean paleolatitude 46.1°) exclusively in the Northern Hemisphere. For the Aptian–Albian interval, the only instance of Pinaceae in the province of Gondwana corresponded to a record in the northeast of the present African continent.

Therefore, the first record of pinacean wood in South American Gondwana, from the Aptian Maceio Formation in the Algoas marginal basin supports some

paleogeographic implications in the framework of the break-up of Gondwana during the Aptian.

The identification of common terrestrial vertebrate biotas in Brazilian and African basins, showing strong similarities (i.e., the sauropod and coelacanth fauna), was consistent with the proximity of the land masses during the Aptian (Calvo and Salgado 1996). In addition, track analysis from Brazilian and African basins in the Aptian-Albian interval indicated that some paleoichthyofaunas were common to both the land masses, as reported by Parmera et al. (2019).

Based on the distribution showed by Peralta-Medina and Falcon-Lang et al. (2012), the wood anatomical data from the Aptian of Brazilian Sergipe-Alagoas basin led to the inference that this conifer group probably irradiated from southern Laurasia landmasses (present-day Iberian Peninsula) to the north African landmasses in the Lower Cretaceous, becoming commom components in African and Brazilian Gondwanan terrestrial floristic provincies during the Aptian.
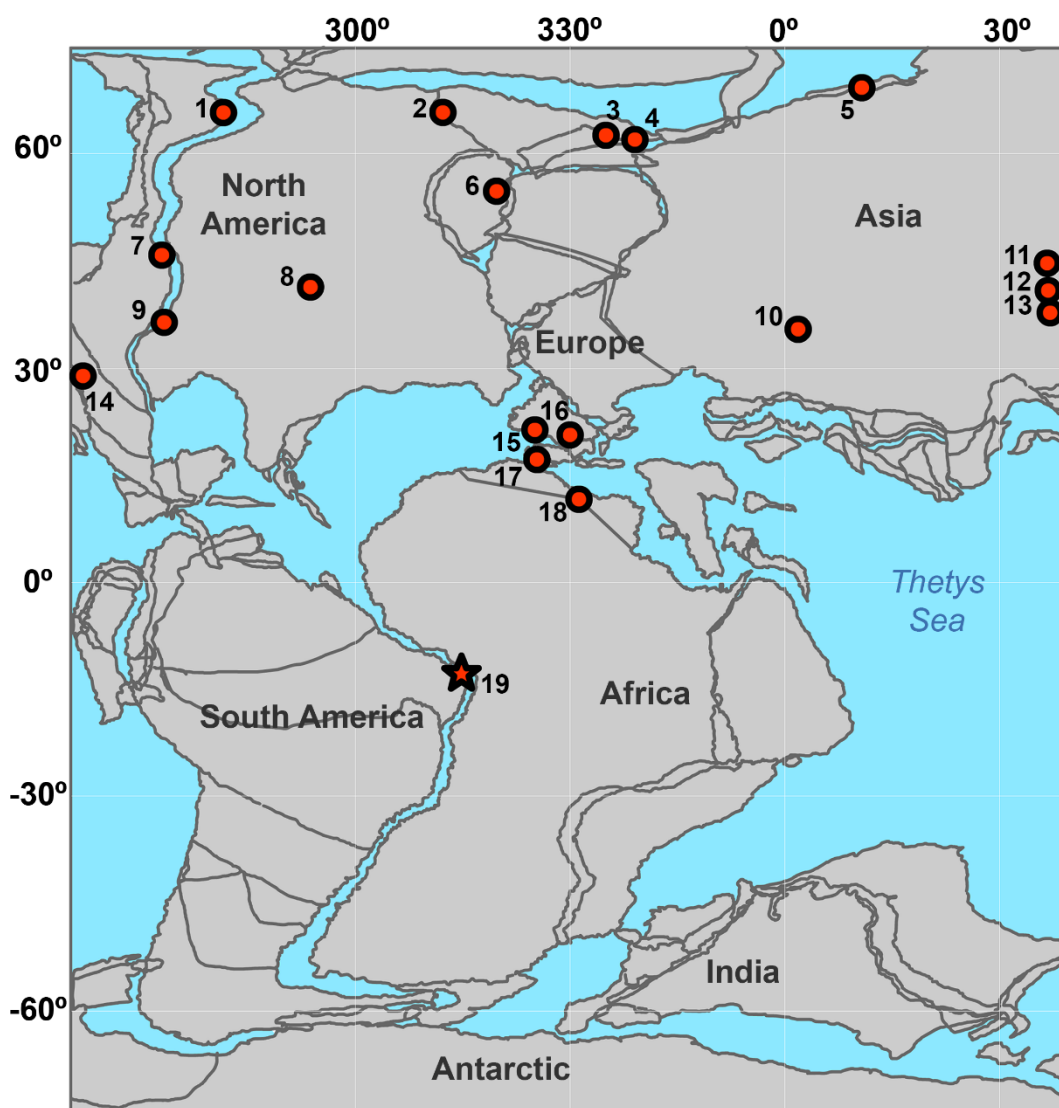
Figure 12. Paleogeographic distribution of Pinaceae woods in the Aptian-Albian (126–99 Ma) continental masses after the general Cretaceous distribution of Conifers of Peralta-Medina and Falcon-Lang (2012) and references cited below. General map modified from Arai (2014). Locality references: 1. Bailey, 1933; 2. Bannan and Fry, 1957; 3, 4, 6. Harland et al., 2007; 5. Blokhina and Afonin, 2007; 7. Tidwell et al., 1967; 8. Berry, 1911; 9. Tidwell and Thayn, 1985; 10. Peralta-Medina and Falcon-Lang, 2012; 11, 12. He, 1995; 13. Shimakura, 1937; 14. Beck, 1871; 15. Stopes, 1915; 16. Fliche, 1897; Lignier, 1913; Carpentier, 1943; Pons 1973,1974,1975; Desplats, 1976; Koeniguer, 1981; Pons et al., 1993; 17. Del Nido et al., 1998; 18. Chudeau,1920; 19. This study.

The occurrence of *Cedripites* Wodehouse pollen grains in the palynological assemblage identified in enclosing sedimentary facies, with botanical affinities to Pinaceae (Grímsson and Zetter, 2011; Stuchlik et al., 2002) reinforces the evidence provided by the anatomical analysis of the wood (Fig. 14E).

Cedripites pollen grains were also registered by Coimbra et al. (2002) for the Cenomanian (Abaiara Formation) of the Araripe Basin*,* in addition to the Aptian/Albian Muribeca and Riachuelo Formations of the Sergipe basin (Carvalho, 2001) and for the Aptian Algamar Formation of Potiguar Basin (Dino, 1992). These palynological data indicate that putative pinaceans were present in the Brazilian Early Cretaceous.

In spite of the importance of conifers in the Brazilian peri-equatorial basins, represented by sterile and fertile fragments of Araucariaceae, Cupressaceae, Podocarpaceae, and Cheirolepidiacea (as synthetized by Santos et al., 2020), there are no published data describing macroremains of Pinaceae for the Cretaceous. This can be attributed to the adaptation of Pinaceae to abiotically stressful environments (Bond, 1989), far from sedimentation basins, rather than to taphonomic bias. In this context, due to their shape, pinacean bisaccate pollen grains can be easily sorted and transported by wind over long distances through the depositional basins.

5. Analyses of Enclosing Sediments

5.1 Palynofacies

The amorphous group (AOM) was absent in the palynofacies association. The particulate organic matter (POM) shows low diversity in both the Facies I light

(medium sandstone forming fining-upward cycles) overlying the fossil wood, and the underlying Facies II dark **(**medium sandstone forming fining-upward cycles).

The OM in both facies is composed of dominant non-opaque phytoclasts (NOP: 93.25–100%), followed by the subgroup of cuticles (26.58–40.00%), and non-opaque, non-biostructured degraded subgroup (10.77–16.08%). (Fig. 13A-F). The palynomorph group (PAL: 0–5.14%) appeared only occasionally, restricted to the Facies I light (Table 1).

Table 1 General composition of the Particulate Organic Matter (POM) in enclosing sedimentary facies

	AOM	Opaq.	PHYTOCLAST					PALYNOMORPH	%C	%S
			Non-Opaque			Total Non Opaq.	Total Phyto.	Sporomorph		
			Non-Biostructured		Cuti.					
			Degrad.	N. Degrad.						
Facies I light	0.00	1.61	16.08	41.80	35.37	93.25	94.86	5.14	0.08	0.10
Facies II dark	0.00	0.00	10.77	49.23	40.00	100.00	100.00	0.00	2.65	0.47
Facies II dark	0.00	0.00	11.96	61.46	26.58	100.00	100.00	0.00	1.44	0.05

Some very thick cuticle fragments, when observed in the transmitted white light mode (MLBT), resemble a dark brown non-opaque phytoclast (Fig. 13G and H). However, in fluorescence mode (MF), these fragments show cuticle structures that are still organically linked to the innermost layers of the epidermis and the leaf mesofilous (Mendonça Filho et al. 2010; 2017). Due to their planar constitution, cuticles remain in suspension, are easily dispersed, and are considered the most buoyant plant debris (Boutler and Roddick 1986; McArthur et al., 2016).
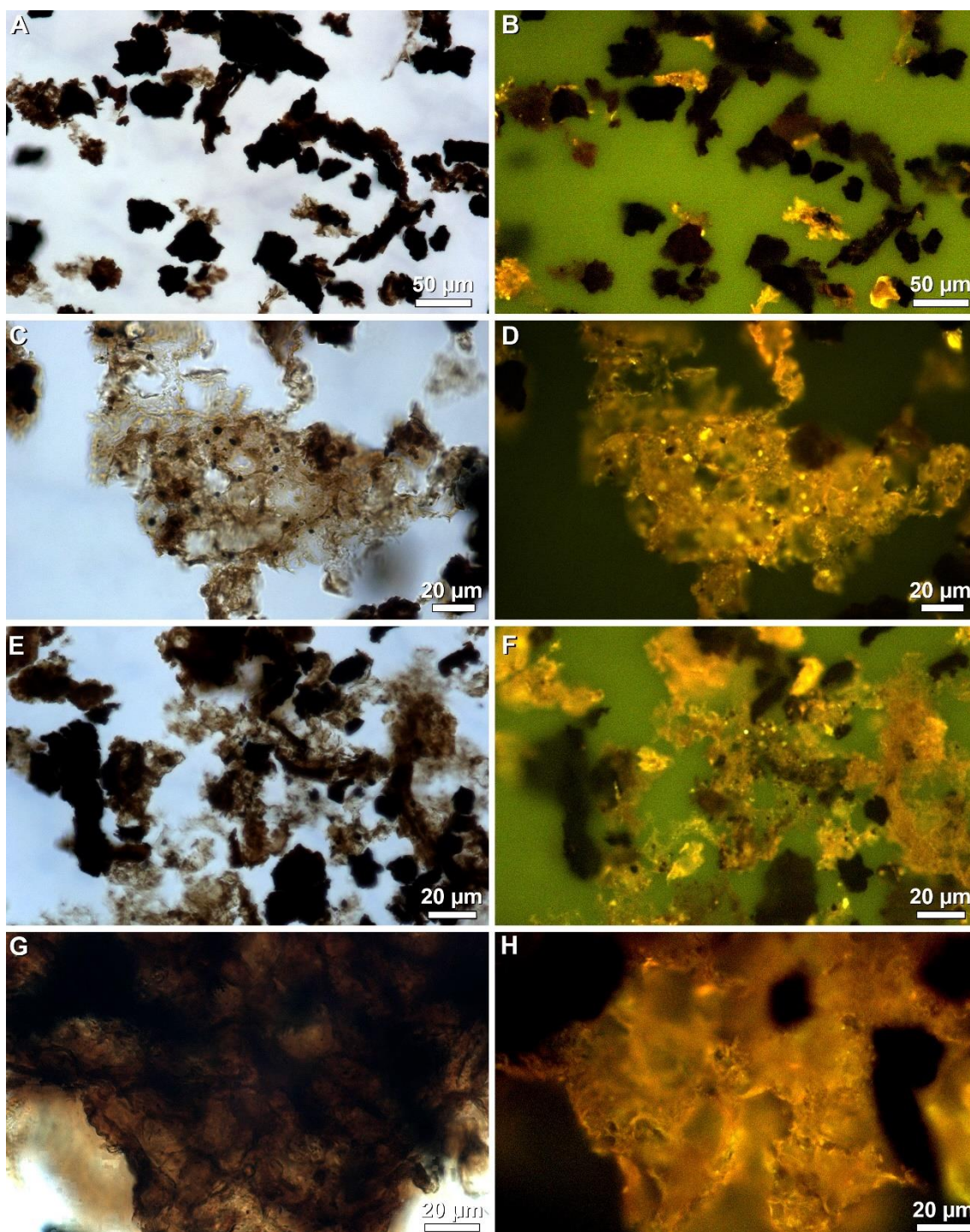
Figure 13- (A), (B): Non-opaque phytoclast. (C), (D): Cuticle. (E), (F): Non-opaque phytoclast and Cuticle. (G), (H): Cuticle. (A), (C), (E) and (G): TWL (Transmitted White Light); B, D, F and H: Incident Blue Light Excitation (Fluorescence Mode).

The Palynomorph group is scarcely represented (5.4%), and exclusively comprises terrestrial sporomorphs (Fig. 14A-E). Botanical affinities of the sporomorph assemblage revealed that gymnosperm pollen grains (95%) largely dominated over pteridophyta spores (5%), reflecting terrestrial contribution from parental vegetation from the hinterland environments (Table 2). This confirmed the presence of Coniferales, including Pinaceae, by the presence of *Cedripites* (Wodehouse) in the source environments. It is important to emphasize that terrestrial sporomorphs have good conditions for buoyancy and are frequently preserved in both proximal and distal settings as exclusive representations of terrestrial environments (Van der Zwan and Van Veen, 1978; Richelot and Streel 1985; Van der Zwan, 1990).

Figure 14- Palynomorphs from the sedimentary facies. Taxa are followed by English Finder coordinates. (A) *Cycadopites* sp. (D11); (B) *Equisetosisporites* sp. (M15-3);

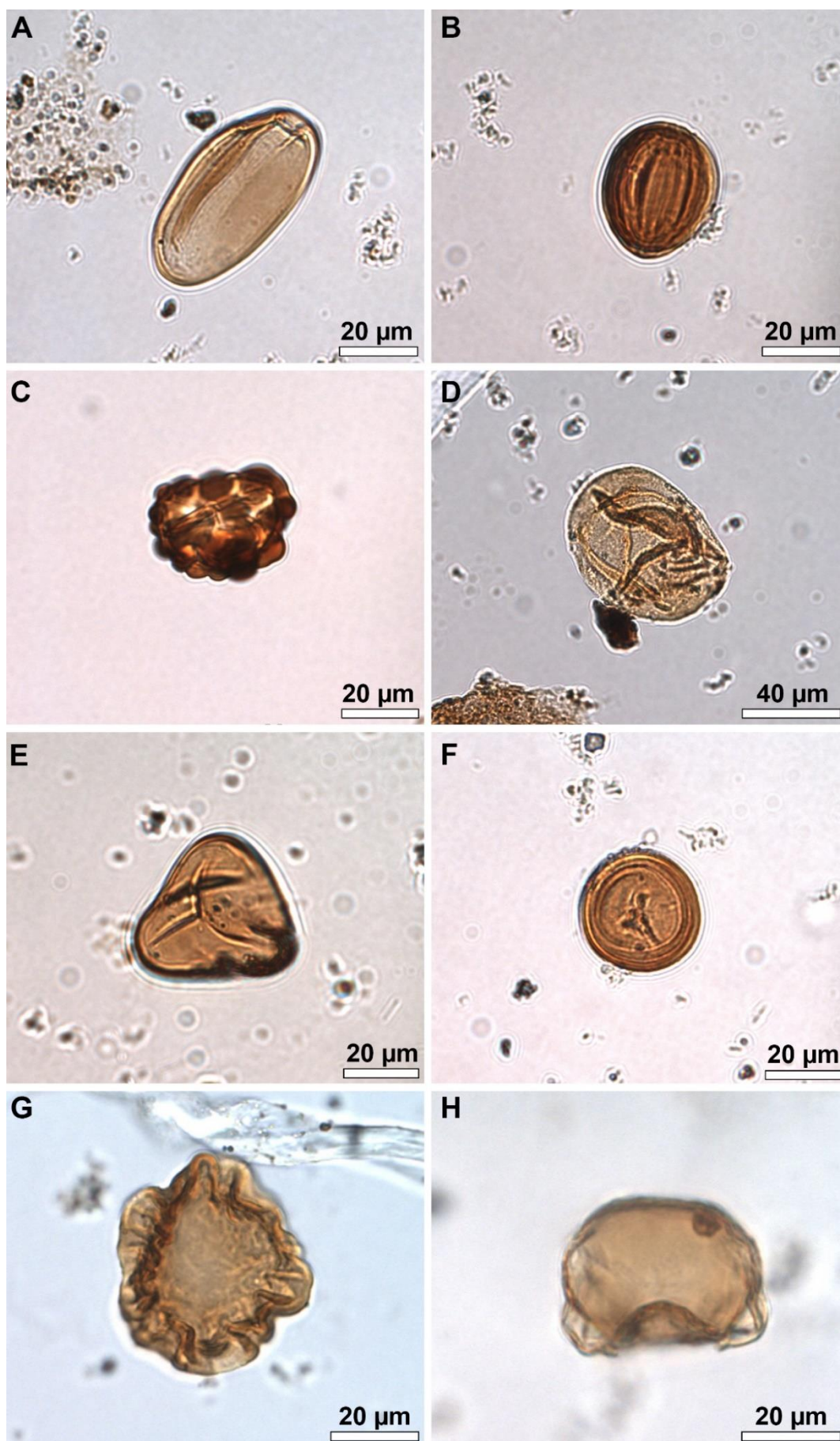(C) *Leptolepidites psarosus* (O42); (D) *Araucariacites australis* (K22); (E). *Deltoidospora* hallii (R16-4); (F). *Classopollis classoides* (R21-2); (G) *Callialasporites segmentatus* (V-4); (H) *Cedripites* sp. (H-5).

Table 2. Botanical affinities of the sporomorph assemblage from the associated sedimentary facies

Taxon	Botanical Affinity	References
Equisetosisporites ovatus	Lycopsyda	Norris (1970)
Deltoidosphora hallii	Cyatheaceae- Dicksoniaceae Dipteridaceae Matoniaceae	Balme (1995) Balme (1995) Guignard *et al.* (2009) Van Konijnenburg-van Cittert (1993)
Leptolepidites psarosus	Pteridophyta	Norris (1970)
Araucariacites australis	Araucariaceae	Balme (1995)
Callialasporites trilobatus *Callialasporites segmentatus*	Araucariaceae Podocarpaceae Pinaceae	Abbink *et al.* (2004) Archangelsky (1994) Batten and Dutta (1997)
Cedripites sp	Pinaceae	Grímsson and Zetter (2011) and Stuchlik *et al.* (2002)
Cycadopites sp 2	Cycadaceae Ginkgoaceae Peltaspermaceae Williamsoniaceae Ginkopsida Pteridospermopsida Bennettitopsida	Balme (1995) Balme (1995) Townrow (1960) Balme (1995) Balme (1995) Balme (1995) Balme (1995)
Classopolis classoides 1	Cheirolepidiaceae	Harris (1979) and Balme (1995)

The palynofacies spectrum allows for correlation with results obtained from an Upper Cretaceous/Paleocene slope channel-levee complex (Rosario Fm., Baja California) developed by McArthur et al. (2016), showing that organic matter was not uniformly spread in turbidite successions. The dominance of well-preserved, non-opaque phytoclasts and plant cuticles, associated with the low contribution of terrestrial sporomorphs in the absence of aquatic microplankton, can be compared with the microscopic distribution of organic matter in channel distal setting deposits, moving away from the channel axis in the model of McArthur et al. (2016). This interpretation agrees with the inferences of Almeida et al. (2017), who considered the deposition of the central dominium of the Camaragibe outcrop as part of the predominantly river-deltaic portions of the system and is closer to the source area.

5.2 Total Organic Carbon (TOC)

The rock packet represented by Facies I light, which overlies the wood sample, was relatively poor in OM content (TOC amount 0.082%), which is attributed to the dilution of organic matter during the depositional process. However, higher TOC values were obtained from the Facies II dark, typically characterized by the occurrence of wood fragments (Table 3).

Tabel 3 - Total Organic Content (TOC) in the wood sample and enclosing facies

Samples	%C	% S	RI	Facies
Sample 1	0.08	0.10	92	Facies I light
Wood	13.72	0.63	86	-
Sample 2	1.44	0.05	88	Facies II dark
Sample 3	2.65	0.47	87	Facies II dark

The higher TOC values of 13.72 % obtained in the sample of gelified pinacean wood are comparable with the values obtained from black shales rich in organic matter, including the dispersed "coaly" wood fragments (14.5%) in the Maceio Formation, from different outcrops on the northern coast of Alagoas state (Nascimento and Lima Filho, 2005).

This led to the speculation that terrestrial conifer wood is an important component of the total organic carbon, and that the type of organic matter is also important in the definition of organic carbon content in sedimentary packets, in addition to the degree of preservation and dilution of organic matter. Total sulfur (S) positively correlated with TOC, and the slightly elevated content of S in the Facies II dark (0.47%) is linked to higher terrestrial influence of OM deposition. In addition, the highest S content (0.63%) found in the wood sample was obtained from humic-derived compounds

5.3 Aromatic Biomarkers

Aromatic biomarkers are common constituents of immature fossil wood samples of different ages and taxonomy (e.g., Otto and Simoneit, 2001; Marynowski et al., 2007; Van Aarssen et al., 2000; Hautevelle et al., 2006).

The samples of wood and the surrounding sediments (Facies I light and Facies II dark) were characterized by the predominance of simonellite, retene, and perylene (Fig. 15 and 16).

Perylene was found in the wood samples and in the overlying Facies I light (Fig. 15). This aromatic biomarker has been mainly used as a molecular tracer product for wood-degrading fungi (Jiang et al., 2000; Grice et al., 2009; Marynowski et al., 2013). Indirect evidence from Holocene sediments and oils supports the hypothesis that there is a strong relationship between perylene and the activity of wood-degrading fungi (Jiang et al., 2000; Grice et al., 2009; Suzuki et al., 2010). In addition, direct evidence from modern lake sediments indicates that perylene originates mainly from the DHPQ *Cenococcumgeophilum,* which corresponds to a resting fungal sclerotium (Itoh et al., 2010, 2012).
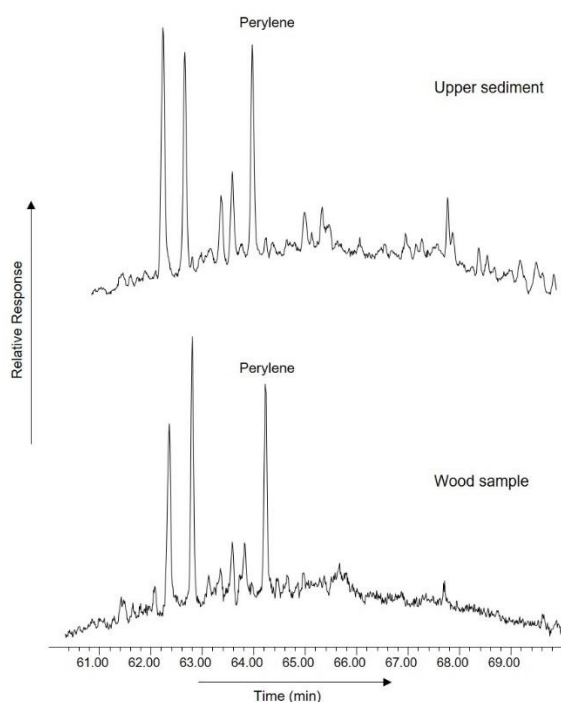

Figure 15- Mass chromatogram for *m/z* 252 showing distribution of perylene.

Retene and simonellite, which have been used in numerous geochemical studies as indicators of higher plant input (Van Aarssen et al., 2000; Otto et al., 2002; Otto and Simoneit, 2001), were found only in the enclosing sediments of Facies I light and Facies II dark (Fig. 16), and were absent in the wood sample.
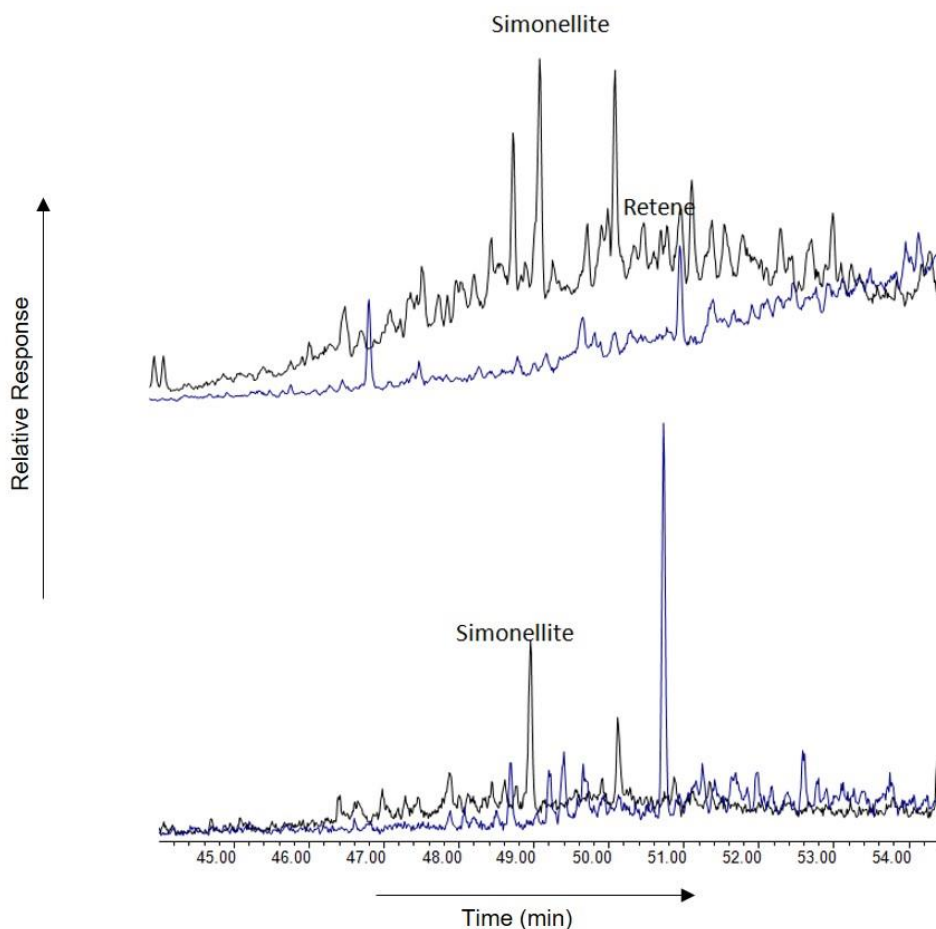
Figure 16- Summed mass chromatogram for *m/z* 219 and 237 showing distribution of conifer wood biomarkers.

However, the simultaneous presence of perylene and simonellite in the surrounding facies is linked to the presence of conifer microfragments dispersed in the sediments, in addition to the products of the fungus-wood decay process, and it is assumed that the absence of simonellites in the wood sample (which would indicate original plant tissues) was a consequence of the fungus-wood decay process.

The present results support the relationship of perylene to the activity of wood-degrading fungi (Marynowski et al., 2013 and citations therein) and contradicts previous hypothesis of Silimann et al. (1998) that considered perylene as an indicator of depositional conditions, rather than the source of organic matter.

6. Conclusions

Based on the analyses of gymnosperm fossil wood and associated sedimentary facies in the Aptian Maceio Formation (Sergipe-Alagoas basin), Northeastern Brazil, the following conclusions can be drawn:

- The gelification process of preservation, despite generating changes in cell architecture in some regions of the wood, preserved almost uncompressed tissues, which allowed for the identification of wood diagnostic anatomical characteristics.

- Anatomical patterns found in the secondary xylem, characterized by intertracheary bordered uniseriate pitting and piceoid cross-field pitting, in addition to physiological axial and radial canals in secondary xylem, led to the establishment of systematic affinities of the wood with Pinaceae conifers.

- The first record of Pinaceae wood in South American Gondwana supports some paleogeographic implications in the framework of the break-up of Gondwana and led to the inference that this conifer group had probably irradiated from southern Laurasian landmasses (present-day Iberian Peninsula) to northern African landmasses in the Lower Cretaceous, becoming commom components in African and Brazilian Gondwanan terrestrial floristic provincies during the Aptian.

- Evidence of xylem decay shows that Pinaceae were available hosts for wood-Basidiomycophyta interactions during the Aptian. Low humidity and high temperature certainly limited fungal activity in the arid and hot equatorial belt. However, the evidence of plant-fungus interaction implies some environmental forces, represented by windows of opportunity in aerobic environments, which boosted water regulation.

- Palynofacies analyses of enclosing sediments revealed the dominance of well-preserved, non-opaque phytoclasts and plant cuticles. Furthermore, the low contribution of terrestrial sporomorphs in the absence of aquatic microplankton suggested that the deposition in channel distal setting

deposits is a part of the predominantly river-deltaic interval of a turbiditc system, as defined for the source of the sediments in the outcrop.

- The identification of perylene as a biomarker in the wood itself and as dispersed elements in associated sediments indicates an association between perylene and the activity of wood-degrading fungi.

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Chart 2020 Chart drafted by K.M. Cohen, D.A.T. Harper, P.L. Gibbard, J.-X. Fan (c) International Commission on Stratigraphy, May 2021.

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ANEXO I

Título da Dissertação/Tese:

ANÁLISES EM LENHOS FÓSSEIS DE CONÍFERAS INTEGRADAS A ANÁLISES GEOQUÍMICAS EM SEDIMENTOS ASSOCIADOS COMO PROXIES PARA INTERPRETAÇÕES PALEOBIOGEOGRÁFICAS E PALEOAMBIENTAIS NO INTERVALO APTIANO DAS BACIAS DO ARARIPE (FORMAÇÃO SANTANA) E SERGIPE-ALAGOAS (FORMAÇÃO MACEIÓ)

Área de Concentração: Paleontologia

Autor: **ÂNGELA CRISTINE SCARAMUZZA DOS SANTOS**

Orientador: Profa. Dra. Margot Guerra Sommer

Examinador: **Profa. Dra. Etiene Fabbrin Pires Oliveira**

Data: 17.08.2021

Conceito: A

PARECER:

A tese analisada consiste de um trabalho robusto, que traz informações paleobotânicas consistentes e inéditas. É um trabalho acadêmico muito bem escrito e desenvolvido de acordo com as normas acadêmicas de escrita e forma. Faz uma apresentação e integração de 3 artigos, sendo um já publicado, que abordam aspectos paleobotânicos relevantes para a caracterização do Aptiano no nordeste do Brasil considerando material fóssil proveniente de duas diferentes bacias sedimentares.

O capítulo de integração contempla o que se propõe, com a análise dos artigos de forma conjunta focando nos objetivos da Tese.

A anatomia de lenhos é muito bem desenvolvida, e é muito satisfatório que tenhamos especialistas nesta área cada vez mais restrita no escopo da paleobotânica.

As sugestões foram realizadas diretamente no arquivo PDF da tese. Aqui, apresento um resumo das contribuições apontadas:

- a colocação dos artigos no final, acaba dificultando um pouco a leitura do texto inicial, visto que as informações acabam se repetindo.

- todas as figuras do capítulo 1 podem ser melhoradas, visto que estão desfocadas.

- a SÍNTESE GEOLÓGICA DAS BACIAS está confusa, e sugere-se uma avaliação da escrita e da quantidade de informações contidas.

Assinatura: *Etiene Fabbrin Pires Oliveira*
Data: 17.08.2021

Ciente do Orientador:

Ciente do Aluno:

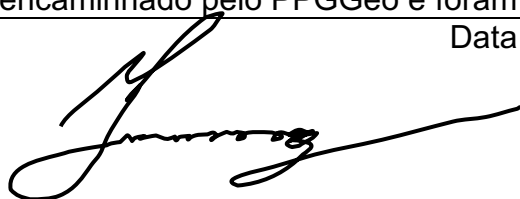| **ANEXO I** |
|---|
| Título da Dissertação/Tese: |
| ANÁLISES EM LENHOS FÓSSEIS DE CONÍFERAS INTEGRADAS A ANÁLISES GEOQUÍMICAS EM SEDIMENTOS ASSOCIADOS COMO PROXIES PARA INTERPRETAÇÕES PALEOBIOGEOGRÁFICAS E PALEOAMBIENTAIS NO INTERVALO APTIANO DAS BACIAS DO ARARIPE (FORMAÇÃO SANTANA) E SERGIPE-ALAGOAS (FORMAÇÃO MACEIÓ) |
| Área de Concentração: Paleontologia |
| Autor: **ÂNGELA CRISTINE SCARAMUZZA DOS SANTOS** |
| Orientador: Profa. Dra. Margot Guerra Sommer |
| Examinador: Prof. Dr. **André Jasper** |
| Data: 17/08/2021 |
| Conceito: A |
| PARECER: |
| Após a leitura atenta do documento apresentado, a defesa verbal dos elementos constantes na tese e a arguição pela banca examinadora, foi possível confirmar que a candidata possui os requisitos necessários para a obtenção do título de Doutora em Ciências (Geociências, Área de Concentração Paleontologia) pela Universidade Federal do Rio Grande do Sul – UFRGS. O trabalho desenvolvido pela candidata tem mérito e demonstra adequação ao método científico, constituindo-se em tese de doutorado. Além do texto integrador, são apresentados três artigos científicos, um deles já publicado e outros dois submetidos. Destaca-se que o texto está muito bem estruturado e, apesar de composto por artigos independentes, é coerente e demonstra o desenvolvimento de um projeto científico robusto, com resultados consistentes e de alto impacto para a paleobotânica nacional e internacional. No momento da defesa e arguição, a candidata demonstrou pleno domínio dos conceitos abordados. Sugestões de retificação e ajustes no documento final foram indicadas no arquivo PDF encaminhado pelo PPGGeo e foram enviadas à candidata via e-mail. |
| Assinatura: Data: 17/08/2021 |
| Ciente do Orientador: |
| Ciente do Aluno: |