



PALEOCLIMATIC INFERENCES BASED ON WOOD GROWTH INTERRUPTIONS IN LATE TRIASSIC FLOOD DEPOSITS FROM THE SOUTHERNMOST BRAZILIAN GONDWANA

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ABSTRACT – The goals of this study were to establish patterns in a silicified wood assemblage to depict the evolution patterns of the Triassic paleoclimate in southern Brazilian Gondwana during an interval of global arid to semi-arid climatic context, and the taphonomic process that led to the preservation of the so-called “Petrified Forest”, which is preserved in the central area of the state of Rio Grande do Sul. Analyses were developed with an assemblage of 13 permineralized conifer wood, using standard thin sections, whose anatomical details were studied in transmitted light. Ground-Penetrating Radar was used to obtain information about the depositional characteristics of the site. Main results are: true growth rings are absent in all samples, and the boundaries of the interruption zones are marked by an abrupt decline in cell diameter, but they are not accompanied by a reduction of cell wall thickness. The subsequent reversion to normal tracheid diameter is also abrupt, revealing the return of the previous growing conditions. Ground-penetrating Radar analyses confirmed that the Mata Sequence deposits correspond to a river. The identification of growth interruption zones in a Late Triassic wood assemblage in southernmost Brazilian Gondwana (Paleobotanic Garden of the city of Mata, RS) indicates the presence of tropical, temporarily dry climate conditions, characterized by irregular, short-term environmental disturbances to growth. The taphonomic process was related to a river-channel infilling depositional process, under the influence of high-energy flood events that dragged and buried the trees.

Keywords: Wood growth patterns, Mata sequence, gymnosperms, Triassic climate, petrified forest.

RESUMO – O objetivo do presente trabalho foi obter assinaturas climáticas por meio da análise de padrões de crescimento em uma associação de lenhos silicificados a fim de retratar os padrões de evolução do paleoclima no Triássico no Gondwana sul-brasileiro durante um intervalo de condições climáticas globais áridas-semiáridas e esclarecer o contexto sedimentar e o processo tafonômico relacionado a preservação da “Floresta Petrificada”, preservada na área central do Estado do Rio Grande do Sul. Seções delgadas foram elaboradas a partir de 13 amostras de lenhos permineralizados, sendo os detalhes anatômicos estudados em microscopia óptica sob luz transmitida. A técnica de Penetração do Solo por Radar (*Ground Penetrating Radar - GPR*) foi utilizada para obter informações sobre as características deposicionais. Os principais resultados foram: ausência de verdadeiros anéis de crescimento nas amostras e todos os espécimes são caracterizados por interrupções de crescimento concêntricas. Os limites das zonas de interrupção são marcados por um declínio abrupto no diâmetro da célula, mas não são acompanhados por uma redução da espessura da parede celular. A reversão subsequente para o diâmetro traqueídeo normal também é abrupta, revelando o retorno das condições de crescimento anteriores. As análises de GPR confirmaram que os depósitos da Sequência Mata correspondem claramente ao preenchimento de canais fluviais. A identificação de zonas de interrupção de crescimento em uma associação de madeira do Triássico Superior no extremo sul do Gondwana brasileiro indica a presença de condições de clima tropical caracterizado por distúrbios ambientais irregulares de curto prazo ao crescimento das plantas, que foram atribuídos principalmente a estresse hídrico temporário. A história tafonômica esteve relacionada a processos de preenchimento de canais fluviais, sob a influência de inundações de alta energia que arrastaram e soterraram as árvores.

Palavras-chave: Zonas de interrupção de crescimento, Sequência Mata, gimnospermas, Triássico, floresta petrificada.

INTRODUCTION

Silicified fossil woods are common in the Triassic at the southernmost Brazilian Paraná Basin in the State of Rio Grande do Sul (RS). They are usually found as rolled pieces on sedimentary outcrops, though they occur rarely

within the sedimentary deposits (Figure 1). The fossil wood record is comprised mainly of conifer-related gymnosperm forms and indicates a mesophytic flora originating during climate changes that took place in global paleogeography where present-day continents formed a single supercontinent, Pangaea, with exposed land extending from about 85°N to

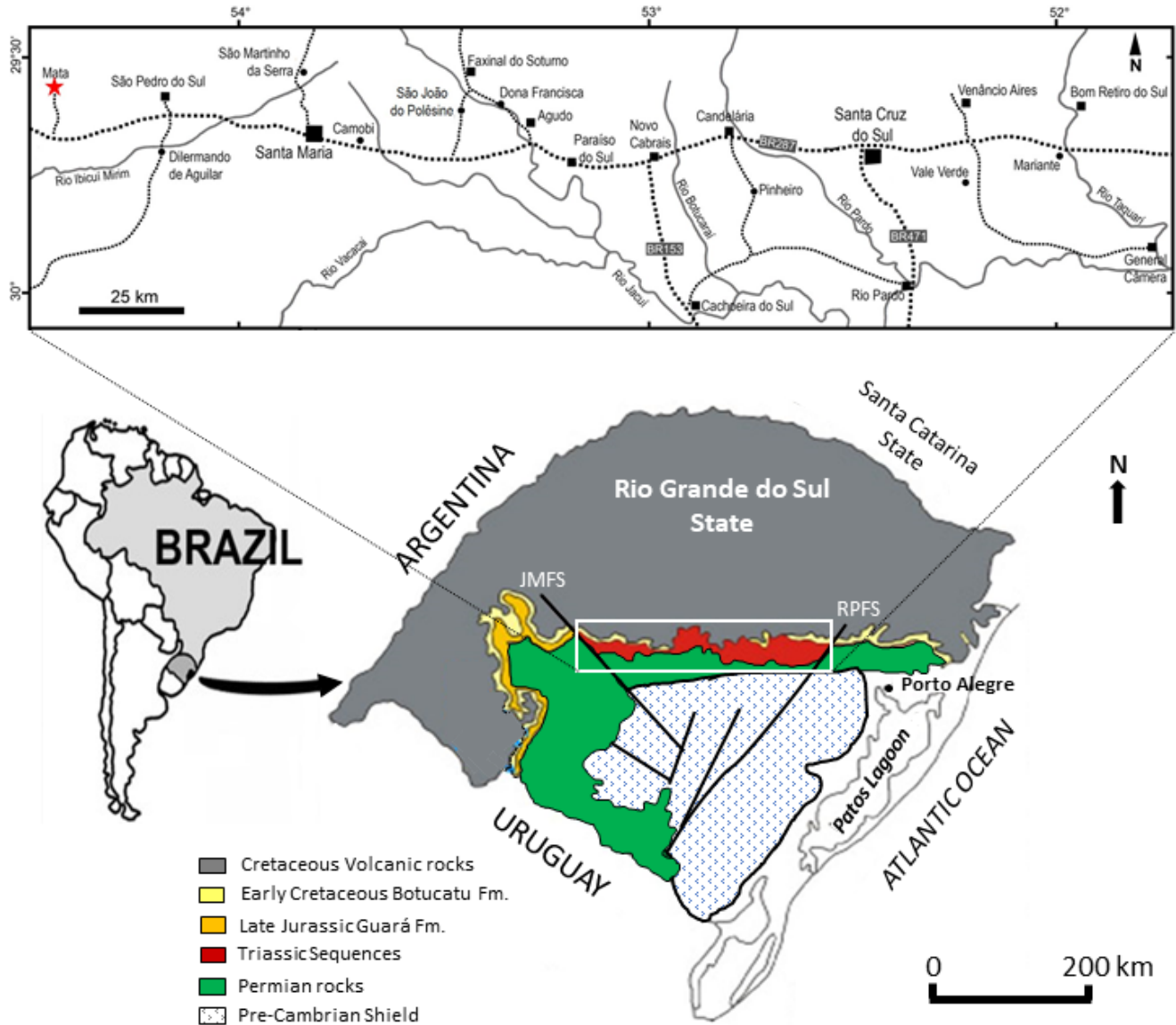


Figure 1. Geographic and stratigraphic positioning of the Triassic sequences in the State of Rio Grande do Sul. The red star indicates the city of Mata, type locality of the Mata Sequence. **Abbreviations:** JMFS, Jaguari-Mata Fault System; RPFS, Rio Pardo Fault System. Modified from Dentzien-Dias *et al.* (2007).

90°S (Ziegler *et al.*, 1983) during an interval of climatic conditions linked to a “hot-house” world with ice-free poles (Spalletti *et al.*, 2003; Preto *et al.*, 2010).

The so-called “petrified forests” that flourish in the E–W belt (Central Depression) of the state of Rio Grande do Sul, mainly in the cities of Mata and So Pedro do Sul (Figure 1), are some of the most important paleobotanical sites in South America and are considered part of the region’s scientific and cultural heritage.

The petrified woods found in several paleontological sites have been correlated with different Triassic, and potentially Jurassic, stratigraphic units (see Crisafulli *et al.*, 2016, 2018, and citations therein). Different wood taxa have been described for distinct localities (Table 1), consisting mainly of gymnosperm pycnoxylic wood belonging to distinct form-taxa. Nevertheless, while taxonomic analyses have been developed previously and already offer an overview of the

floristic diversity, attempts to infer climatic patterns using paleobotanical proxies are still uncommon.

A review of the anatomical studies of wood samples (Table 1) from southernmost Brazil described so far reveals that growth patterns have been identified only briefly and have not been discussed as climatic signatures by the various authors (Minello, 1994; Guerra-Sommer & Scherer, 2002; Bardola *et al.*, 2009; Crisafulli & Dutra, 2009; Crisafulli *et al.*, 2016, 2018).

The working hypothesis of this study is based on an assemblage of silicified gymnosperm pycnoxylic wood from sandy layers of the Norian/Rethic Mata Sequence (Horn *et al.*, 2018a, b), preserved within the geographic limits of the Paleobotanic Garden in the city of Mata, that shows anatomical evidence of growth processes (Figures 2 and 3). The main goal of the study was to obtain signatures by analyzing these growth patterns, as they are relevant proxies

to the predictions of paleoclimate patterns, offering tools for calibration between wood assemblages found in distinct depositional sequences, in order to depict the evolution patterns of the Triassic climate in southern Brazilian Gondwana. Additionally, this study aimed to clarify aspects of the taphonomic process that generated this impressive “Petrified Forest” through stratigraphic analysis coupled with Ground Penetrating Radar.

GEOLOGICAL SYNTHESIS

Stratigraphic framework

Since the publication of Huene & Stahlecker’s (1931) work almost a century ago, the sandstone layers containing

silicified fossil logs in the central region of Rio Grande do Sul, Brazil, especially in the municipalities of Santa Maria, São Pedro do Sul, and Mata (Figure 1), have been mentioned in the literature. However, the stratigraphic position and age of these fossiliferous levels have been quite controversial ever since.

According to Huene & Stahlecker (1931), the fossil logs occurred in the same sedimentary layers, the so-called “Rio do Rasto Red Beds,” *sensu* White (1908), that contain tetrapod remains interpreted as Triassic due to the presence of the rhynchosaurs (*Scaphonyx* Woodward, 1907, *Hyperodapedon* Huxley, 1859). However, a year earlier, Moraes-Rego (1930) had already recognized that the upper levels of the Rio do Rasto Red Beds (precisely those where Triassic vertebrates and silicified logs occurred) that outcropped in Rio Grande

Table 1. Wood taxa described for the Upper Triassic in southernmost Brazilian Gondwana and indicated growth patterns.

Wood Taxa	Location /site	Growth pattern	References
<i>Chapmanoxylon jamuriense</i> (Conifera)	Not informed	Growth rings	Crisafulli <i>et al.</i> (2018)
<i>Chapmanoxylon</i> sp. cf. <i>C. jamuriense</i> (Conifera)	Rio Soturno	Growth rings absent	Crisafulli <i>et al.</i> (2016)
<i>Megaporoxylon kaokense</i> (Conifera)	Rio Soturno	Growth rings	Crisafulli <i>et al.</i> (2016)
<i>Agathoxylon africanum</i> (Conifera)	Rio Soturno	Growth rings	Crisafulli <i>et al.</i> (2016)
<i>Labatoxylon kaokense</i> (Conifera)	Not informed	Growth rings	Crisafulli <i>et al.</i> (2018)
“ <i>Araucarioxylon</i> ” spp. (Conifera)	Cerro da Ermida	Growth zones	Minello (1994)
<i>Baieroxylon cicatricum</i> (Gingkoaceae)	Chiniquá/Água Boa	Growth zones	Bardola <i>et al.</i> (2009)

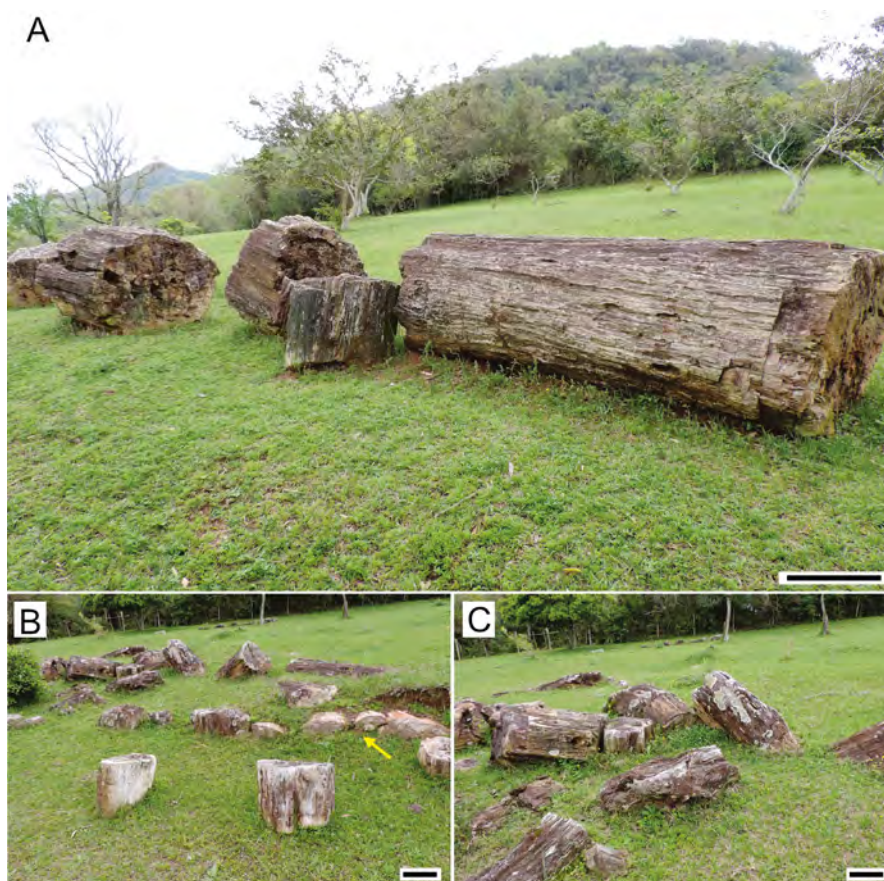


Figure 2. A, general view of the Paleobotanical Garden; B–C, fossil woods of different sizes occur randomly dispersed at ground level and in the subsurface (arrow). Scale bars: A = 60 cm; B, C = 30 cm.

do Sul were distinct from those that occurred in the central and northern portions of Paraná Basin. Moraes-Rego (1930) named these upper levels the Santa Maria Beds (Figure 4). Later, Gordon Jr. (1947) identified a Permian unconformity separating the Santa Maria Beds (Triassic) from the underlying layers, which he called the Rio do Rasto Formation. From his

work, the package of red beds containing both vertebrates and silicified logs came to be called the Santa Maria Formation, restricted to Rio Grande do Sul and the Triassic age.

The first author to propose a stratigraphic separation between the red beds containing vertebrate bones and those where the fossil logs occurred was Bortoluzzi (1974),

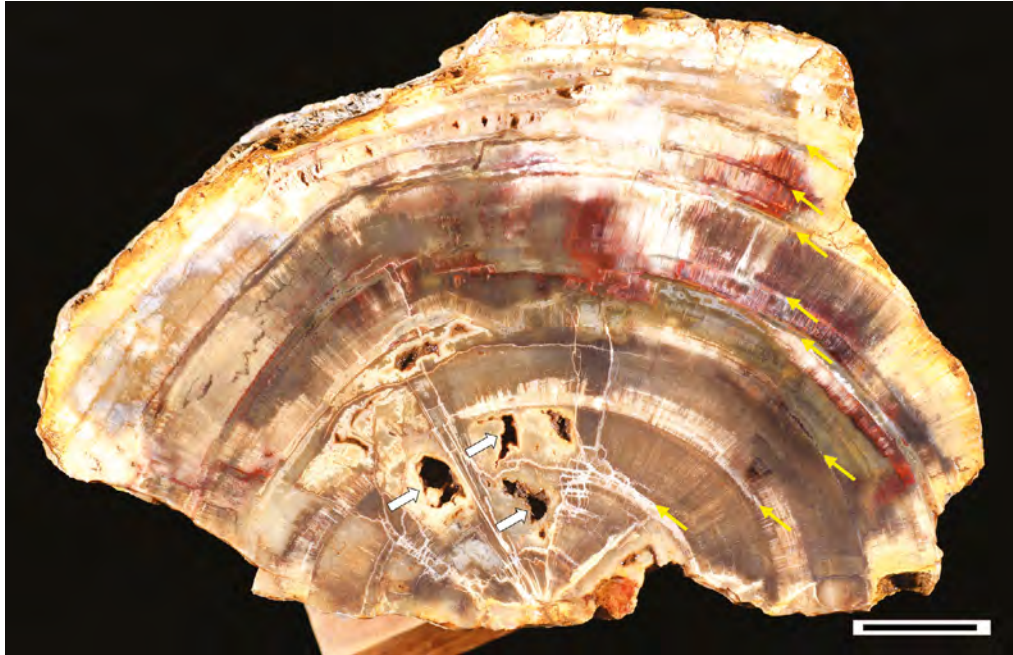


Figure 3. Transversal section showing distinct growth interruptions zones along the wood (yellow arrows) and irregular boring with preferential radial orientation (white arrows). Scale bar = 2 cm.

	MORAES-REGO (1930)	GORDON Jr. (1947)	BORTOLUZZI (1974)	ANDREIS <i>et al.</i> (1980)	FACINNI (1989)	ZERFASS <i>et al.</i> (2003)	HORN <i>et al.</i> (2014)
JURASSIC			<div style="background-color: #cccccc; width: 100%; height: 10px;"></div> BOTUCATU FORMATION CATURRITA MEMBER	BOTUCATU FORMATION	SEQUENCE IV	<div style="background-color: #cccccc; width: 100%; height: 10px;"></div>	NOT STUDIED
TRIASSIC	SÃO BENTO SERIES	SERRA GERAL VOLCANIC	SÃO BENTO GROUP	CATURRITA FORMATION	SEQUENCE III	SANTA MARIA III SEQUENCE	MATA SEQUENCE
		BOTUCATU SANDSTONE				CAIUÁ SANDSTONE	SANTA MARIA II SEQUENCE
	RIO DO RASTO GROUP	SANTA MARIA BEDS	SERRA GERAL FORMATION	SANTA MARIA FORMATION	SEQUENCE II	SANTA MARIA I SEQUENCE	SANTA MARIA I SEQUENCE
	SERRINHA BEDS	BOTUCATU SANDSTONE	RIO DO RASTO FORMATION	SANTA MARIA FORMATION		SANTA MARIA I SEQUENCE	PINHEIROS/CHINIQUÁ SEQUENCE
	TEREZINA BEDS	SANTA MARIA FORMATION		SANGA DO CABRAL FORMATION		SANGA DO CABRAL SUPERSEQUENCE	SANGA DO CABRAL SUPERSEQUENCE
PERMIAN	PASSA DOIS SERIES	RIO DO RASTO FORMATION	PASSA DOIS GROUP	PASSA DOIS GROUP	SEQUENCE I	RIO DO RASTO/PIRAMBOIA FORMATIONS	NOT STUDIED
	ESTRADA NOVA GROUP	ESTRADA NOVA FORMATION				NOT STUDIED	NOT STUDIED
	IRATI GROUP	IRATI SHALE					

Stratigraphic levels containing silicified logs
 Hiatuses

Figure 4. Some lithostratigraphic and sequence stratigraphic frameworks proposed for the upper Permian–Jurassic package from the State of Rio Grande do Sul including the levels bearing silicified logs.

who recognized that these two rock packages were separated by an erosive unconformity. Furthermore, for Bortoluzzi (1974), the levels containing the fossil logs (which he called the Caturrita Member) constituted the basal portion of the Jurassic Botucatu Formation, as it was known at the time, the stratigraphic unit that overlays the Santa Maria Formation (Figure 3). Later on, Andreis *et al.* (1980) proposed the name “Caturrita Formation” to include those layers with fossil logs corresponding to Bortoluzzi’s (1974) Caturrita Member as well as others bearing fossil vertebrates (such as rhynchosaurs, cynodonts, dicynodonts and a thecodont) that overlay the Santa Maria Formation further south than those mapped by Bortoluzzi (1974). Based on the fossil vertebrate content of the latter, Andreis *et al.* (1980) considered the Caturrita Formation Late Triassic in age. This dating was based mainly on the presence of the dicynodont *Jachaleria candelariensis* Araujo & Gonzaga, 1980, which would be correlated with the earlier-identified *Jachaleria colorata* Bonaparte, 1971 that occurred at the base of the Los Colorados Formation in Argentina. The name of the dicynodont from the Caturrita Formation was not mentioned by Andreis *et al.* (1980) because the paper proposing *Jachaleria candelariensis* was not yet published at the time.

The first proposal of a stratigraphic framework for the Paraná Basin infilling in Rio Grande do Sul based on sequence stratigraphy was carried out by Faccini (1989), who divided the Upper Permian–Lower Cretaceous package into four depositional sequences, numbered I to IV from bottom to top (Figure 4). In this arrangement, Sequence II (Middle–Upper Triassic) would encompass the entire Santa Maria Formation and the basal layers of the Caturrita Formation, *i.e.* those containing *Jachaleria* and other vertebrates (*sensu* Andreis *et al.*, 1980), while those bearing the fossil logs (corresponding to the Caturrita Member from Bortoluzzi (1974)) corresponded to the Sequence III. In turn, Sequence IV corresponded to the Upper Jurassic–Lower Cretaceous Botucatu Formation.

Subsequently, Milani (1997) performed extensive work throughout the Paraná Basin, proposing a series of second-order depositional sequences to subdivide the basin’s entire filling. Milani (1997) included the rocks corresponding to the Santa Maria and Caturrita Formations (*sensu* Andreis *et al.*, 1980) in what he called the Gondwana II Supersequence, whose occurrence was restricted to Rio Grande do Sul.

Zerfass *et al.* (2003) refined part of this framework, focusing on the south Brazilian Triassic package, which they divided into three third-order depositional sequences called Santa Maria I, II, and III, of Ladinian, Carnian and Rhaetian ages, respectively (Figure 4), based on regional unconformities and biostratigraphic dating. The set of these three third-order sequences, in turn, composed a second-order sequence they called the Santa Maria Supersequence, which corresponded to Milani’s (1997) Gondwana II Supersequence. In this stratigraphic framework, the Santa Maria I and II Sequences included the layers containing the Triassic vertebrates, while the Santa Maria III Sequence corresponded to the package containing the silicified logs, just as Faccini (1989) had earlier proposed.

Horn *et al.* (2014) improved the stratigraphic framework established by Zerfass *et al.* (2003), recognizing a distinct third-order sequence between Santa Maria Sequences I and II and renaming them all (Figure 4). In this new arrangement, the package containing the fossil logs came to be called the Mata Sequence, whose age could be located between the Late Triassic (Rhaetian) and the Late Jurassic. However, it is more likely Triassic due to its fossiliferous content and restricted geographical occurrence, which is limited to the west by the Jaguari-Mata Fault System (JMFS), like the Triassic sequences including vertebrates and unlike the younger units, which extend beyond that line or occur just west of it.

Studied area

The Paleobotanical Garden outcrop is located within the urban area of the city of Mata (Figures 2, 5 and 6), whose subsoil has revealed the presence of hundreds of silicified logs that are discovered each time an excavation is made for the construction of a street or building. Mata city is the type locality and represents the westernmost point of occurrence of the Mata sequence, which, together with the other Triassic sequences of the Paraná Basin in the extreme south of Brazil, is limited by the JMFS, a great geological alignment with a SE–NW orientation (Figure 1). However, this is not true in the opposite direction, where the Middle and Upper Triassic sequences containing fossil vertebrates extend much further east to the vicinity of the city of General Câmara, where they are limited by another major SW–NE lineament called the Rio Pardo Fault System (RPFS). The last records of the Mata Sequence, in turn, are located to the east in the Agudo region, in the center of the W–E Triassic outcrop belt.

In the studied outcrop, the fossil woods occur dispersed at ground level and in the subsurface within fine to medium pinkish-whitish sandstones with through cross-bedding, often presenting conglomeratic levels with reddish mud clasts at the base.

Four wells (0553-COR-MAT-0, 0557-COR-MAT-021, 0846-COR-MAT-03, and 3027-COR-MAT-04), drilled within the city limits by the state sanitation company (CORSAN-RS) to assess the aquifer, showed (in all drillings) that the Mata Sequence is covering a thick pack of red muds, which are interbedded with reddish sandstone levels, typically representing one of the older Middle–Upper Triassic sequences that contain the fossil vertebrates. The depth of this contact varies from 6 to 11 m among the different wells. In the city of São Pedro do Sul, about 60 km east of Mata, it is possible to see the contact between the Mata Sequence and the underlying red mudstone package at the surface. The presence of the rhynchosaur *Hyperodapedon* in the red mudstone package indicates that those mudstones represent the lower portion of the Candelária Sequence, whose faunal content characterizes the *Hyperodapedon* Assemblage Zone (upper Carnian/lower Norian). From this, the erosive and discordant character of the contact between the Candelária and Mata sequences is once again apparent, since the entire upper part of the Candelária Sequence (the *Riograndia* Assemblage Zone middle–upper Norian) is absent in that region.

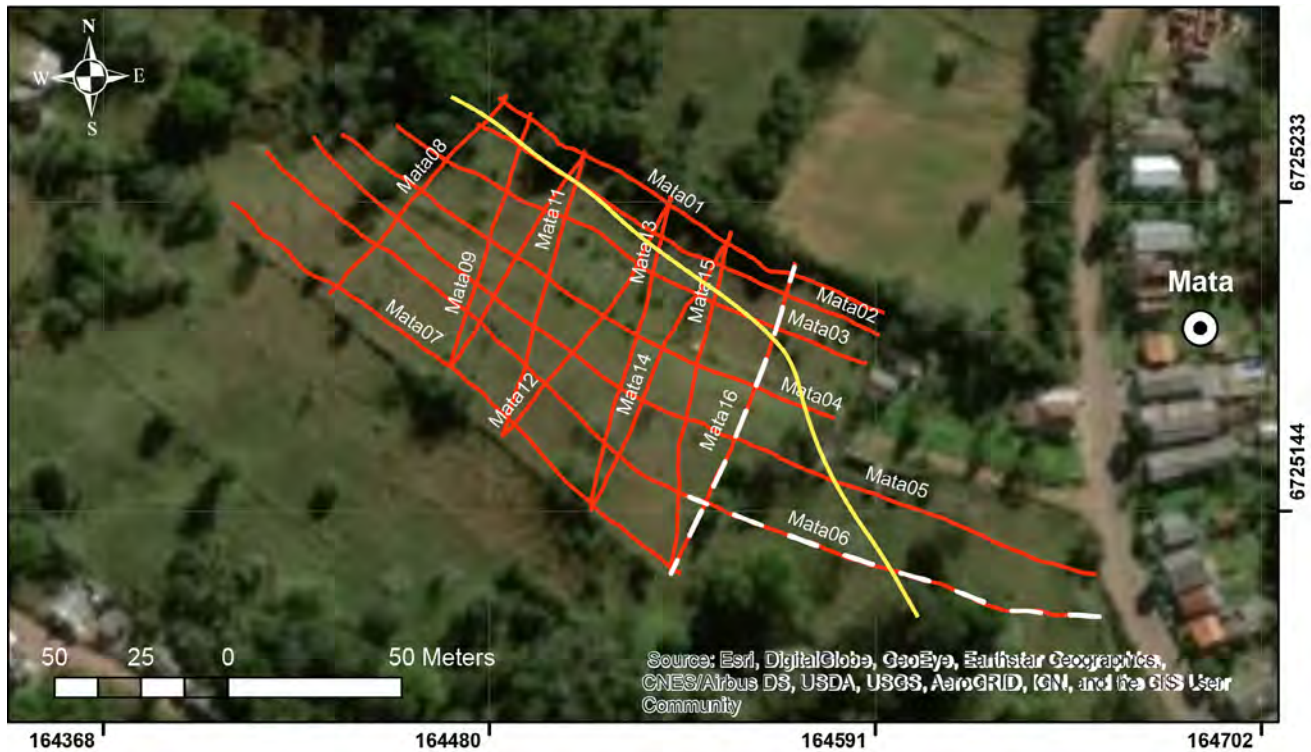


Figure 5. Location map of the GPR sections made at the Paleobotanical Garden in the city of Mata. Red-white lines indicate the selected orthogonal sections (6 and 16). The yellow line indicates the position of the structural height at NE against which the layers of the Mata sequence prograde in onlap.

MATERIAL

Thirty samples were collected from different areas of the Paleobotanic Garden of Mata, RS, with authorization from the Institute of Historical and Cultural Heritage of the State of Rio Grande do Sul (IPHAE), no. 243/2019/IPHAE. The site has an area of 36,391 m² and was listed by IPHAE in April 2018 (IPHA013/2018) as a site of cultural importance. It is located in the urban area of the city of Mata (29°32'58"S, 54°27'32"W).

The wood specimens were preserved by the permineralization process of silica (Dietrich *et al.*, 2013). These large wood pieces with circular diameters ranging from 0.20 to 0.80 cm, are disposed semi-horizontally, randomly dispersed, and frequently semi-included in sediments (Figure 2). The specimens are mostly decorticated, and irregularly bordered cracks are observed in the region of the pith, which is not preserved. There was no recorded occurrence of roots organically associated with these fragments or as isolated fragments. Given the legal restrictions for working in areas protected by IPHAE, fragments of wood were collected in a manner to minimize damage to the great stems exposed in the Paleobotanical Garden.

METHODS OF STUDY

Ground-Penetrating Radar (GPR)

The electromagnetic method GPR was used to obtain information on the site's depositional characteristics and to elaborate on its subsurface profile. This technique was

previously used by Silva (2009) and Bardola (2011), with good results in Triassic sites of southernmost Brazil, to identify subsurface fossil material. The GPR profiles were acquired using Cobra Plug-In GPR (Radar team Sweden AB) and YUMA 2 (Trimble®) data acquisition systems with a SUBECHO SE-70 aerial antenna with a central frequency of 80 MHz and a two-way travel time (TWTT) range of 500 ns. This configuration penetrated 23.5 m deep. High-pass, stacking, and gain filters were applied during the time of data acquisition. Altitudes were determined by a Global Navigation Satellite System (GNSS) Trimble® ProXRT unit, datum WGS84.

The data was post-processed with Reflex-Win®, Radan™, and Prism2® software packages, followed by trace analysis (Leandro *et al.*, 2019), background removal, band-pass frequency filter (ORMSBY), gain equalization, time to depth conversion, and topography correction. A dielectric constant of 10 for dry sand was used to convert travel time to depth, which represents a velocity of 0.09 m/ns (Davis & Annan, 1989). The stratigraphic interpretation was based on the method of seismic stratigraphy adapted to GPR (Neal, 2004). The method is based on termination (onlap, downlap, toplap, and truncations), geometry, internal configuration, and reflection patterns (Abreu *et al.*, 2010; Barboza *et al.*, 2014).

Anatomical analyses of the woods

Given the poor preservation of their internal structures, only 13 of the 30 samples collected were analyzed anatomically. The material was prepared according to standard procedures, *i.e.* with the elaboration of polished blocks and thin sections of the polished three surfaces (transversal, longitudinal radial,

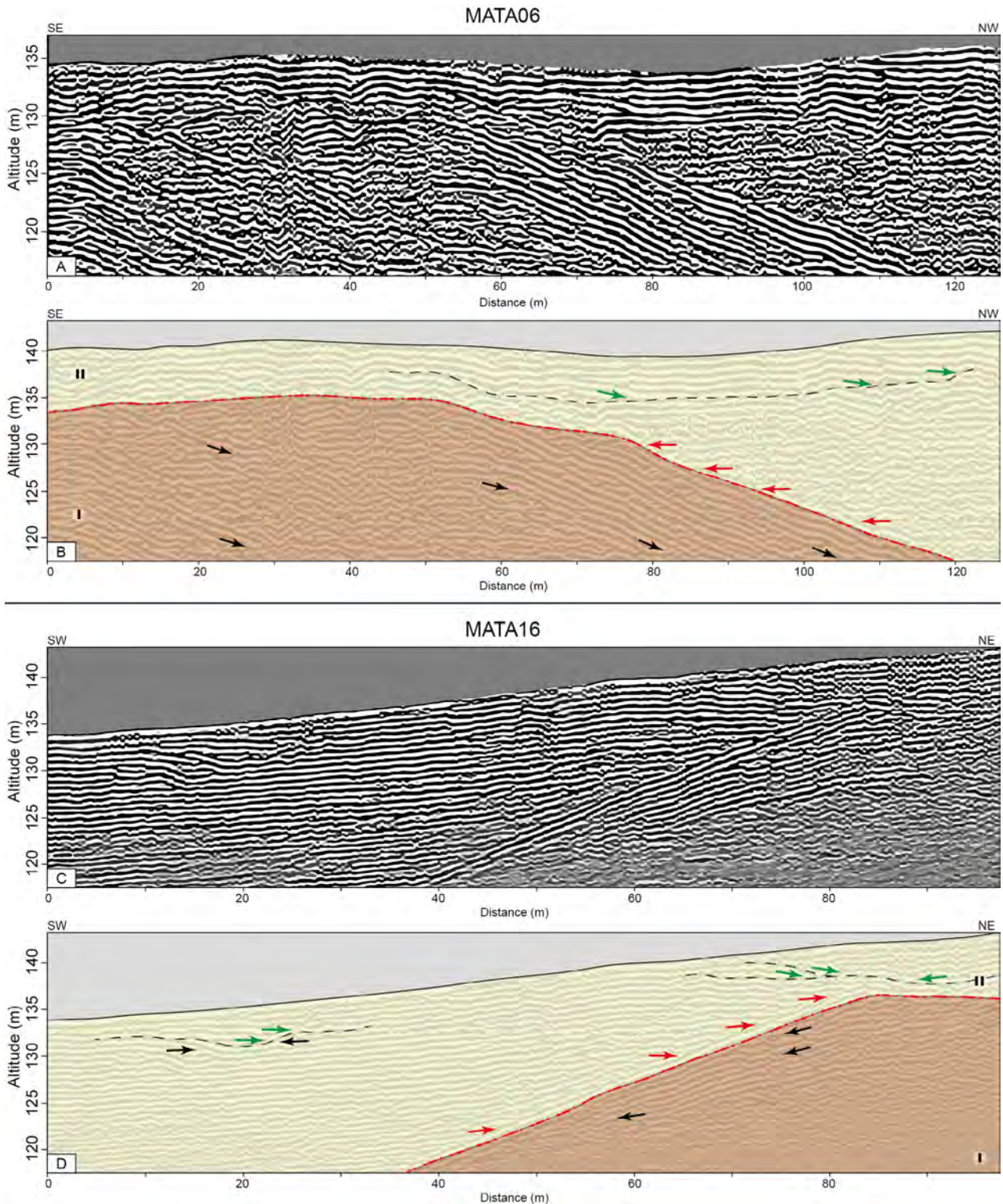


Figure 6. Two selected GPR sections (MATA06 above and MATA16 below) showing the structural relationships between the Mata Sequence (above) and the presumed Candelária Sequence in the subsurface. The arrows show the progradation pattern of the deposition of the Mata Sequence over a structural height at NE, as well as a channel structure (black dashed lines) running parallel to the border of the height (indicated by the yellow line presented in Figure 5).

and longitudinal tangential) mounted in Canada balsam and observed with optical microscopy in transmitted light in a Carl Zeiss MC80 microscope. Photomicrographs were taken using a digital camera (AxioCamMRc) and the software *AxioVision LE* at the Instituto de Geociências (IG), Departamento de

Paleontologia e Estratigrafia, Universidade Federal do Rio Grande do Sul (UFRGS).

The woods' anatomical patterns were described according to the list of microscopic features for softwood identification (IAWA Committee, 2004). For the identification of wood

growth patterns and paleoclimate inferences, we consulted Douglass (1928), Creber & Chaloner (1984), Falcon-Lang (2003), IAWA Committee (2004), and Schweingruber (1992, 1996, 2007).

Macroscopic specimens are housed in the Paleontological Museum of Mata, RS, and petrographic slides are housed under the acronym PB-5496 to 5510 at the Paleobotanical Collection of the Paleontological Museum of the Departamento de Paleontologia e Estratigrafia, IG/UFRGS.

RESULTS

GPR

The GPR grid from the locality (Paleobotanical Garden) is excellent, and two representative sections were selected for interpretation, identified as MATA06 and MATA16, respectively. From these samples, we were able to identify a paleochannel and two units, as shown in Figures 5 and 6.

Unit I was identified in a subsurface at the 135-meter altimetric quota in both sections, and its portion closest to the surface is located in the MATA06 section, between 0 and 50 m, with a NW inclination. Additionally, in the MATA16 section, the altimetric quota was located between 80 and 97 m, showing a reflection dipping to SW.

In both sections, MATA06 and MATA16, Unit I is characterized by high amplitude and continuous, parallel cross reflections with downlap terminations, which indicate that this unit has depositional structures such as large cross-stratifications. Unit II presents continuous reflections with high amplitude, with parallel and onlap on the surface that delimits the top of Unit I. In the MATA16 section, erosive truncations are delimited by characteristics, and surface excavations are observed at distances between 10 and 30 m. Downlap reflections are identified on this surface, as well as stratifications, but with lower angles than in the MATA06 section.

Wood analyses

Given the poor preservation, very few of the fragments exhibit anatomical preservation to provide some taxonomical data and, consequently, formal taxonomic analyses have not been developed. However, despite the poor preservation, two gymnosperm wood xylotypes were recognized mainly based on patterns of radial pitting on the tracheids.

The Xylotype 1 occur in three specimens and exhibited a decorticated pycnoxylic wood with canals and ducts absent. In the longitudinal radial section, the pits on tracheid walls are of the araucarian type, uniseriate, biseriate alternate, and contiguous (Figures 7A–C); cross-field were not preserved (Figure 7C). The anatomical features point to a conifer wood with araucarioid anatomy, showing similarities with *Agathoxylon* type of wood according to the morphotype criteria of Philippe & Bamford (2008) for Mesozoic secondary woods. This wood pattern has been included by different authors within the Araucariaceae family (Sagasti *et al.*, 2019 and citations therein). Nevertheless, the non-preservation of crossfield pits precludes the establishment of secure affinities.

The Xylotype 2, showed by 10 specimens, is also a decorticated, homoxylic, and pycnoxylic wood; canals or ducts are absent. Areolate pitting in the tracheid walls presents a dominant uniseriate, isolated disposition (Figures 7D, E), and slight spiral thickening (Figure 7E). Cross-field pits are inconspicuous oculipores seemingly irregularly disposed with one or two pits per cross-field (Figures 7D, E) and, in some areas, the end of tracheids radially appears like golf clubs (Figure 7F), suggesting an affinity with Gynkgoacea trees.

Despite the limitations for establishing taxonomic sources of variability within the wood assemblage, given that silicified woods are the unique type of fossil found in the rock packet being studied (the Mata Sequence), we decided to use the woods' growth patterns as indicators of climate.

Of the 30 wood specimens collected from the Paleobotanical Garden in the city of Mata, only 13 specimens had sufficient anatomical preservation to examine their growth patterns. Growth patterns from the wood assemblage are quite unlike true "growth rings" as defined by Greguss (1972), Fritts (1976), Creber & Chaloner (1984), and Schweingruber (1992, 1996), which are produced by a complete cessation of cambial activity and appear continuously around the trunk circumference, displaying well-marked, asymmetrical ring boundaries defined by numerous latewood cells with cell wall thickening.

Instead, the wood growth patterns present in our specimens were identified as "growth interruptions", as defined by Schweingruber (1992), which result from a temporary slowing down of cambial activity and are different in origin from true growth rings (Figures 3, 8, 9).

The observation of continuous sequences was highly impaired in our material given the irregular preservation of single specimens caused by distinct silicification processes along with the samples, characterized in some levels by the occurrence of large silica crystals that were associated with randomly dispersed elongated cracks (Figure 3), cellular crushing, and, in some cases, extreme wood deformation processes. Cell-by-cell measurements in cross-sections of adjacent rows detected distinct growth zone boundaries, which were informally identified as morphologic types according to some of the criteria established by Falcon-Lang (2003). However, it was difficult to draw clear boundaries between the two types because some wood displayed a great variation in patterns within a single specimen.

The interruption Zone Type I is inconspicuous and subtle and is only represented in some punctual sections of the wood. Its boundaries cannot be traced laterally and these zones are absent for a considerable distance within the horizontal sections. They are distinguished by a sudden decline in cell diameter followed by a rapid rise back to the tracheid diameter compatible with wood-tracheids of analogous earlywood (Figure 8). In each zone, the tracheids equivalent to the initial wood have radial diameters ranging from 39 to 57 μm (mean 47.7 μm) and walls from 5 to 8.5 μm (mean 6.6 μm) thick. In the analogous latewood, 3 to 5(7) rows of tracheids are flattened with radial diameters of 21 to 35 μm (mean 29.7 μm) and walls from 5.2 to 9.0 μm (mean 8 μm) thick. The tracheids that mark the interruptions do not have thickened cell walls in relation to the earlywood tracheids (Figures 8A, B).

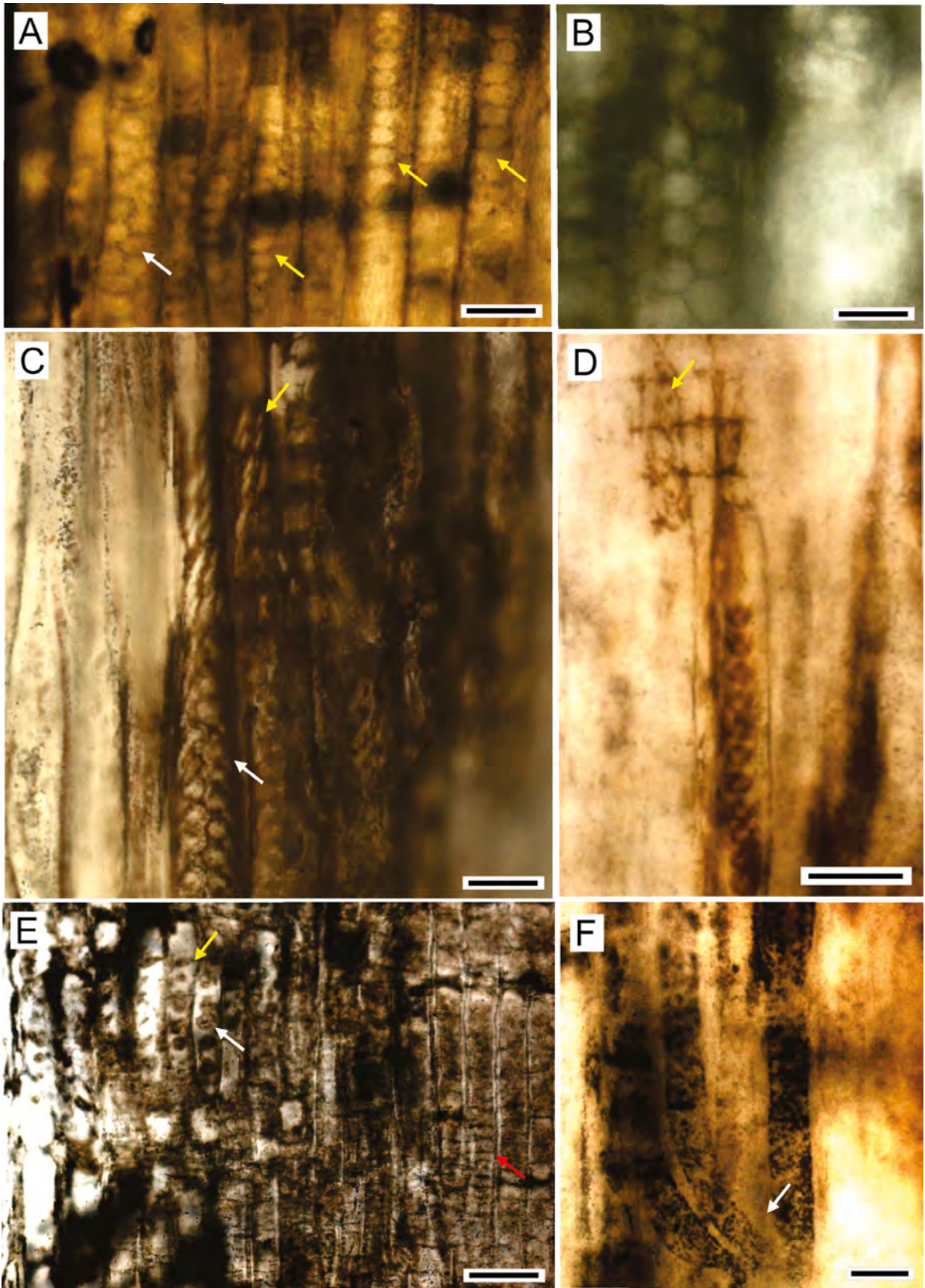


Figure 7. Wood radial sections. Xylotype 1: **A**, tracheid walls showing bordered pitting, with araucarian disposition from contiguous uniseriate (yellow arrow), to alternate biseriate (white arrow). **B**, detail of a biseriate, alternate, polygonal-shaped areolate pitting on tracheid walls. **C**, cross-field pits poorly preserved (white arrow) and biseriate pits (yellow arrow). Xylotype 2: **D**, uniseriate isolated to areolate pitting in the tracheid walls associated with spiral thickening and cross-field pits showing two pits per cross-field (yellow arrow). **E**, uniseriate isolated areolate pitting in the tracheid walls spiral thickening (red arrow); cross-field pits inconspicuous (yellow arrow). **F**, terminalization of tracheids resembling golf clubs (white arrow). Scale bars: A, C, D, F = 50 μm ; B = 25 μm ; E = 100 μm .

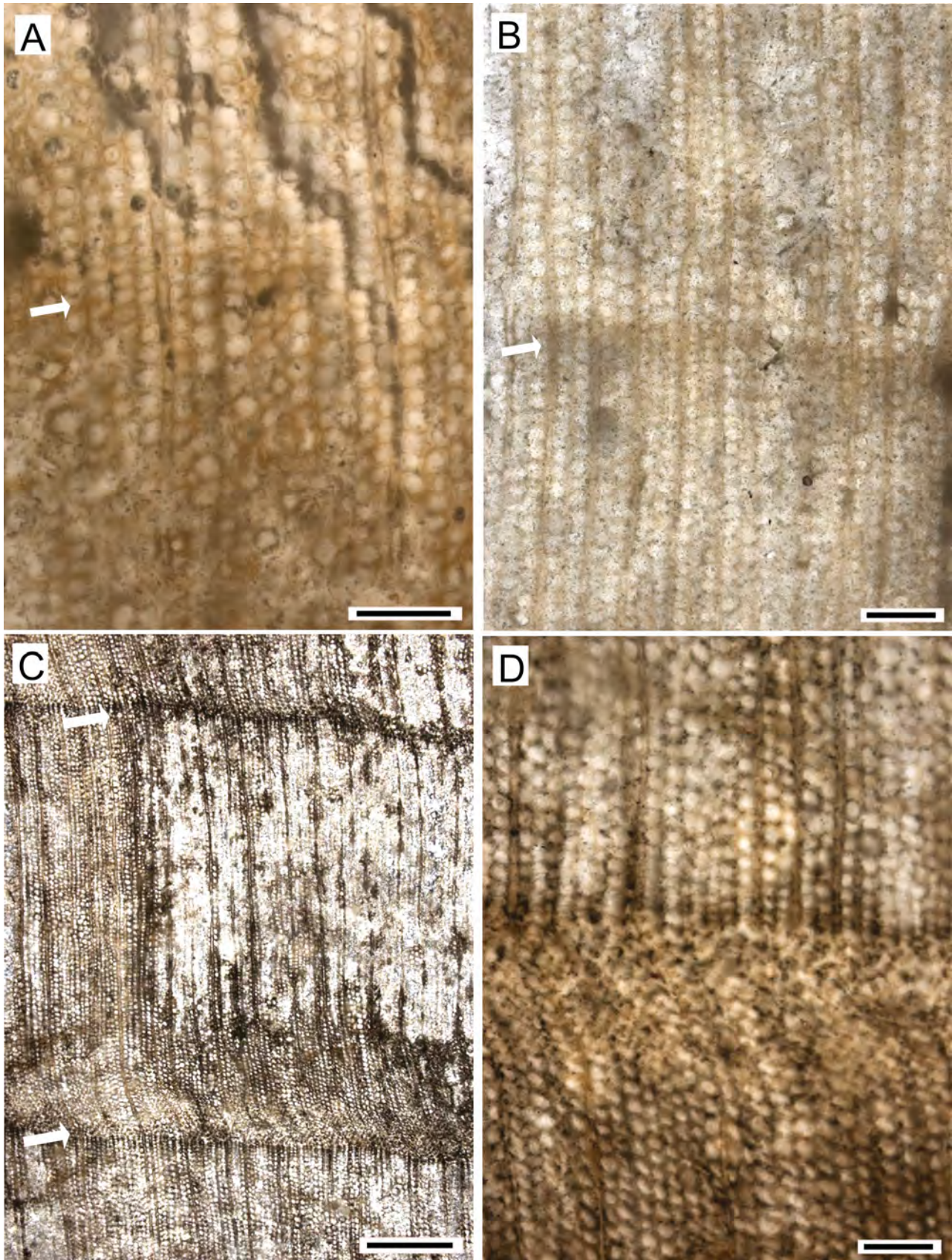


Figure 8. Growth interruption types (indicated by the arrows). **A**, growth interruption locally almost absent. **B**, typical weakly interruption boundaries which cannot be traced laterally. **C**, marked interruption traced laterally along cross-section. **D**, zone boundaries marked by an abrupt decline in cell diameter and subsequent abrupt reversion to normal tracheids diameter. Scale bars: A, B, D = 200 μm , C = 1000 μm .

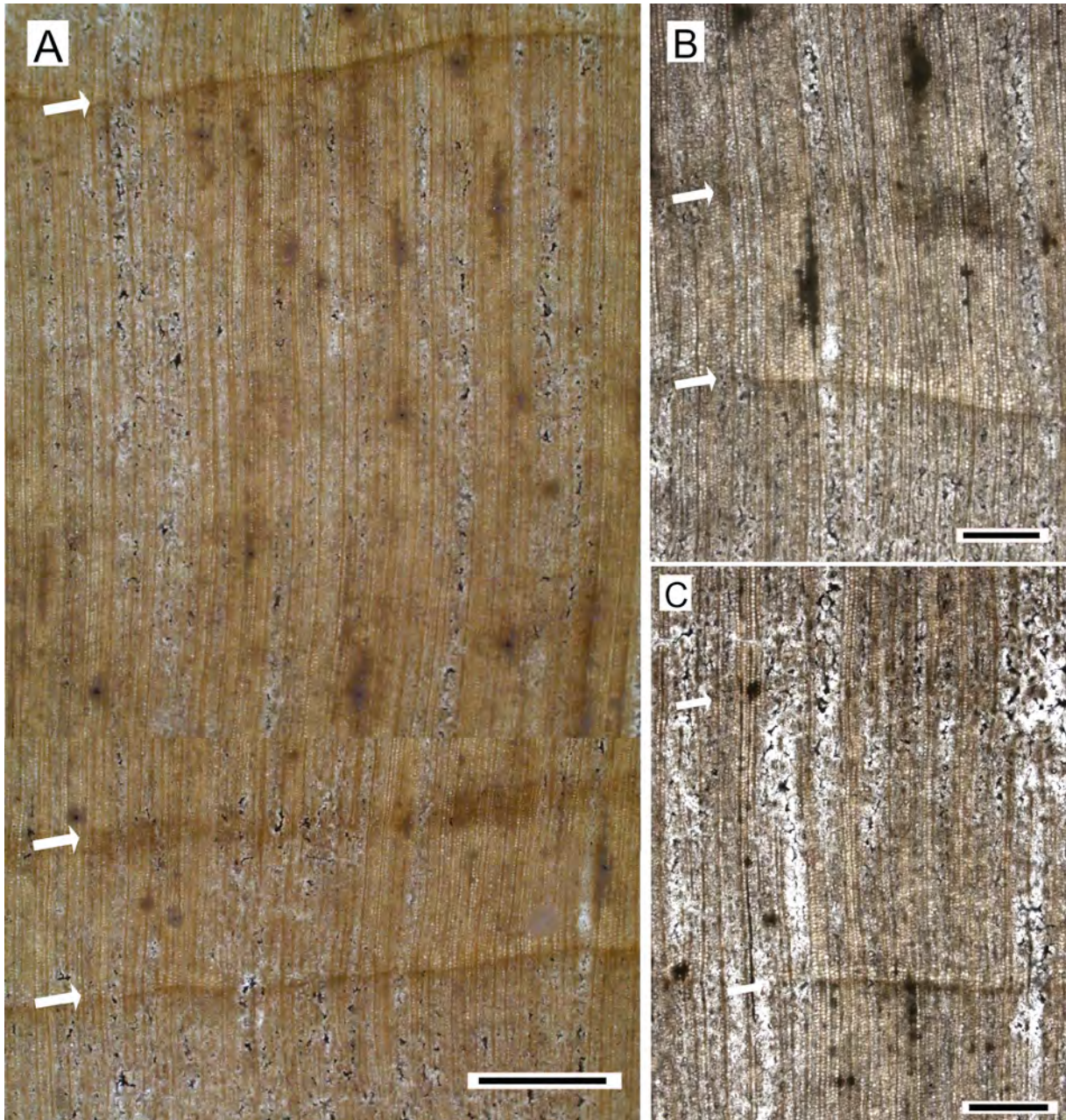


Figure 9. The spacing of wood growth interruption (indicated by the arrows). **A**, general view boundary spacing from marked growth interruptions in a single specimen. **B**, marked growth interruptions interspersed with very weakly ones in a single specimen. **C**, inconspicuous boundary spacing between two weakly zones. Scale bars: A = 2 mm; B, C = 1 mm.

Given the inconspicuous nature of these zones, it was not possible to describe the ring boundary spacing.

Type II is dominant and characterized by marked growth boundaries which are observable continuously along with the thin slides (Figure 8) and in polished cross-sections (Figure 3). The tracheids equivalent to the initial wood have radial diameters of 39 to 65 μm (mean 52.9 μm) and walls from 5 to 8.5 μm (mean 6.6 μm) thick. In the analogous latewood, two to three rows of tracheids are flattened with radial diameters between 24.7 and 35 μm (mean 29.7 μm) and walls between 5.2 and 9.0 μm (mean 8 μm) thick. Similar to those found in Type I, the tracheids that mark the interruptions in Type II do not have thickened cell walls in relation to the

earlywood tracheids. Their boundaries are marked by an abrupt decline in cell diameter, and the subsequent reversion to normal tracheid diameter is equally abrupt (Figures 8C, D). The growth interruptions in the wood fragments are constant but irregularly spaced (Figure 9A), and individual growth zones are spaced between 1 and 9 mm apart (mean 4.5 mm). Additionally, distinct types of boundary patterns can be recognized throughout the same cross-section of a single specimen. It was then possible to observe along the secondary xylem the occurrence of well-demarcated growth interruptions interspersed with very weakly developed growth interruptions (Figures 9B, C).

In an attempt to make greater contributions to climatic inferences, mean sensitivity statistical analysis was applied unconventionally to the growth interruption sequences, since its application by Falcon-Lang (2003) yielded good results in spacing variability using Fritts' (1976) equation:

$$MS = \frac{1}{n-1} \sum_{t=1}^{t=n-1} \left| \frac{2(x_{t+1} - x_t)}{x_{t+1} + x_t} \right|$$

where x is the distance between adjacent growth interruptions, n is the number of growth increments in the analyzed sequence, and t is the year number of each increment.

The statistical analysis of 13 wood fragments, obtained from the 70 growth zones (measured in polished blocks and confirmed under the transmitted light microscope) spaced between 1 and 13 mm apart (mean 5.9 mm in total), showed mean sensitivity values of 0.221 to 1.225 (mean of 0.687) (Table 2).

According to Fritts (1976), average sensitivities greater than 0.3 ($MSR > 0.3$) indicate that the woods were sensitive to fluctuating climate parameters.

Deformation of wood structures

In all samples, the anatomical structures of the secondary wood show distinct patterns of anomalies and were often deformed, crushed, and sometimes extensively distorted. Wide and continuous undulations along the secondary wood are present in some specimens, however, they do not significantly alter the tracheid and rays morphology (Figure 10A).

Several specimens displayed laterally interconnected cracks produced by a few levels of collapsed tracheid rows, interspersed in rows of non-compressed cells, sometimes giving these samples the appearance of false rings (Figure 10B).

The dominant wood deformation anomaly throughout the entire assemblage is a strong zigzag, chevron-like pattern, caused by strong compression of the tracheids (Figure 10C). Frequently, individual tracheids are highly tangentially compressed, and cells are sinuous in the transverse section, seemingly having gelatinous walls (Figure 10D).

Evidence of wood decay

In the transverse and longitudinal sections, the secondary xylem in several specimens shows irregular cavities (2.2 to

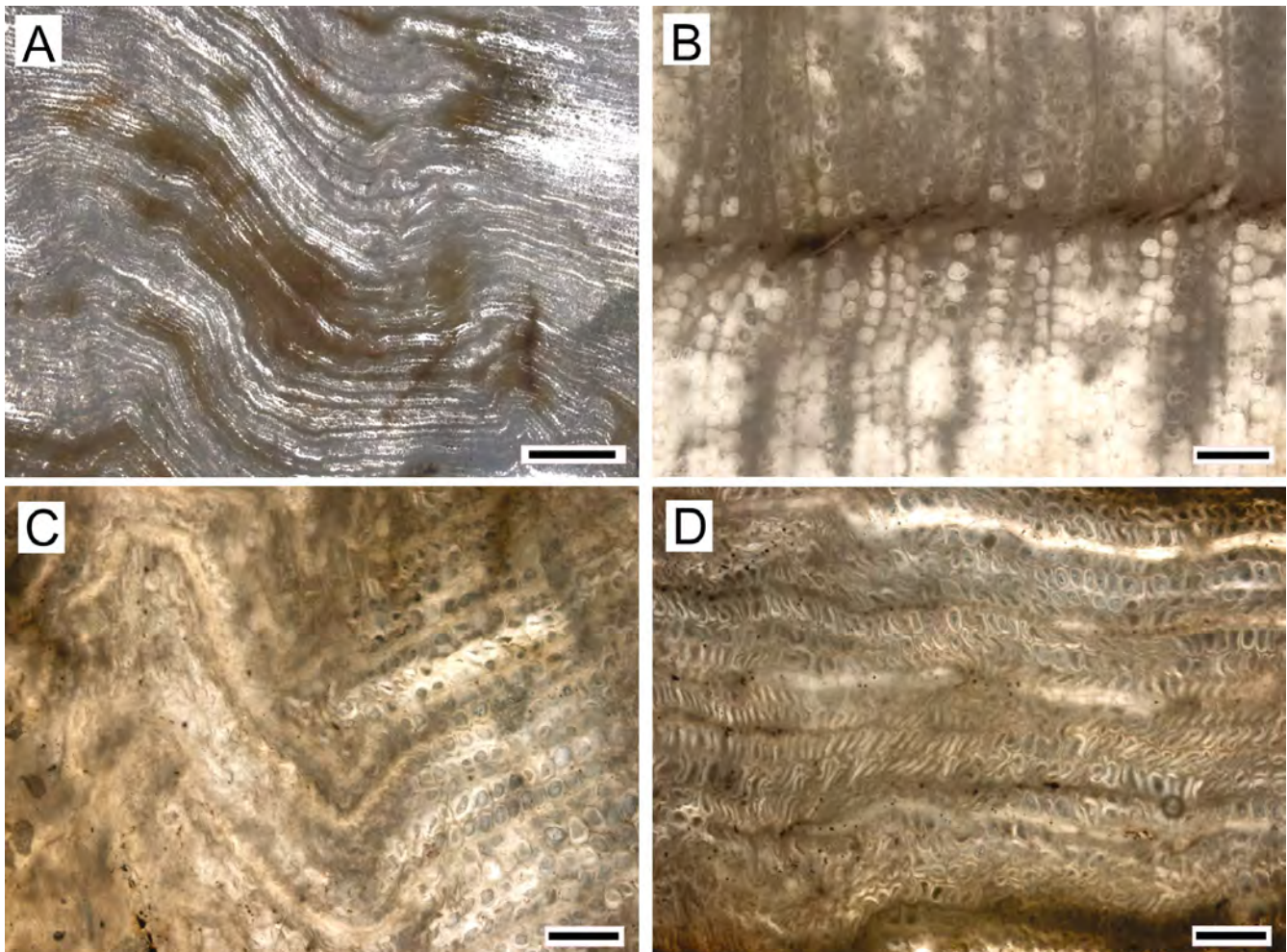


Figure 10. Deformation wood structures in cross-section. **A**, wide and continuous undulations along the wood tissue. **B**, abrupt linear compression along few rows of tracheids. **C**, strong zigzag, chevron-like pattern, elongated parenchyma cells of the rays curved but not broken. **D**, very compressed cells showing sinuous cell-walls. Scale bars: A = 1000 μ m; B, C, D = 200 μ m.

3.1 mm, average 2.7 mm × 0.8 to 2.5 mm, average 1.6 mm) of different sizes randomly distributed throughout it (Figures 11A, B). Furthermore, the walls of the tracheids that bordered the borings have been gnawed, and the frass is composed of discernible plant material, mainly degraded tracheid wall fragments (Figure 11C) and, rarely, isolated, non-clustered bodies, typically dark in colour, with a fairly regular circular to oval outline, ranging from 297 to 303 µm in length and 141 to 207 µm in width (Figure 11D). These bodies were identified

as arthropod coprolites because of their similarities with faecal pellets produced by living phytophagous arthropods (Snyder, 1924).

Tracheids filled with dark contents clustered as massive bands were observed, which are typically associated with boring (Figures 11B, C) and likely document host cell reactions to fungal attacks in fossil woods (Aist, 1976; Pujana *et al.*, 2009; Gnaedinger *et al.*, 2015), similar to the reaction seen in extant woods (Blanchette, 1990; Schwarze, 2007).

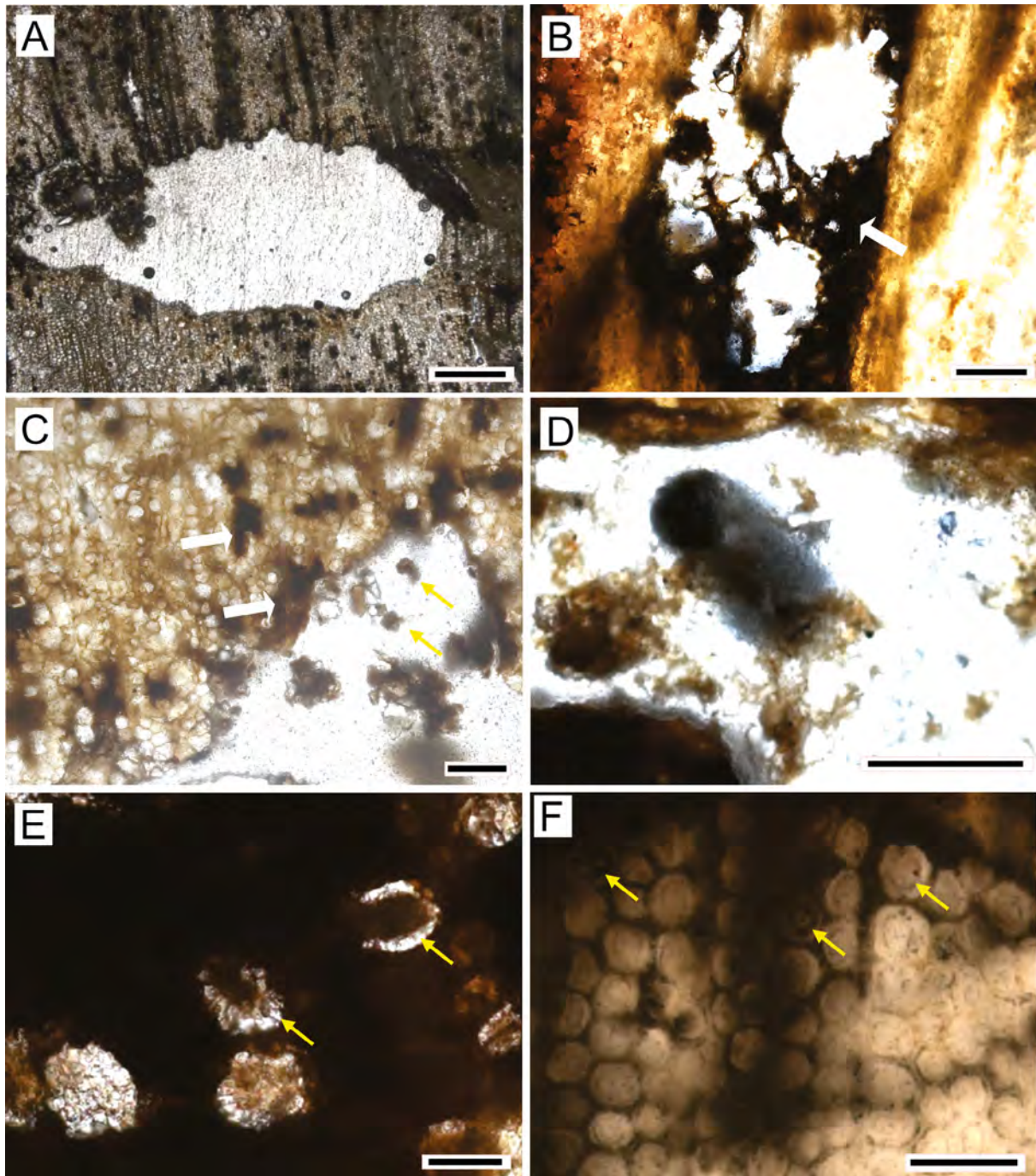


Figure 11. Evidence of wood decay. **A**, transverse view of a boring. **B**, longitudinal view of different borings with irregular borders, encircled by dark bands (white arrow). **C**, irregular borders of the boring, encircled by dark tracheid bands (white arrow) and frass inside the lumen (yellow arrow). **D**, coprolite. **E**, fungal spores included in tracheid lumina (yellow arrow). **F**, transverse circular section of elongated hyphae bordering walls, inside cellular lumen (yellow arrow). Scale bars: A = 1000 µm; B, C, D = 200 µm; E = 50 µm; F = 100 µm.

Table 2. Results of growth interruptions analysis.

Samples	Number of growth rings	Minimum ring width (mm)	Maximum ring width (mm)	Mean ring width (mm)	Mean sensitivity MS	Minimum annual sensitivity	Maximum annual sensitivity
1 PB 03	7	1	5	2.7	0.654	0	1.333
2 PB 05	4	2	6	4.3	0.693	0.222	1.000
3 PB 09	5	2	11	6.8	1.073	0.588	1.385
4 PB 13	2	5	11	8	0.75	0.750	0.750
5 PB 14	4	3	13	8	0.765	0.476	0.909
6 PB 15	6	3	11	5.2	0.515	0	1.143
7 PB 17	13	2	6	3.9	0.285	0	1.000
8 PB 18	7	2	13	7	1.125	0.933	1.385
9 PB 19	2	6	9	7.5	0.4	0.400	0.400
10 PB 20	4	3	9	6.3	0.468	0.154	1.000
11 PB 21	5	1	11	4.6	0.968	0.222	1.333
12 PB 22	5	2	13	6.2	1.011	0.666	1.467
13 PB 23	6	4	9	6.2	0.221	0	0.545
Total	70		Mean	5.9	0.687		

Fungal bodies corresponding probably to spores (Figure 11E) and hyphae (Figure 11F) were found growing inside tracheid lumina along the secondary xylem. Nevertheless, poor preservation hampered diagnostic affinities for this fungal remains.

DISCUSSION

The GPR sections, described previously, were interpreted on-site (Figures 5 and 6) and indicated that the Mata Sequence is overlapping another sedimentary unit that configures a structural high in the subsurface located northeast of the outcrop, which is characteristic of an erosive discordant contact. Additionally, GPR section MATA16 (Figures 6C, D) shows a clear channel structure running parallel to this high, whose orientation is consistent with the preferred orientation of the outcropping trunks, which are perpendicular to the channel identified in the GPR section. This confirms that Mata Sequence deposits clearly correspond to river channel infilling, and the logs must have been dragged into these channels during flood events.

Conventionally, the Triassic has been considered a “hot-house warm equable” world, with no major climate oscillations or trends, and was seemingly arid to semi-arid in interior Gondwana during the Middle to Late Triassic (Sellwood & Valdes, 2006). In agreement with the general global scale context, a general semi-arid climate for the deposition of the Santa Maria Supersequence was accepted based on chemical indices of alteration (Horn *et al.*, 2018a, b). However, despite the chemical indices, results based on field, chemical, and fossil vertebrates data suggest a climate marked by great seasonal changes during the deposition of the Middle/Upper Triassic sequences of the Santa Maria Supersequence (Horn *et al.*, 2018a, b). Results for the Candelaria Sequence (Carnian/Norian), which underlies the Mata Sequence (Rhaetian) in the stratigraphic framework of Horn *et al.*

(2018a, b), indicate a strongly seasonal, semi-arid climate with seasonal rainfall. Nevertheless, several indicators such as a change in depositional systems (eolian/fluvial to fluvial-deltaic sheet deltas in lacustrine environments), climate-sensitive sediments, and faunal change point to an increase in humidity from the upper part of the sequence (Global Carnian Wet Interval). However, the presence of calcrete at the topmost levels suggests a return to semi-arid/arid conditions.

According to Zerfass *et al.* (2003), facies data to define the depositional processes linked to fluvial style for the Mata sequence (then called the Santa Maria III Sequence) were inconclusive due to the small number of exposures. However, the lack of floodplain facies and the coarse-grained nature of the sandstone suggested high-energy flows to Zerfass *et al.* (2003). The stratigraphic analyses developed in the present study confirm that Mata Sequence deposits clearly correspond to river channel infilling processes associated with high-energy flows.

A change to fluvial depositional systems during the deposition of the Mata Sequence, as accepted by Horn *et al.* (2018b), would certainly lead to the establishment of climatic trends somewhat different from those of the lower units. Nevertheless, climatic signatures data that should be provided by fossil woods (the unique fossils preserved in the Mata Sequence) have not been discussed. Growth rings or growth zones (Table 1) are only documented for single specimens and are not accompanied by climatic inferences (Minello, 1994; Guerra-Sommer & Scherer, 2002; Bardola *et al.*, 2009; Crisafulli *et al.*, 2016; Crisafulli *et al.*, 2018), and many of these structures were likely the consequence of taphonomic processes rather than caused by wood growth patterns.

The absence of true growth rings in the wood assemblage preserved in the Paleobotanical Garden locality, included in the Mata Sequence (Horn *et al.*, 2018a, b), point to climatic conditions with minimal year-round variability. Nevertheless, the common occurrence of wood growth interruption interspersed with relatively long cycles of homogeneous

growth in all sampling (Figure 3) indicates frequent short-term environmental disturbances to growth that have mainly been attributed to droughts (Fritts, 1976; Schweingruber, 1992, 1996).

The large diameter of the tracheids that commonly follow the growth interruptions was linked with a rapid return to good growing conditions at the end of disturbance events and a consequent increase in water availability. While irregular spacing of growth interruptions implies irregular periods of drought, the interspersed occurrence of marked growth interruptions with tenuous ones in a single wood sample reflects the different intensities of these stress events throughout the life of the plant.

The growth pattern is distinct from that formed under monsoonal conditions, even taking into account the inferences of several authors (*e.g.* Robinson, 1973; Wang, 2009) who considered this interval to be marked by a maximum expression of a monsoonal climate. As observed by Horn *et al.* (2018a), reconstructions of the paleolatitudes for South America placed the Santa Maria Supersequence in higher southern latitudes (over 30°S) than would be expected for a monsoonal influence.

Mean sensibility data ratified the results from a cell by cell analysis and, according to Fritts' criteria (1976), the paleoenvironment where these gymnosperms developed was not uniform and included short-term aperiodic disturbances, which caused irregular growth rates, and had variable water supply conditions throughout the life of the plant. The common occurrence of growth interruptions in almost all of the wood samples did not necessarily represent annual increments of growth and was in response to climatic stress caused by erratic rainfall.

The absence of anatomical evidences (*e.g.* rounded tracheids with intercellular spaces in the latewood) which are typical answers to flooding events, means that drought, not flooding, caused this growth interruption during the tree's life. The general characteristics of the growing pattern point to an ecological niche related to inter-channel environments that were relatively far from meso-hygrophilous sites.

Biological interactions present in several specimens indicate that wood damage is probably attributable to arthropod bores and fungal decay, and involved pathogenic and saprophytic processes. Given that wood-boring arthropods generally attack trees that are already suffering from moisture or other physical or biotic stresses (Bonello *et al.*, 2006; Drees *et al.*, 2006), they were likely secondary invaders during drought intervals under stressful environmental conditions.

Statistical analyses by Pires *et al.* (2005) in a wood assemblage with Taxaceae affinity from the Faxinal do Soturno outcrop, included by Zerfass *et al.* (2003) in the Triassic Santa Maria III, is a unique study that allowed for more reliable paleoclimate information. Unlike the present study, Pires *et al.* (2005) found true growth rings in their sample, indicating periodic growth related to clear seasonal cycles under temperate climatic conditions. Nevertheless, the distinct growth pattern shown in the studied assemblage reflects not only a paleoecological distinction but a distinct age interval, given that an Early Jurassic age for the Faxinal do Soturno

outcrop has been strongly suggested based on paleontological and sedimentological data (Barboni & Dutra, 2013; Rohn *et al.*, 2014; Soares *et al.*, 2014; Jenisch *et al.*, 2017).

Considering the general context of semi-arid conditions for the Middle/Late Triassic of the southernmost Brazilian Gondwana, which indicates seasonal variations between long periods of drought and short, but intense, flood events (Horn *et al.*, 2018a), wood growth patterns from the Mata Sequence (Rhaetian) indicate a relative increase in water availability intervals interspersed with very short, irregular drought intervals.

The aperiodic high-energy flow events did not cause the anatomical responses in the wood during the life span of the trees but, instead, were closely related to their preservation process. The interpretation of GPR analyses, coupled with stratigraphic data, was vital to clarifying the taphonomic process involved in this petrified wood assemblage, which was closely associated with the drag and burial of trees by very high-energy flood events under fluvial environments with a high sediment load.

Additionally, the environmental indicator value of the intense wood deformation, represented by a strong zigzag, chevron-like pattern found in all samples (Figure 10), is linked to their compression by a heavy layer of high-energy flows of channel infilling sediments before the wood was permineralized during the burial process. Based on their morphologies, these anomalous features could not be linked to reactions during the life span of the trees (*e.g.* reaction wood, frost rings, density fluctuations, and scars) caused by climatic/environmental anomalies such as extreme weather, avalanches, landslides, storms and erosion, fire, mechanical damages, parasites, or lack of light and water (Baas & Schweingruber, 1987; Schweingruber, 2007; Butler & Sawyer, 2008; Gärtner & Heinrich, 2013). These structures are present in Holocene and Pleistocene conifers that ended up in glacial sediments that were later covered by ice and were under high pressure, which caused the wood cells to collapse (Schweingruber, 2007). Such structures were also noticed by Gnaedinger & Zavattieri (2020) in coniferous woods from the Upper Triassic of southwestern Gondwana and the Triassic of Antarctica (Del Fueyo *et al.*, 1995) and were attributed to wood compression caused by burial before the permineralization process.

A review of the general tree growth pattern of coeval Upper Triassic assemblages in South America at relatively higher latitudes (45°S) indicated distinct growth conditions. Wood analyses in the Tronquimalal Group (Neuquén Basin, Mendoza Province) led Gnaedinger & Zavattieri (2020) to identify a wood growth pattern composed of continuous true growth rings with well-marked ring boundaries defined by numerous latewood cells showing radial thickening of the walls. This evidence, along with other paleobotanical data, indicated a seasonal temperate-warm and humid to sub-humid climate for the western margin of the continent.

Closer comparisons with the Upper Triassic of Antarctica are hampered due to the absence of fossil woods described for this interval. However, true growth rings were identified in wood specimens from the Middle Triassic Fremouw Peak

(Ryberg & Taylor, 2007), attributed to a rapid transition to dormancy under the strong influence of the annual light/dark cycle within the Antarctic Circle. However, some environmental stresses in the polar region were indicated by epicormic shoots and traumatic growth zones in some woods (Decombeix *et al.*, 2018).

The only fossil records in the Upper Triassic that show similarities with our material are those found in conifer woods of the Northern Hemisphere in the Upper Triassic Chinle Formation of Arizona (USA), 15° north of the paleoequator near the west coast of Pangaea. Those wood assemblages showed no true growth rings and instead displayed irregular growth interruptions that were attributed to periods of drought in a tropical climate (Ash & Creber, 1990, 1992).

Given the evidence, the growth pattern found in the studied assemblage points to climatic conditions more consistent with tropical/subtropical climatic belts rather than with warm temperate zones. Similar wood patterns have been described for extant subtropical and tropical conifer woods (Schweingruber, 1992).

The exclusive occurrence of gymnosperms with a non-pteridospermophyta affinity during the deposition of the Mata sandstone, attributed to the latest Triassic (Rhaetian), seems to indicate the development of a forest where the corystosperms disappeared, suggesting a temporal change in the plant composition in communities of the long-lasting endemic Triassic *Dicrodium*-dominated floras. Zhang & Grant-Mackie (2001) considered the replacement of *Dicrodium*-dominant floras by conifer forests in the Gondwanan southern hemisphere to be a gradual affair associated with increased humidity, in contrast with the dramatic climate changes attributed to hot-house conditions evidenced by data from northwestern Europe.

CONCLUSIONS

The report of growth interruption zones in a Late Triassic wood assemblage from fluvial depositional environments in southernmost Brazilian Gondwana (Paleobotanic Garden of the city of Mata, RS) indicates the presence of tropical climate conditions under the influence of a variable and irregular water supply.

These irregular, short-term environmental growth disturbances were attributed to drought fluctuation, which caused temporary water stress and probably influenced the water table. Nevertheless, the return to suitable growing conditions and increased water availability at the end of temporary stress conditions was rapid.

The wood anatomical proxies from the Mata Sequence (Rhaetian) indicate a relative increase in water availability intervals and irregular short-term drought periods, suggesting some climatic change in relation to the conditions in the underlying unit Candelaria Sequence (Carnian/Norian), which was subject to seasonal variations characterized by long dry periods and short, but intense, flood events.

Stratigraphic analysis coupled with GPR ratified the river-channel infilling depositional process for the Mata Sequence and clarified some stages of the taphonomic process of the

wood assemblage, which occurred under the influence of high-energy flood events that dragged and buried the trees originally adapted to ecological niches linked to inter-channel environments.

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CONTRIBUTIONS

A.M.S and M.G.S. conducted the paleobotanical analyses; E.G.B. conducted the GPR analyses; C.L.S. wrote the geological synthesis and established the stratigraphic interpretation of the GPR results.

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