



## Climate change during the deposition of the Aptian Santana Formation (Araripe Basin, Brazil): Preliminary data based on wood signatures

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### ABSTRACT

This paper presents preliminary results of paleoclimatic signatures of conifer woods during the deposition of the basal Crato and topmost Romualdo members of the Santana Formation within the Tropical Equatorial Hot Arid Belt (late Aptian, Araripe Basin, Brazil). Analysis was carried out using standard thin sections, and the anatomical details were studied in transmitted light. The wood growth pattern from the lowermost laminated lacustrine carbonate level of the Crato Member was characterized by the absence of true growth rings and the common presence of wood growth interruptions, and could be linked to a tropical, equable but erratically humid environment. In an interlayered fine-to-coarse sandstone level attributed to a fluvio-deltaic interval, the wood growth pattern was homogeneous, lacking true growth rings, with weakly delineated growth interruptions over long radial distances. In this level the growth pattern could be related with a transition to a more equable tropical climate during a relatively humid period. In contrast, the wood pattern from the carbonate succession of the uppermost Romualdo Member, interpreted as a lagoon area with marine influence, showed true growth rings with abrupt ring boundaries and rings of variable width, also including frequent growth interruptions. This pattern could be linked to a monsoonal-like climate, subjected to distinct cyclical conditions and periodical droughts during the growing season.

### 1. Introduction

Semi-arid to arid climatic conditions have been assumed to be predominant during the deposition of the Mesozoic Brazilian Araripe Basin, which was located within the Tropical Equatorial Hot Arid Belt in the late early Cretaceous according to Scotese (2014).

Climatic inferences have been based on the widespread occurrence of evaporites along the evolving South Atlantic rift system, on the absence of coal deposits, and on the dominance of drought-resistant, xerophytic plants, as evidenced by morphological parameters such as sunken stomata, increased cuticle and epidermis thickness, and the development of papillae and hairs (Dilcher et al., 2005; Mohr et al., 2006, 2007). Alternation of humid/dry cycles, probably associated with seasonal

precipitation, have been proposed for the heterolytic Araripe succession based on sedimentological and organic matter evidence (Neumann et al., 2003 and citations therein).

Scherer et al. (2015) integrated sedimentological and paleoclimatic data for the Aptian succession in the Araripe Basin and found evidence of consistently high temperatures, albeit with variable humidity. Their sedimentological evidence indicated that, despite variations in the oxygenation degrees of the lakes, the climate could be relatively humid or sub-humid, and that no major climatic changes occurred during the deposition of the basal sequences.

The fossil-bearing deposits of the Lower Cretaceous (late Aptian) of the Araripe Basin found in the Crato and Romualdo members granted to the Santana Formation the title of best-known Mesozoic Lagerstätte of

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Gondwana (Grimaldi, 1990; Heimhofer and Martill, 2007; Martill and Bechly, 2007; Naish, 2007; Pinheiro et al., 2012; Barling et al., 2015; Carvalho et al., 2019; Dias and Carvalho, 2020). Nevertheless, records of permineralized woods, which provide the most sensitive geological data for assessing paleoclimatic seasonality (Chaloner and Creber, 1988) have so far been virtually absent within the Aptian interval of the basin. Martill et al. (2012) already noted that while petrified woods are abundant in the coarser siliciclastic units beneath the Araripe Group (e.g., the pre-rift Missão Velha Formation), they rarely occur as three-dimensional fossils of large diameter within the Santana Formation. Martill et al. (2012) suggested the development of hinterland vegetation with small, poorly lignified plants, but some taphonomic sorting could not be ruled out.

The presence of growth rings was recorded by Santos et al. (2020) in a petrified araucarian conifer branch showing preserved xylem and bark from the basal, fine laminated carbonates of the Crato Member, but further details of the growth pattern were not presented. The additional recovery of anatomically preserved petrified woods from a fine-to-coarse sandstone interlayered in the lowermost fine laminated carbonates, and two wood fragments from the uppermost silty-shale interval of the Romualdo Member led to the present working hypothesis that woods from different stratigraphic levels of similar anatomical identity could enable climatic inferences.

It is known that analysis of wood growth patterns can be problematic if the approach is based on a low number of samples. However, the studied material has important attributes such as good preservation, provenance from well-defined stratigraphic and sedimentological intervals and biological affinity of all samples with the single morphogenus *Agathoxylon* Hartig. Thus, despite the scarcity of sampling (that prevails throughout the studied interval), the present study was carried out aiming to provide preliminary clues, although still partly speculative, to the interpretation of the regional paleoclimate conditions during the depositional intervals within the Aptian Santana Formation (Araripe Basin, NE Brazil).

## 2. Geological setting

The Araripe Basin (Fig. 1) is a hinterland basin covering an area of 12,200 km<sup>2</sup> that originated during a Berriasian–Hauterivian tectonic phase connected with the first stages of the South American and African rifting (Matos, 1992; Carvalho, 2000). It is located in the southern part of the Ceará state, spreading through the northwestern of Pernambuco state to the east of Piauí state, northeastern Brazil. The basin is filled with conglomerates, sandstones, siltstones, shales, mudstones, marls, limestones, gypsum and anhydrite. The lithostratigraphic subdivision of these rocks has been discussed and reviewed by many authors (Mabe-soone, 2000; Machado Jr. et al., 1990; Martill, 2007; Martill et al., 2007; Neumann and Cabrera, 2002; Neumann et al., 2002). The most accepted terms for the lithostratigraphic units are, from base to top, the Cariri, Brejo Santo, Missão Velha, Rio da Batateira, Santana, and Exu formations (Beurlen, 1963, 1971, 1971; Ponte, 1992; Ponte and Appi, 1990; Paula-Freitas and Borghi, 2011; Rios-Netto et al., 2012).

The permineralized woods analyzed here come from the depositional interval of the early Cretaceous included in the post-rift stage (Ponte and Appi, 1990), which is up to 180 m thick (Peulvast et al., 2011). This carbonate and gypsum interval was defined by Beurlen (1963, 1971) as one lithostratigraphic unit named Santana Formation, divided from base to top in Crato, Ipubi and Romualdo members.

The Crato Member is mainly composed of gray, dark brown to black shales and light gray to light brown laminated limestones. Its mean thickness is approximately 50 m (up to 80 m) and it overlies the Rio da Batateira Formation conformably, and the Abaiara Formation unconformably, or lies directly on the basement. The contact with the overlying Ipubi Member is gradational. The Ipubi Member (30 m mean thickness) is mainly composed of gypsum and anhydrite with interbedded dark shales. This evaporitic layer represents the climax of a

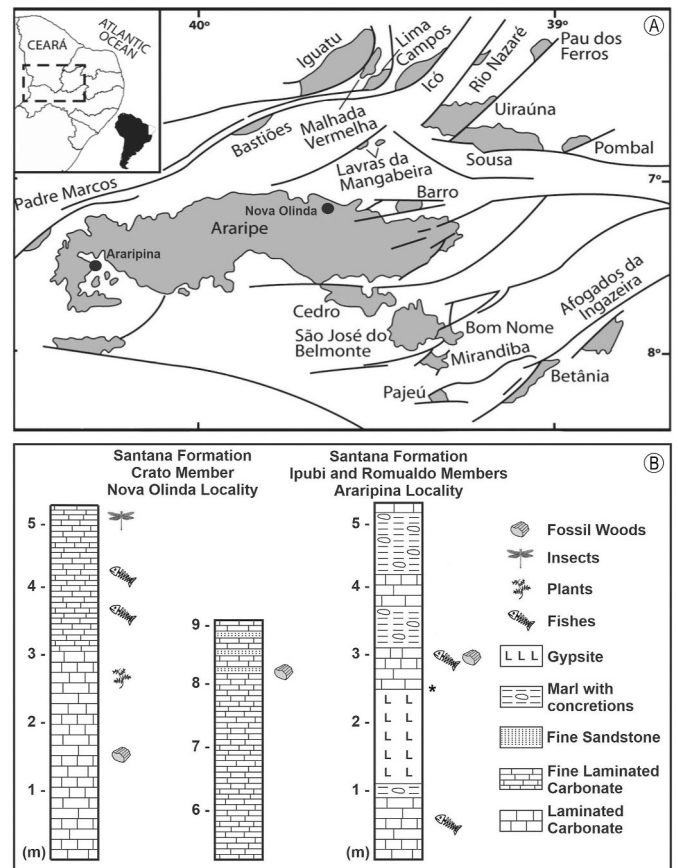


Fig. 1. Location map of the Araripe Basin (A) and simplified stratigraphic column of the Santana Formation (B) at Nova Olinda and Araripina outcrops. \*Transition from the Ipubi to the Romualdo Member.

sedimentary sequence in an inland lake, whose waters have become progressively saline due to increasing evaporation. In this environment, gypsum and anhydrite precipitated in salt layers and on sabkha-type plains. The contact with the overlying Romualdo Member is abrupt and is interpreted as a regional erosive unconformity (Ponte and Appi, 1990).

The Romualdo Member consists of intercalations of shales, marls, limestones and lenses of whitish friable sandstones. The shales and marls are greenish-gray and very fossiliferous, with a horizon abundant in limestone concretions. Although the fossil fishes are exceptionally abundant and well preserved within the concretions, (Brito and Yabu-moto, 2011; Martill, 1998; Martill and Brito, 2008), other vertebrates such as turtles, pterosaurs and crocodyliforms, invertebrates, and rare plants are also typical of this unit (Martill, 1988; Wilby and Martill, 1992). The occurring limestones are usually clayey, fossiliferous and are found predominantly in the upper part of the unit. The lower contact with the Ipubi Member is marked at the base by a thin layer (1–2 m) of whitish microconglomerate or conglomeratic sandstone, recognized as the marker of a regional erosive unconformity. The new lithological sequence that begins there is considered as the record of a new sedimentary cycle of shallow and ephemeral lakes. At the top of the unit there is a 12 m thick layer of marls and limestones with fossiliferous content (gastropod and bivalve shells and echinoids) evidencing marine deposition (Ponte and Appi, 1990).

One permineralized wood sample (UFRJ-DG 2443-Pb) comes from the lowest portion of the Crato Member, considered of late Aptian in age (Heimhofer et al., 2010; Rios-Netto et al., 2012). The deposition in these strata is interpreted by Martill et al. (2007) and Selden and Nudds (2012) as a microbially induced precipitation of carbonate in a shallow, hypersaline lacustrine environment.

The specimen UFRJ-DG 2792-Pb comes from a fine-to-coarse sandstone layer interlayered in the basal, fine laminated carbonates of the Crato Member, interpreted by Selden and Nudds (2012) as originated by episodic influx of water from seasonal rivers which allowed the salt dissolution and the flourishing of a freshwater invertebrate and vertebrate biota.

The two wood specimens (UFRJ-DG 2963-Pb and ANMRJ-E-418) from the uppermost late Aptian Romualdo Member come from a laminated carbonate deposited after the gypsum interval (Fig. 1). The depositional environment of this carbonate succession was interpreted as a lagoon area with restricted marine influence, coupled with increasing freshwater input during phases of lowstand sea-level (Fürsich et al., 2019).

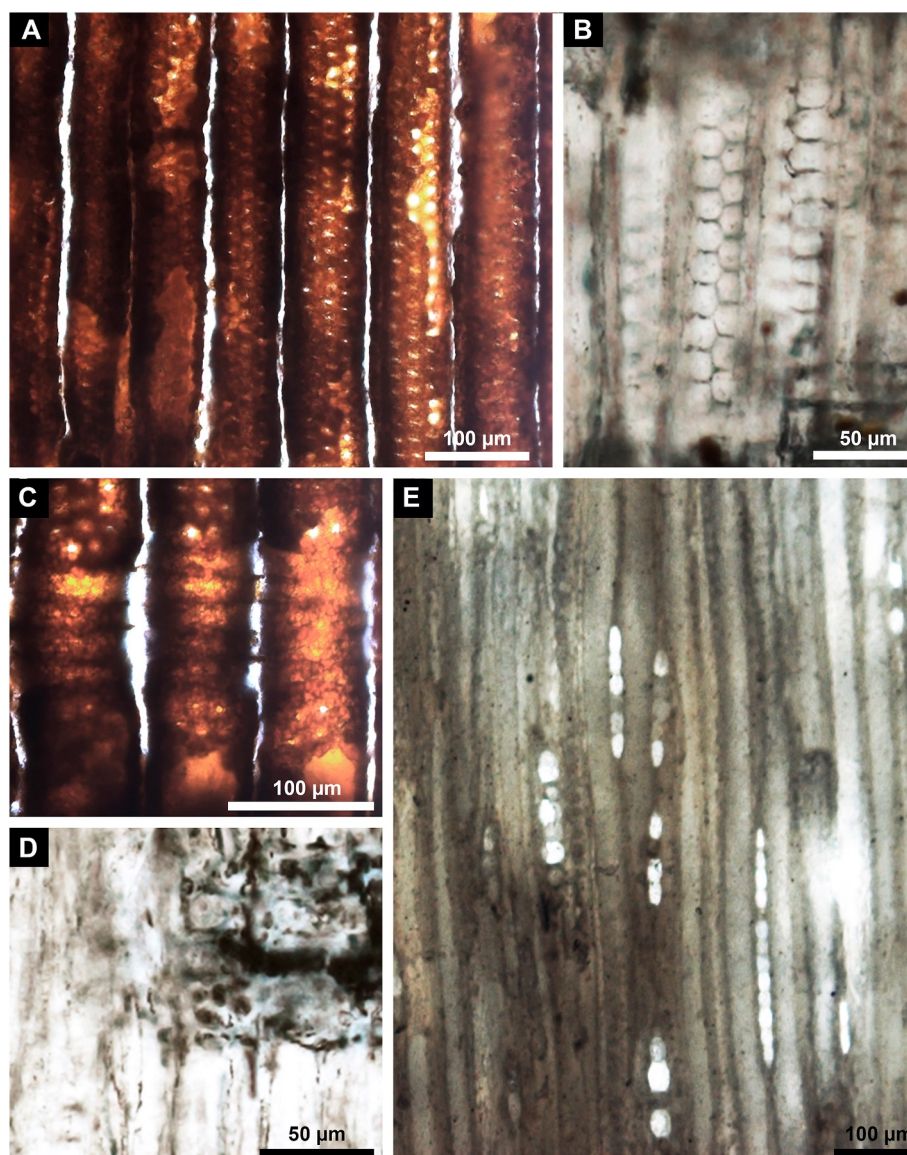
### 3. Material and methods

The petrified wood specimens were prepared according to standard procedures, i.e., with the elaboration of polished blocks and thin sections of three polished surfaces, namely transversal (TS), radial

longitudinal (RLS), and tangential longitudinal sections (TLS) mounted on Canada balsam and observed with optical microscopy in transmitted light with a Carl Zeiss MC80 microscope. Photomicrographs were taken using a digital camera (AxioCam MRC) and measurements made with the AxioVision software. The specimens under the acronyms UFRJ-DG 2443-Pb, 2792-Pb and 2963-Pb are housed in the paleontological collection of the Departamento de Geologia, Instituto de Geociências, Universidade Federal do Rio de Janeiro, and the specimen under the acronym ANMRJ-E-418 is housed in the paleontological collection of the Museu de Ciências da Terra – Agência Nacional de Mineração/RJ.

The wood anatomical patterns were described according to the list of microscopic features for softwood identification by Richter et al. (2004) and morphotype criteria established by Philippe and Bamford (2008).

For the identification of wood growth patterns and paleoclimate inferences, Douglass (1928), Creber and Chaloner (1984), Schweingruber (1992, 1996, 2007), Falcon-Lang (2003) and Richter et al. (2004) were consulted.



**Fig. 2.** *Agathoxylon*-type woods from the Santana Formation. (A, C) UFRJ-DG 2443-Pb; B, (B, D-E) UFRJ-DG 2963-Pb. (A) RLS showing uniseriate, biseriolate alternate, polygonal bordered tracheid pitting; (B) RLS showing triseriate, alternate, bordered pitting in hexagonal shape, the pit spacing on the tracheid radial walls in compact arrangement between margins; (C–D) RLS showing araucarioid cross-field pitting; (E) TLS with homogeneous parenchymatous uniseriate rays.

#### 4. Wood anatomical patterns and affinities

The gymnospermous wood UFRJ-DG 2443-Pb (39.5 cm in length x 2.1 cm in diameter) from the lowest laminated carbonate level of the Crato Member was previously informally described by Santos et al. (2020) as a non-compressed conifer branch. RLS showed triseriate alternate, bordered pitting of hexagonal shape (Fig. 2A), with the pits completely packing the tracheid radial walls, and crowded araucarioid cross-field pits (Fig. 2C). Resin plugs are common features in the tracheids, and axial parenchyma was not observed. TLS showed homogeneous uniseriate parenchymatic rays. Axial parenchyma was not observed in either radial or tangential sections. In TS the small, heterogeneous pith (ca. 0.5 mm in diameter) was composed of parenchymatous cells and clusters of sclerenchyma cells. The secondary xylem was composed by square to polygonal tracheids and uniseriate parenchymatic rays. The growth pattern observed in TS was characterized by frequent zones of wood growth interruption and is described in detail in Section 5. The collapsed phloem was characterized by axial physiologic resin ducts and a continuous band of sclereids.

The log UFRJ-DG 2792-Pb (20 cm in length x 25 cm in diameter) collected from the fine-to-coarse sandstone interlayered in the fine laminated carbonates of the Crato Member is a pycnoxylic, gymnospermous wood composed of secondary xylem, bark absent. In RLS the tracheid pitting can be uniseriate (48%), round, sometimes slightly compressed, 14.6  $\mu\text{m}$  average diameter, showing rounded apertures. Adjacent tracheid pits are all contiguous, not spaced. When biseriate (52%), pits are alternate, and adjacent pit borders are polygonal. Cross-field pitting with 2–5 pits, densely arranged in araucarioid pattern. In LTS, density of parenchymatous rays is 2–6 rays per millimeter (4 rays on average), always uniseriate, typically 1 to 8 cells high (5 cells on average). The tangential surfaces of the ray cells are not pitted and axial parenchyma is absent. Diagnostic resin ducts are absent in the xylem. In TS tracheids are polygonal, arranged in regular rows, limited by elongated, parenchymatous ray cells with thin walls in uniseriate disposition. Axial parenchyma cells are absent. The homogeneous growth pattern observed in TS is described in detail in Section 5.

The specimens UFRJ-DG 2963-Pb (20 cm in length x 12 cm in diameter) and ANMRJ-E-418 (18 cm in length x 15 cm in diameter) from the uppermost Romualdo Member are also conifer woods represented by fragments of secondary xylem, showing very similar anatomical features, being thus included in a single taxon. In RLS the intratracheal pits are contiguous, uniseriate (73%), non-compressed, showing rounded apertures, and when biseriate (27%) are alternate with hexagonal outline (Fig. 2B), ranging from 12 to 19  $\mu\text{m}$  in diameter (14.8  $\mu\text{m}$  on average). Bars of Sanio, secondary spiral thickening and trabeculae are absent. Cross-fields are composed exclusively of parenchyma cells with smooth horizontal walls and perpendicular end walls. Cross-field pits are crowded, in araucarioid pattern, consisting of 4–8 pits densely arranged, smaller than the tracheid pitting (Fig. 2D). TLS shows exclusively uniseriate rays ranging from 2 to 13 cells high (6.2 cells on average) with density of 3–6 rays per millimeter (Fig. 2E). Some of the parenchymatous cells of the rays are filled with dark content, suggesting the occurrence of resiniferous parenchyma (Fig. 2E). The tangential walls of the tracheids are not pitted. In TS the secondary xylem is composed of tracheids and parenchyma rays. The tracheids are square, arranged in regular rows, limited by elongated, parenchymatous ray cells with thin walls in uniseriate disposition. The wood growth pattern, characterized by typical growth rings, is detailed in Section 5.

The affinity of all the specimens from both the Crato and the Romualdo members point to the single morphogenus *Agathoxylon* Hartig (1848), according to the morphotype criteria of Philippe and Bamford (2008) for Mesozoic secondary woods. Among extant conifers, the *Agathoxylon*-type wood occurs exclusively in the Araucariaceae family. However, this anatomical pattern also occurred in other plant groups in the Jurassic – early Cretaceous, e.g., Pteridospermales and Cheiridolepidiaceae (Philippe et al., 2004; Vera and Césari, 2012; Greppi et al.,

2020). Nonetheless, the collapsed phloem in the specimen UFRJ-DG 2443-Pb from the basal Crato Member, characterized by canals and a continuous band of sclereids points to Araucariaceae.

#### 5. Wood growth patterns and climatic approaches

The growth pattern of the conifer branch UFRJ-DG 2443-Pb collected from the lowest laminated carbonate of the Crato Member was identified as growth rings with high variability by Santos et al. (2020), characterized by an extremely low proportion of latewood (one or two tracheids) showing no increases in wall thickness, implying stressful conditions. However, a more detailed analysis revealed that the growth pattern is very unlikely to be composed of “true growth rings” as defined by Greguss (1972), Fritts (1976), Creber and Chaloner (1984) and Schweingruber (1996), and corresponds to “wood growth interruption zones” resulting from a temporal slowing down, but not switching off, of cambial activity (Creber and Chaloner, 1984; Schweingruber, 1992, 1996, 1996; Wan 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, 1996; Young et al., 1993; Falcon-Lang, 2003; Wan et al., 2014).

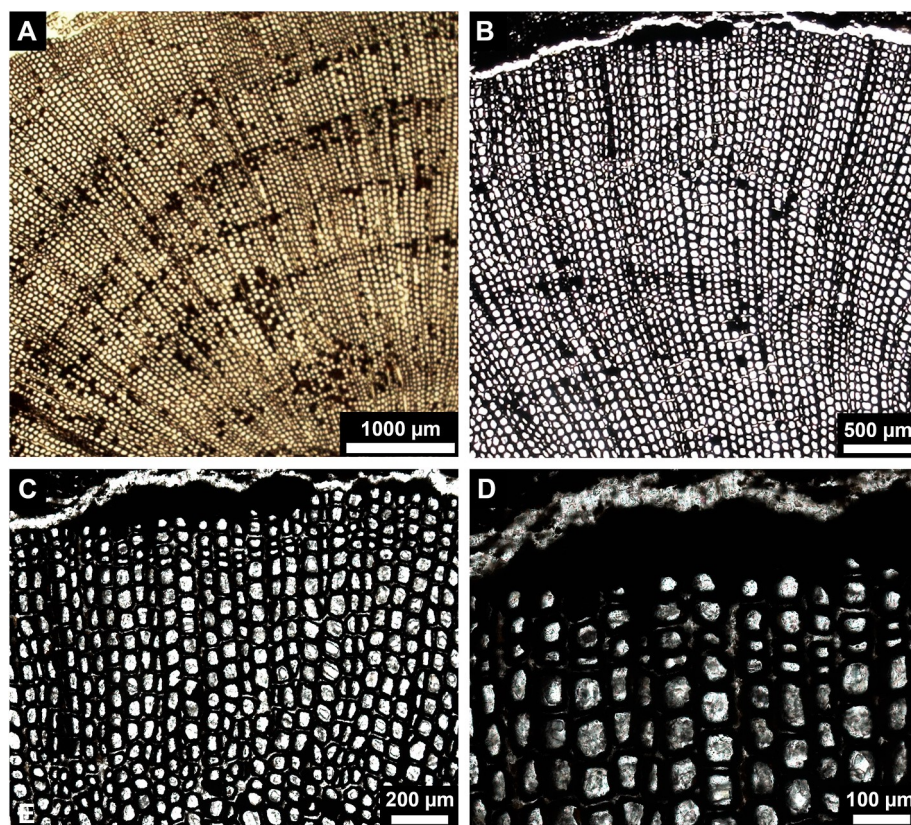
Cell-by-cell measurements in TS detected growth interruptions ranging from 680 to 948  $\mu\text{m}$  wide (Fig. 3A). In each zone the tracheids of the earlywood range from 60 to 95  $\mu\text{m}$  (average 75  $\mu\text{m}$ ) in radial diameter and the walls from 6 to 13  $\mu\text{m}$  (average 9  $\mu\text{m}$ ) in thickness (Fig. 3B). In the latewood, 1 to 3 rows of tracheids are flattened, ranging from 29 to 50  $\mu\text{m}$  (average 36  $\mu\text{m}$ ) in radial diameter and the walls from 6 to 13  $\mu\text{m}$  (average 9  $\mu\text{m}$ ) in thickness (Fig. 3C–D). The interruption boundaries are distinguished by a sudden, abrupt decline in cell diameter also followed by a rapid rise back up in the tracheid diameter compatible with wood-tracheids of earlywood. Some zones are inconspicuous, subtle, and the boundaries cannot be traced laterally (Fig. 3B).

The absence of true growth rings found in the branch fragment could be linked to climatic conditions where variability was minimal year-round, but the abrupt growth interruption zones could be a signal of common and abrupt cycles of water shortage interspaced with intervals of favorable growing conditions. The wide diameter of earlywood tracheids testifies for relatively mild conditions during the growing interval. Correlations between drought and growth-interruption formation in wood were probably indirect and linked to the physiological water stress through the depression of the local water table as a consequence of the actual aperiodicity of the rainfall (Yamamoto et al., 1993; Donaldson, 2002). Consequently, we speculate that the growth interruptions may have mainly been triggered by drought, but their narrow width (1–3 cells) suggests that the growth disturbance was short-lived.

Closer comparisons of the growth pattern with coeval Aptian woods included in the periequatorial belt (ca. 5°S) are hampered due to the lack of studies during this interval at low latitudes. However, irregular growth patterns like this were registered across a broad latitudinal belt in woods from the Upper Cretaceous of the US Western interior, indicating that they resulted from regional climatic forcing (Falcon-Lang, 2003). For Wan et al. (2014), the occurrence of numerous growth interruptions and absence of true growth rings in a gymnospermous stem from the Upper Permian of mid-latitude continental deposits of NW China (*Septomedullopitys szei* Wan, Yang et Wang) suggests weak seasonality of annual precipitation and short-term, non-periodic droughts.

In addition, wood growth patterns similar to the one described here are present in conifers from extant megathermal regimes in periequatorial East Africa settings when annual temperature variability is minimal, and irregular growth interruption patterns are entirely due to erratic rainfall and seasonal droughts (Jacoby, 1989; Schweingruber, 2007).

As the material under study is a branch, potential differences in the definition of juvenile and adult wood could falsify the results. However, different authors (Forward and Nolan, 1961; Krause and Eckstein, 1992;



**Fig. 3.** Wood growth patterns in TS. (A) General view of specimen UFRJ-DG 2443-Pb showing growth interruptions (B–D) Details of (A) showing the abrupt decline in cell diameter.

Grabner and Wimmer, 2006; Schweingruber, 2007) concluded that typical anatomical patterns of a tree are also recognizable in branches and twigs that are not mechanically stressed.

The wood fragment UFRJ-DG 2792-Pb from the fine-to-coarse sandstone interlayered with the fine laminated carbonates of the Crato Member showed, in TS, uniform-sized rows of tracheids from 28.8 to 36.4  $\mu\text{m}$  in radial diameter  $\times$  27.3–33.8  $\mu\text{m}$  in tangential diameter (average 30  $\mu\text{m}$ ). This anatomical pattern persists throughout the specimen (Fig. 4A). The occurrence of wood deformation structures that could be interpreted as growth interruptions is attributed to wood compression caused by burial during early taphonomic process (Fig. 4B). Weak growth interruptions are very rare, distinguished by a sudden decline in cell size, with no increases in wall thickness, along one to three cells and are locally absent for a considerable distance (Fig. 4C–D).

The general wood growth spectrum is characterized by the absence of true growth rings and exhibits continuous, uninhibited growth. The virtual absence of growth rings indicates that the tree grew under potentially favorable conditions with continuous, year-round cambial activity in a climatic zone with no distinct seasonality.

Based on macro and microfossils described for the Crato Member, included in the Tropical-Equatorial Hot Arid Belt (Chumakov et al., 1995), Bernardes-de-Oliveira et al. (2014) detected the presence of morphoadaptive features in fossil plants to a semiarid to arid climate, probably under torrential and sporadic rains. However, the presence of “humidity windows” for this interval was indicated by Santos et al. (2020) based on the analysis of fungus-plant interactions in araucarian woods in addition to climatic signatures of growth ring patterns. Based on multiproxies (i.e., vascular plants, arthropods, fishes, and tetrapods), Ribeiro et al. (2021) detected a seasonal, semi-arid, shallow lacustrine wetland where aquatic zones were surrounded by periodically flooded mesophytic ecotones and outer xeric habitats. Salgado-Campos et al.

(2021) recognized a marginal paleolagoon facies succession coincident with a clay mineral association with higher kaolinite contents in the Crato succession that was probably deposited in wetter conditions.

The wood growth patterns found in both lacustrine and fluvio-deltaic environments of the Crato Member in a low latitude belt (ca. 5°S) are distinct from those found in conifer woods from the Lower Cretaceous at relatively higher latitudes of South America in warm temperate climates, such as central Patagonia (45°S), where growth patterns are typically composed of true growth rings (Passalia, 2009; Greppi et al., 2020).

True growth rings were observed in the two wood samples from the uppermost Romualdo Member (UFRJ-DG 2963-Pb and ANMRJ-E-418). Ring increments range from 0.3 mm to 1.94 mm (mean 0.8 mm), but the width from one increment to the next is variable (Fig. 5A). Each growth ring begins with earlywood cells 24.7–37.8  $\mu\text{m}$  (mean 30  $\mu\text{m}$ ) in radial diameter. The diameter declines slightly to 24.7  $\mu\text{m}$  with an abrupt reduction to 14–18  $\mu\text{m}$  (mean 16  $\mu\text{m}$ ) in the final stage of the ring along latewood tracheids. The low-density latewood is composed of 2–4 tracheids with maximum 7  $\mu\text{m}$  thick radial walls, and at the start of a new ring values return to 24–37.8  $\mu\text{m}$  (mean 30.5  $\mu\text{m}$ ) in radial diameter (Figs. 5B) and 4.5  $\mu\text{m}$  thick radial walls.

Although the occurrence of true growth rings is mainly linked to temperate latitudes, they occur in conifers from extant seasonal tropical regions, but do not necessarily represent annual increments of growth (Duke et al., 1981; Ash, 1983; Falcon-Lang, 1999). In these tropical latitudes, seasonality is largely the product of intra-annual variations in rainfall (Rumney, 1968; Worbes, 1995; Schweingruber and Poschold, 2005; Brienen et al., 2016). Wood growth interruptions composed of 1–2 rows of cells, irregularly spaced (between 0.1 and 0.5 mm apart) are also a characteristic feature along radial diameters of the wood, and occur most commonly associated to the growing phase (Fig. 5C–D). However, some of the growth rings observed here contain no interruption zones,

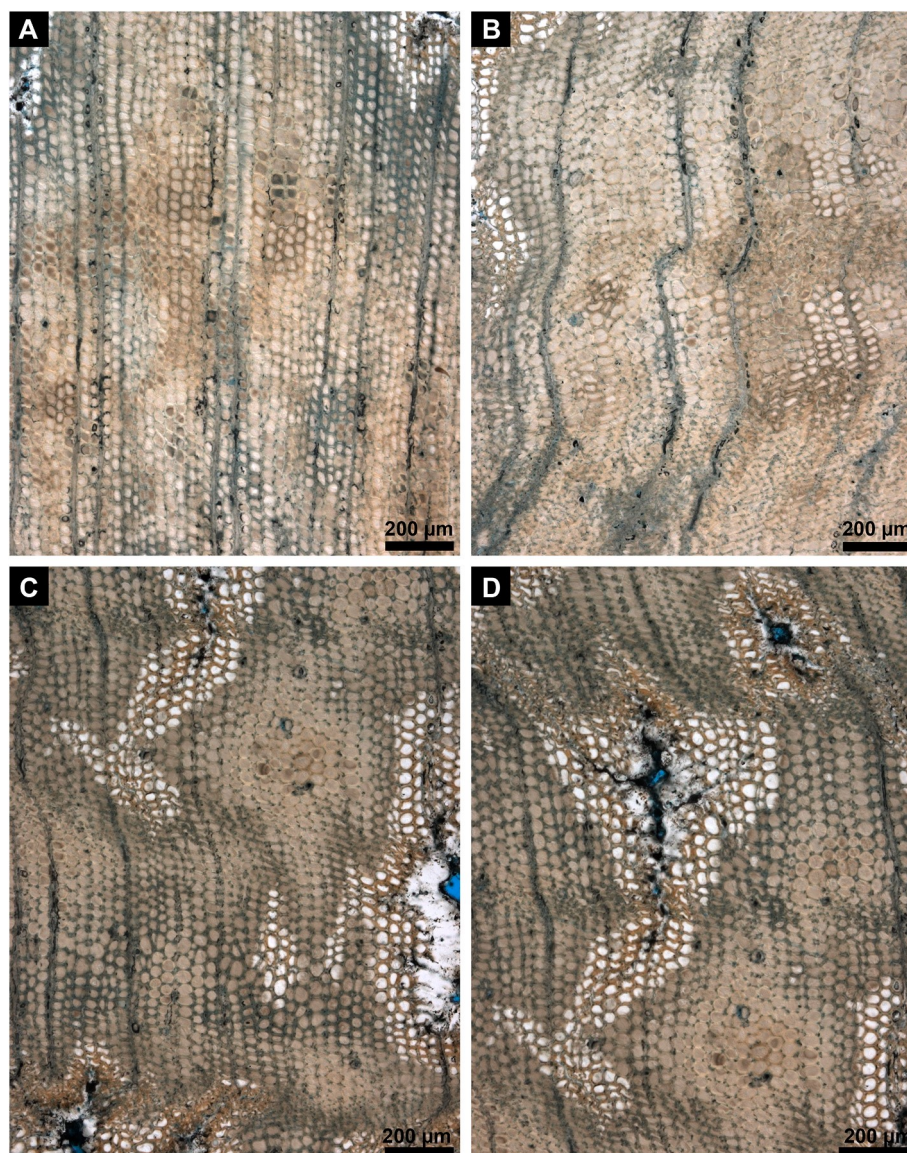


Fig. 4. Wood growth pattern in TS of specimen UFRJ-DG 2792-Pb. (A) Virtually homogeneous pattern; (B) wood deformation structures; (C–D) wood growth interruption zones.

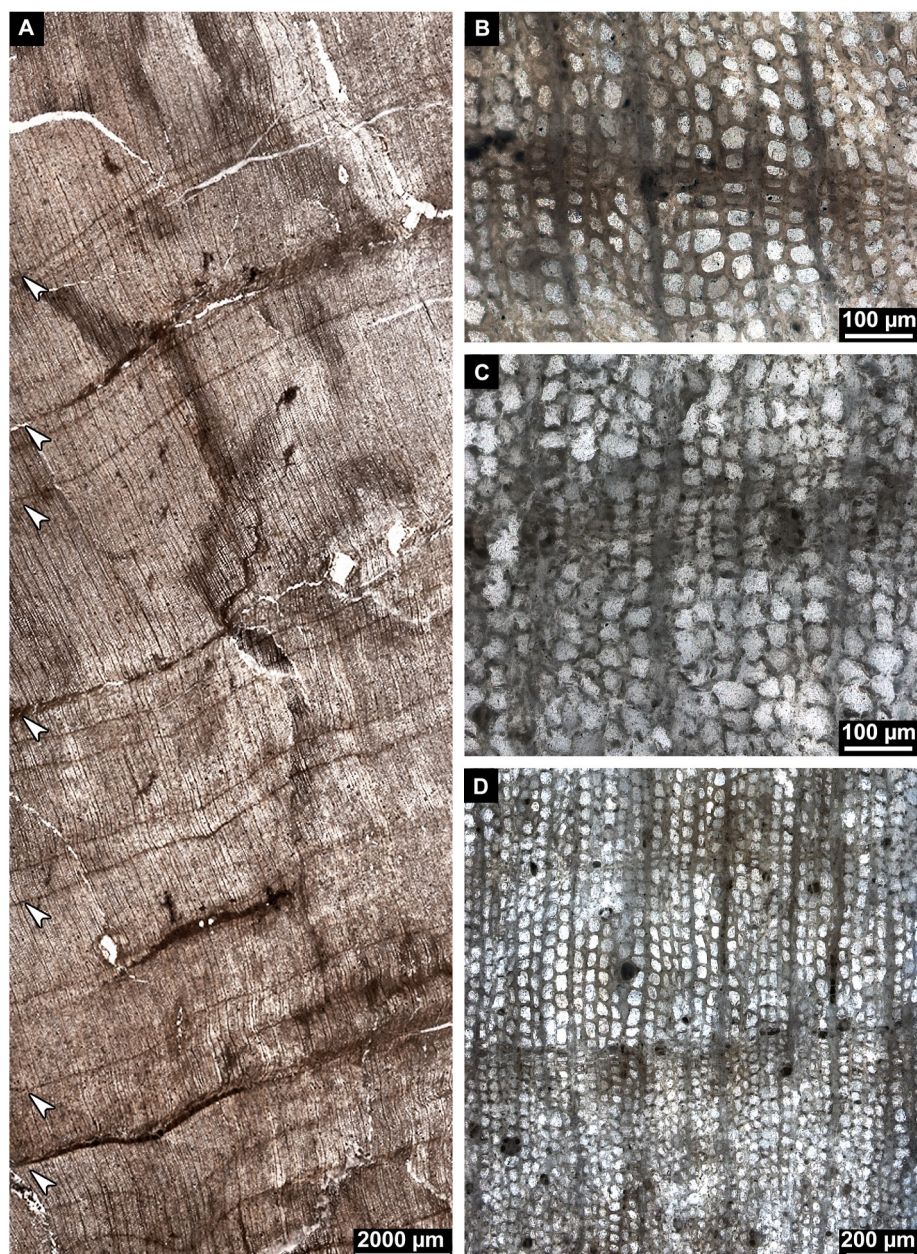
while others contain double interruption zones.

Even though the wood anatomical signatures were defined based on restricted sampling, and consequently still speculative, they suggest that during the deposition of the uppermost Romualdo Member the paleoclimate was characterized by distinct cyclical conditions, with inter and intra-annual density fluctuations typical of extant Mediterranean and monsoonal climates (Cherubini et al., 2003; De Micco and Aronne, 2007; De Micco et al., 2016). The periodic occurrence of true growth rings associated with growth interruption zones and followed by the increment of earlywood before terminal growth point to monsoonal conditions (Schweingruber, 1996, 2007).

Under these conditions, the summer drought usually starts in the beginning of summer and the tree reacts with an intra-annual density fluctuation. When the monsoon starts, growth takes up again, and in the late autumn the tree ring is terminated by latewood with thick-walled cells (Schweingruber, 2007). The reduced occurrence of latewood in each growth ring matches the evidence found in woods from extant monsoonal climates linked to marked dry season in the fall, where conifers have marked growth rings but latewood is only a few cells wide (Falcon-Lang, 1999). Detailed analysis of inter and intra-annual wood

fluctuations as a consequence of extant climates have been hardly discussed (e.g., De Micco and Aronne, 2007; De Micco et al., 2016).

The speculation about changing climatic conditions from tropical with intermittent drought events to monsoonal is in line with sedimentary analysis which considered the deposition of the Romualdo Member as the record of a new sedimentary cycle within the Santana Formation, corresponding to shallow and ephemeral lakes under marine influence (Ponte and Appi, 1990). Falcon-Lang (1999) inferred a monsoonal climate for western Ireland and southern Scotland at a paleolatitude of 4° S during the early Carboniferous based on a conifer wood pattern similar to that found in extant monsoonal-influenced regions. This inference was supported by global paleogeographic data, dominated by the large, mid-latitude, equator-parallel Gondwanan continent. Additionally, the influence of Pangaeon megamonsoonal climates in the wood signatures of coniferous woods, associated to other paleontological data, was demonstrated by Dubiel et al. (1991) for the Upper Triassic Chinle Formation (EEUU). However, Ash and Creber (1992) concluded that the absence of true growth rings and the exclusive presence of interruption zones in the woods from the Triassic Chinle Formation would indicate that the trees were not greatly affected by the



**Fig. 5.** Wood growth patterns in TS in the specimens UFRJ-DG 2963-Pb (A) and ANMRJ-E-418 (B–D) from the Romualdo Member. (A) General view showing the presence of growth rings (arrows) intercepted by growth interruptions; (B) true growth ring with low-density latewood; (C) growth interruption zone; (D) successive growth interruption zones.

monsoonal climate.

The monsoon-like climate inferred here during the deposition of the Romualdo Member can be supported by the results of [Ohba and Ueda \(2010\)](#) who performed climate simulations for the early and latest Cretaceous using an atmospheric general circulation model (AGCM). They explained how the changing paleocontinental configuration in the Cretaceous affected the atmospheric circulation, especially over the tropics. Their results indicated that the birth process of the Atlantic Ocean caused moisture convergence over the northern part of South America, and consequently the paleogeography would have been particularly conducive for monsoonal circulation over the tropics, and a South American monsoon was thus established over the continent.

## 6. Conclusions

Preliminary analysis on growth signatures of a restricted assemblage

of petrified conifer woods from the basal Crato and topmost Romualdo members of the Santana Formation (Araripe Basin) included in the Tropical Equatorial Hot Arid Belt allowed to speculate about changing climate patterns along the depositional interval as summarized in [Fig. 6](#).

The lowermost deposition of the fine laminated carbonates of the Crato Member, interpreted as a shallow lacustrine environment, would occur, according to the wood growth data analyzed here, under a tropical, equable, erratically humid environment. During the deposition of a fine-to-coarse sandstone level, interpreted as a fluvio-deltaic environment interlayered in the fine laminated carbonates, wood signatures point to a transition to a tropical, more equable climate which occurred during a relatively humid period.

Wood signatures point to a distinct monsoon-like climate during the deposition of the uppermost Romualdo Member, interpreted as a lagoonal area with marine influence subjected to distinct cyclical conditions and periodical droughts during the growing season.

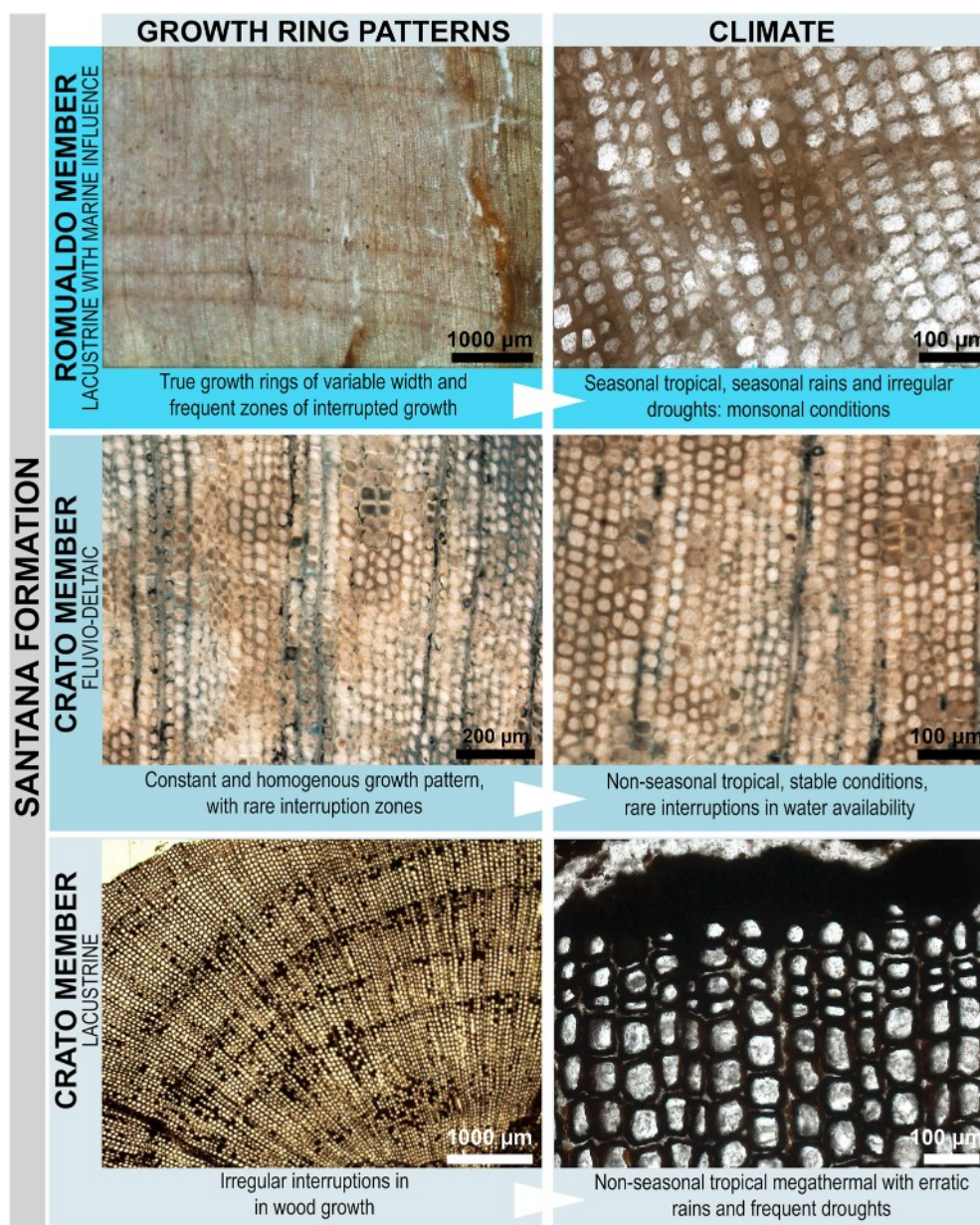


Fig. 6. Wood growth signatures and climate inferences for the Santana Formation.

#### Author contributions

M. Guerra-Sommer: Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing M. Sieglöcher: Data curation, Formal analysis, Investigation, Validation, Visualization, Writing – original draft I. Degani-Schmidt: Formal analysis, Validation, Visualization, Writing – original draft, Writing – review & editing A. C. S. Santos: Formal analysis, Writing – original draft I. S. Carvalho: Funding acquisition, Resources, Writing – original draft J. A. F. G. Andrade: Resources F. I. Freitas: Resources.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### References

- Ash, J., 1983. Growth rings in *Agathis robusta* and *Araucaria cunninghamii* from tropical Australia. *Aust. J. Bot.* 31, 269–276.
- Ash, S.R., Creber, G.T., 1992. Palaeoclimatic interpretation of the wood structures of the trees in the Chinle Formation (upper Triassic), petrified forest National Park, Arizona, USA. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 96 (3–4), 299–317.



- Barling, N., Martill, D.M., Heads, S.W., Gallien, F., 2015. High fidelity preservation of fossil insects from the Crato formation (lower Cretaceous) of Brazil. *Cretac. Res.* 52, 605–622.
- Bernardes-de-Oliveira, M.E.C., Sucerquia, P.A., Mohr, B., Dino, R., Antonioli, L., Garcia, M.J., 2014. Indicadores paleoclimáticos na paleoflora do Crato, final do Aptiano do Gondwana Noroccidental. In: Carvalho, I.S., Garcia, M.J., Lana, C.C., Strohschoen, O. Jr (Eds.), *Paleontologia: Cenários de Vida e Paleoclimas*, vol. 5. Interciência, Rio de Janeiro, pp. 101–119.
- Beurlen, K., 1963. Geologia e estratigrafia da Chapada do Araripe. In: 17 Congresso Nacional de Geologia, SBG/SUDENE (Recife, Brazil).
- Beurlen, K., 1971. As condições ecológicas e fisiológicas da Formação Santana na Chapada do Araripe (Nordeste do Brasil). *An Acad. Bras Ciências* 43 (Suppl. o), 411–415.
- Brienen, R.J., Schöngart, J., Zuidema, P.A., 2016. Tree rings in the tropics: insights into the ecology and climate sensitivity of tropical trees. In: Goldstein, G., Santiago, L.S. (Eds.), *Tropical Tree Physiology: Adaptations and Responses in a Changing Environment*. Springer, Cham, pp. 439–461.
- Brito, P.M., Yabumoto, Y., 2011. An updated review of the fish faunas from the Crato and Santana formations in Brazil, a close relationship to the Tethys fauna. *Bullet. Kitakyushu Mus. Nat. Hist. Ser. A* 9, 107–136.
- Carvalho, I.S., 2000. Geological environments of dinosaur footprints in the intracratonic basins of northeast Brazil during the Early Cretaceous opening of the South Atlantic. *Cretac. Res.* 21, 255–267.
- Carvalho, I.S., Agnolin, F., Rolando, M.A.A., Novas, F.E., Xavier-Neto, J., Freitas, F.I., Andrade, J.A.F.G., 2019. A new genus of pipimorph frog (Anura) from the Early Cretaceous Crato Formation (Aptian) and the evolution of South American tongueless frogs. *J. S. Am. Earth Sci.* 92, 222–233.
- Chaloner, W.G., Creber, G.T., 1988. Do fossil plants give a climatic signal? *J. Geol. Soc. Lond.* 147, 343–350.
- Cherubini, P., Gartner, B.L., Tognetti, R., Bräker, O.U., Schoch, W., Innes, J.L., 2003. Identification, measurement and interpretation of tree rings in woody species from Mediterranean climates. *Biol. Rev.* 78 (1), 119–148.
- Chumakov, N.M., Zharkov, M.A., Herman, A.B., Doludenko, M.P., Kalandadze, N.N., Lebedev, E.L., Ponomarenko, A.G., Rautian, A.S., 1995. Climatic belts of the mid-Cretaceous time. *Stratigr. Geol. Correl.* 33, 42–63.
- Creber, G.T., Chaloner, W.G., 1984. Influence of environmental factors on the wood structure of living and fossil trees. *Bot. Rev.* 50, 357–448.
- Dechamps, R., 1984. Evidence of bush fires during the Plio-Pleistocene of Africa (Omo and Sahabi) with aid of fossil woods. In: Coetzee, J.A., Van Zinderen Bakker, E.M. (Eds.), *Palaeoecology of Africa and Surrounding Islands*, vol. 16 (Rotterdam).
- De Micco, V., Aronne, G., 2007. Anatomical features, monomer lignin composition and accumulation of phenolics in 1-year-old branches of the Mediterranean *Cistus ladanifer* L. *Bot. J. Linn. Soc.* 155 (3), 361–371.
- De Micco, V., Campelo, F., De Luis, M., Bräuning, A., Grabner, M., Battipaglia, G., Cherubini, P., 2016. Intra-annual density fluctuations in tree rings: how, when, where, and why? *IAWA J.* 37 (2), 232–259.
- Dias, J.J., Carvalho, I.S., 2020. Remarkable fossil crickets preservation from Crato formation (Aptian, Araripe Basin), a Lagerstätten from Brazil. *J. S. Am. Earth Sci.* 98, 102443.
- Dilcher, D.L., Bernardes-de-Oliveira, M.E.C., Pons, D., Lott, T.A., 2005. Welwitschiaceae from the lower Cretaceous of northeastern Brazil. *Am. J. Bot.* 92, 1294–1310.
- Donaldson, L.A., 2002. Abnormal lignin distribution in wood from severely drought stressed *Pinus radiata* trees. *IAWA J.* 23 (2), 161–178.
- Douglas, A.E., 1928. *Climatic Cycles and Tree Growth: a Study of the Annual Rings in Trees in Relation to Climate and Solar Activity*, vol. 289. Carnegie Institution of Washington Publication, pp. 1–127.
- Dubiel, R.F., Parrish, J.T., Parrish, J.M., Good, S.C., 1991. The Pangaeen megamonsoon: evidence from the upper Triassic Chinle Formation, Colorado plateau. *Palaios* 6, 347–370.
- Duke, N.C., Birch, W.R., Williams, W.T., 1981. Growth rings and rainfall correlations in a mangrove tree of the genus *Diospyros* (Ebenaceae). *Aust. J. Bot.* 29, 135–142.
- Falcon-Lang, H.J., 1999. The Early Carboniferous (Coureycan–Arundian) monsoonal climate of the British Isles: evidence from growth rings in fossil woods. *Geol. Mag.* 136 (2), 177–187.
- Falcon-Lang, H.J., 2003. Growth interruptions in silicified conifer woods from the Upper Cretaceous Two Medicine Formation, Montana, USA: implications for palaeoclimate and dinosaur palaeoecology. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 199, 299–314.
- Forward, D.F., Nolan, N.J., 1961. Growth and morphogenesis in the Canadian forest species: IV. Radial growth in branches and main axis of *Pinus resinosa* Ait. under conditions of open growth, suppression, and release. *Can. J. Bot.* 39, 413–436.
- Fritts, H., 1976. *Tree Rings and Climate*. Academic Press, San Francisco, p. 567.
- Fürsich, F.T., Custódio, M.A., Matos, S.A., Hethke, M., Quaglio, F., Warren, L.V., Assine, M.L., Simões, M.G., 2019. Analysis of a Cretaceous (late Aptian) high-stress ecosystem: the Romualdo formation of the Araripe Basin, northeastern Brazil. *Cretac. Res.* 95, 268–296.
- Grabner, M., Wimmer, R., 2006. Variation of different tree-ring parameters in samples from terminal shoot of a Norway spruce tree. *Dendrochronologia* 23, 111–120.
- Greguss, P., 1972. *Xylotomy of the Living Conifers*. Akademiai Kiado, Budapest, p. 329.
- Greppi, C.D., Pujana, R.R., Scasso, R.A., 2020. Fossil woods from the lower Cretaceous Tres Lagunas formation of central Patagonia (Chubut Province, Argentina). *Cretac. Res.* 108, 104322.
- Grimaldi, D.A. (Ed.), 1990. *Insects from the Santana Formation, Lower Cretaceous of Brazil*. Bulletin of the American Museum of Natural History 195, 1–191.
- Hartig, T., 1848. Beitrag zur Geschichte der Pflanzen und zur Kenntnis der norddeutschen Braunkohlen-Flora. *Bot. Zeitung* 6, 185–190.
- Heimhofer, U., Ariztegui, D., Lenniger, M., Hesselbo, S.P., Martill, D.M., Rios-Netto, A.M., 2010. Deciphering the depositional environment of the laminated Crato fossil beds (early Cretaceous, Araripe Basin, north-eastern Brazil). *Sedimentology* 57, 677–694.
- Heimhofer, U., Martill, D.M., 2007. The sedimentology and depositional environment of the Crato Formation. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), *The Crato Fossil Beds of Brazil*. University Press, Cambridge, pp. 44–62.
- Jacoby, G.C., 1989. Overview of tree-ring analysis in tropical regions. *IAWA J.* 10, 99–108.
- Krause, C., Eckstein, D., 1992. Holzzuwachs an Ästen, Stamm und Wurzeln bei normaler und extremer Witterung. In: Michaelis, W., Bauch, J. (Eds.), *Lutverunreinigungen und Waldschäden am Standort "Postturm"*. Forstamt Farchau/Ratzeburg. GKSS-Forschungszentrum Geesthacht GmbH, 92/E/100, pp. 215–242.
- Mabesoone, J.M., 2000. Abertura do Oceano Atlântico Sul: como, onde, quando? XVIII Simpósio de Geologia do Nordeste, Recife, Brazil.
- Machado Jr., D.L., Dehira, L.K., Carneiro, C.D.R., Almeida, F.F.M., 1990. Reconstruções paleoambientais do Juro-Cretáceo do nordeste oriental brasileiro. *Rev. Bras. Geociências* 19, 470–485.
- Martill, D.M., 1988. Preservation of fish in the Cretaceous Santana Formation of Brazil. *Palaeontology* 31, 1–18.
- Martill, D.M., 1998. Fidelity of fossilisation: the Santana Formation of Brazil. In: Donovan, S.K. (Ed.), *The Fidelity of the Fossil Record*. Bellhaven Press, London, pp. 55–74.
- Martill, D.M., 2007. The age of the Cretaceous Santana Formation fossil Konservat Lagerstätte of north-east Brazil: a historical review and an appraisal of the biostratigraphic utility of its palaeobiota. *Cretac. Res.* 28, 895–920.
- Martill, D.M., Bechly, G., 2007. Introduction to the Crato formation. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), *The Crato Fossil Beds of Brazil: Window into an Ancient World*. University Press, Cambridge, pp. 3–7.
- Martill, D.M., Bechly, G., Loveridge, R., 2007. The Crato Fossil Beds of Brazil: Window into an Ancient World. University Press, Cambridge, p. 624.
- Martill, D.M., Brito, P.M., Washington-Evans, J., 2008. Mass mortality of fishes in the Santana Formation (lower Cretaceous, ?Albian) of northeast Brazil. *Cretac. Res.* 29, 649–658.
- Martill, D.M., Loveridge, R.F., Mohr, B.A., Simmonds, E., 2012. A wildfire origin for terrestrial organic debris in the Cretaceous Santana Formation fossil Lagerstätte (Araripe Basin) of north-east Brazil. *Cretac. Res.* 34, 135–141.
- Matos, R.M.D., 1992. The northeast Brazilian rift system. *Tectonics* 11, 766–791.
- Mohr, B.A.R., Bernardes-de-Oliveira, M.E.C., Barale, G., Ouaja, M., 2006. Biogeographic distribution and ecology of *Klitzschophyllites*, an early Cretaceous angiosperm in southern Laurasia and northern Gondwana. *Cretac. Res.* 27, 464–472.
- Mohr, B.A.R., Bernardes-de-Oliveira, M.E.C., Loveridge, R.F., 2007. The macrophyte flora of the Crato Formation. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), *The Crato Fossil Beds of Brazil: Window into an Ancient World*. University Press, Cambridge, pp. 537–565.
- Naish, D., 2007. Turtles of the Crato formation. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), *The Crato Fossil Beds of Brazil: Window into an Ancient World*. University Press, Cambridge, pp. 452–457.
- Neumann, V.H., Borrego, A.G., Cabrera, L., Dino, R., 2003. Organic matter composition and distribution through the Aptian–Albian lacustrine sequences of the Araripe Basin, northeastern Brazil. *Int. J. Coal Geol.* 54, 21–40.
- Neumann, V.H., Cabrera, L., 2002. A tendência expansiva do sistema lacustre Aptiano-Albiano do Araripe durante sua evolução: dimensões e morfologia. *IG Sér. B, Estudos Pesquisas, Recife – PE* 11, 176–188.
- Neumann, V.H., Cabrera, L., Mabesoone, J.M., Valença, L.M.M., Silva, A.L., 2002. Ambiente sedimentar e fácies da sequência lacustre aptiana-albiana da Bacia do Araripe, NE do Brasil. 6º Simpósio sobre o Cretáceo do Brasil e 2º Simpósio sobre el Cretáceo de América del Sur, Rio Claro. *Anais. UNESP, Rio Claro*, pp. 37–51.
- Ohba, M., Ueda, H., 2010. AGCM study on effects of continental drift on tropical climate at the early and late Cretaceous. *J. Meteorol. Soc. Jpn.* 88, 869–881.
- Passalía, M.G., 2009. Cretaceous pCO<sub>2</sub> estimation from stomatal frequency analysis of gymnosperm leaves of Patagonia, Argentina. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 273, 17–24.
- Paula-Freitas, A.B.L., Borghi, L., 2011. Estratigrafia de alta resolução do intervalo siliciclástico Aptiano da Bacia do Araripe. *Geociências* 30, 529–543.
- Peulvast, J.P., Bétard, F., Magalhães, A.O., 2011. Scarp morphology and identification of large-scale mass movements in tropical tablelands: the eastern Araripe Basin (Ceará, Brazil). *Geomorphologie* 17, 33–52.
- Philippe, M., Bamford, M.K., 2008. A key to morphogenera used for Mesozoic conifer-like woods. *Rev. Palaeobot. Palynol.* 148, 184–207.
- Philippe, M., Bamford, M., McLoughlin, S., Alves, L.S.R., Falcon-Lang, H.J., Gnaedinger, S., Ottone, E.G., Pole, M., Rajanikanth, A., Shoemaker, R.E., Torres, T., 2004. Biogeographic analysis of Jurassic–early Cretaceous wood assemblages from Gondwana. *Rev. Palaeobot. Palynol.* 129, 141–173.
- Pinheiro, F.L., Horn, B.L.D., Schultz, C.L., Andrade, J.A.F.G., Sucerquia, P.A., 2012. Fossilized bacteria in a Cretaceous pterosaur headcrest. *Lethaia* 45, 495–499.
- Ponte, F.C., 1992. Sistemas deposicionais na Bacia do Araripe, nordeste do Brasil. Simpósio sobre as Bacias Cretácicas Brasileiras, 2, Resumos Expandidos. UNESP, Rio Claro, pp. 81–84.
- Ponte, F.C., Appi, C.J., 1990. Proposta de revisão da coluna litoestratigráfica da Bacia do Araripe. *Anais 36. Congresso Brasileiro de Geologia, SBG, Natal, Brazil*, pp. 211–226.
- Ribeiro, A.C., Ribeiro, G.C., Varejão, F.G., Battirola, L.D., Pessoa, E.M., Simões, M.G., Warren, L.V., Riccomini, C., Poyato-Ariza, F.J., 2021. Towards an actualistic view of the Crato Konservat-Lagerstätte paleoenvironment: a new hypothesis as an Early Cretaceous (Aptian) equatorial and semi-arid wetland. *Earth Sci. Rev.* 216, 103573.

- Richter, H.G., Grosse, D., Heinz, I., Gasson, P.E., 2004. IAWA list of microscopic features for soft wood identification. *IAWA J.* 25, 1–70.
- Rios-Netto, A.M., Regali, M.S.P., Carvalho, I.S., Freitas, F.I., 2012. Palinoestratigrafia do intervalo Alagoas da Bacia do Araripe, Nordeste do Brasil. *Rev. Bras. Geociencias* 42, 331–342.
- Rumney, G.R., 1968. *Climatology and the World's Climate*. MacMillan, London, New York, p. 656.
- Salgado-Campos, V.M.J., de Souza Carvalho, I., Bertolino, L.C., Duarte, T.A., Araújo, B. C., Borghi, L., 2021. Clay mineralogy and lithochemistry of lutites from the lower Cretaceous Crato member, Araripe Basin, NE Brazil: implications for paleoenvironmental, paleoclimatic and provenance reconstructions. *J. S. Am. Earth Sci.* 110, 103329.
- Santos, A.C.S., Guerra-Sommer, M., Degani-Schmidt, I., Sieglöcher, A.M., Carvalho, I.S., 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). *Cretac. Res.* 114, 104525.
- Scherer, C.M.S., Goldberg, K., Bardola, T., 2015. Facies architecture and sequence stratigraphy of an early post-rift fluvial succession, Aptian Barbalha Formation, Araripe Basin, northeastern Brazil. *Sediment. Geol.* 322, 43–62.
- Schweingruber, F.H., 1992. Annual growth rings and growth zones in woody plants in southern Australia. *IAWA J.* 13, 359–379.
- Schweingruber, F.H., 1996. *Tree Rings and Environment: Dendroecology*. Paul Haupt AG, Bern, p. 609.
- Schweingruber, F.H., 2007. *Wood Structure and Environment*. Springer, Berlin, p. 291.
- Schweingruber, F.H., Poschold, P., 2005. Growth rings in herbs and shrubs: life span, age determination and stem anatomy. *For. Snow Landsc. Res.* 79 (3), 195–415.
- Scotese, C.R., 2014. Atlas of Early Cretaceous Paleogeographic Maps, PALEOMAP Atlas for ArcGIS, Mollweide Projection. PALEOMAP Project, Evanston, IL.
- Selden, P., Nudds, J., 2012. *Evolution of Fossil Ecosystems*. Academic Press, London, p. 288.
- Vera, E.I., Césari, S.N., 2012. Fossil wood (Coniferales) from the Baqueró group (Aptian), Santa Cruz Province, Argentina. *An. Acad. Bras. Cienc.* 84, 617–625.
- Wan, M., Yang, W., Wang, J., 2014. *Septomedullopitys szei* sp. nov., a new gymnospermous wood from Lower Wuchiapingian (Upper Permian) continental deposits of NW China, and its implication for a weakly seasonal humid climate in mid-latitude NE Pangaea. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 407, 1–13.
- Wilby, P.R., Martill, D.M., 1992. Fossil fish stomachs: a microenvironment for exceptional preservation. *Hist. Biol.* 6, 25–36.
- Worbes, M., 1995. How to measure growth dynamics in tropical trees a review. *IAWA J.* 16 (4), 337–351.
- Yamamoto, F., Shimizu, S., Hashizume, H., 1993. Anatomy of stem hyperplasia called tokkuri disease in *Chamaecyparis obtusa*. *IAWA J.* 14 (3), 227–237.
- Young, P.J., Megonigal, J.P., Sharitz, R.R., Day, F.P., 1993. False ring formation in baldcypress (*Taxodium distichum*) saplings under two flooding regimes. *Wetlands* 13 (4), 293–298.