Journal of South American Earth Sciences 111 (2021) 103490

Contents lists available at ScienceDirect

Journal of South American Earth Sciences

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

Multidisciplinary approach as a key for paleoenvironmental interpretation in a *Weichselia*-dominant interval from the late Aptian Codó Formation (Parnaíba Basin, Brazil)

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ARTICLE INFO

Keywords:
Early Cretaceous
Ferns
Mosses
Paleobiogeography

ABSTRACT

The presence of the fern *Weichselia* in a restricted sedimentary interval of a drilling core in the Parnaíba Basin (Brazil) was used as a lead for paleoenvironmental interpretation integrating paleobotanical, palynofacies, palynological, organic petrography and clay mineralogy analyses. The fern paleobiogeography was amplified and its association with terrestrial bryophyte gametophytes (*Muscites*) indicated depositional conditions corresponding to marginal areas of freshwater bodies subjected to frequent flooding under the general fluvial-deltaic conditions so far accepted for the intermediary portion of the Codó Formation. The high dominance of non-opaque phytoclasts and very scarce autochthonous non-marine palynomorphs pointed to a shallow water body linked to marginal areas of fluvial systems in the river outlets, channel margins in estuarine systems, and/or shallow floodplain lakes connected/open to fluvial canals. The very scarce marine palynomorphs (dinoflagellate cysts) suggest a limited influence from unstable environments on coastal margins or estuarine canals. The terrestrial vegetation surrounding the depositional setting, deciphered by palynological analysis, reflected distinct environmental conditions prevailing simultaneously in 1) humid areas dominated by fern communities, and 2) dry-xerophytic areas dominated mainly by Araucariaceae and Cheirolepidiaceae gymnosperms, both as components of a wider Aptian paleoenvironment within the periequatorial latitudes in South America. The results were supported by clay mineralogy that showed abundance of detrital kaolinite over montmorillonite and suggest the dominance of a climatic humidification process and a less expressive semiarid climate in a regional context.

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https://doi.org/10.1016/j.jsames.2021.103490
Received 20 April 2021; Received in revised form 12 July 2021; Accepted 24 July 2021

1. Introduction

Weichselia Stiehler, a fern that became extinct during the Mesozoic, shows a chronostratigraphic range from the Middle Jurassic to the Early Cretaceous and a broad paleogeographic distribution. Its scleromorphic features, such as sporocarps protecting the spores (angiosporangy), gave rise to conflicting interpretations, from xeromorphism to adaptation against excessive moistening or salinity (Silantieva and Krassilov, 2006 and citations therein).

Consequently, habitat reconstructions range from dry land to shallow continental and coastal margins (Barale, 1979; Daber, 1968; Krassilov, 1972; Retallack and Dilcher, 1981; Watson and Alvin, 1996). Despite this divergence – mainly arisen from sedimentary analysis – *Weichselia* has been recognized as an important paleoenvironmental proxy and its presence in fossil plant associations has been used to guide the interpretation of the corresponding depositional environments, from continental savannah-like to marginal marine settings (Blanco-Moreno et al., 2018).

In this way, the fern-dominated assemblages containing *Weichselia* remains, especially in the Cretaceous, were reported from continental lacustrine carbonates from the Barremian of Las Hoyas Formation and from the middle Albian Escucha Formation, Spain (Diéguez and Meléndez, 2000; Sender et al., 2005). In addition, paleofloras characterized by the presence of *Weichselia* from other European sites of Barremian age were linked to environments of channel deposits and of brackish water by Coiffard et al. (2007).

The presence of *Weichselia* as a prominent element in marginal marine habitats was reported for the upper Aptian–lower Albian of south Tunisia and for the Barremian–early Aptian delta plain, tidal flat and near-shore marine facies of the Hatira Formation, Israel (Barale and Ouaja, 2001; Silantieva and Krassilov, 2006). The dominance of *Weichselia* fronds in a lignite layer led Abu Hamad et al. (2016) to recognize the genus as dominant in mangrove coastal systems in the northern Gondwana (Jordan) during the Barremian.

Blanco-Moreno et al. (2018) recovered information about the paleogeography, chronostratigraphy and ecology of the genus and ratified the previous proposition of Alvin (1974) and Daber (1953, 1968), who suggested the occurrence of *Weichselia*-dominated plant associations in both continental and coastal marine deposits. New data from morphological and anatomical analyses of rachises performed by Blanco-Moreno et al. (2020) confirmed the presence of adaptations to stressful environments.

According to Blanco-Moreno et al. (2018), *Weichselia* first appeared in the fossil record during the Middle Jurassic in North Africa and Georgia; in Europe, it was more common during the Berriasian–Barremian. After appearing in North America in the Aptian, those authors suggested that the genus would have apparently vanished in South America and India before the Aptian, with the last records corresponding to the Cenomanian in Europe and the north of the African Province (Vakhrameev, 1991). For South America, *Weichselia* figured in the early Aptian paleobiogeographic map of Blanco Moreno et al. (2018) in deltaic environments of Colombia (Pons, 1988) and Peru, and Venezuela in unknown environments of "Neocomian" age (Berry, 1922, 1937; Zeiller, 1914). For the Brazilian Albian, the presence of *Paradoxopteris* Hirmer (the stem of *Weichselia* according to El Atfy et al., 2020 and citations therein) was described by Mussa et al. (2000) from the Itapecuru Formation (São Luís Basin, NNE Brazil).

Well-preserved adpression pinna fragments of *Weichselia* are reported here for the first time for the Brazilian Cretaceous from a 1.55 m segment of a drill core from the late Aptian Codó Formation (Parnaíba Basin). By means of the integration of paleobotany with palynofacies and palynological analyses, the present study aimed to refine the specific associated depositional environment within the general fluvio-deltaic conditions so far accepted for the encompassing intermediary package of the Codó Formation in the context of the Parnaíba Basin (Rossetti et al., 2001a), as well as contributing to the knowledge on the paleobiogeography of this peculiar fern.

Additionally, clay mineral analysis was conducted in three lutite samples genetically related to the macrofossil remains allowing for comparison with previous paleoclimatic analyses for the Codó Formation outcrops (Rossetti et al., 2001b; Gonçalves et al., 2006).

2. Geologic and Paleontological setting

The sedimentary and magmatic succession of the Parnaíba Basin, with a total area of 600,000 km^2, located in the northern and northeastern regions of Brazil (Fig. 1), is divided into five supersequences: Silurian, Middle Devonian–lower Carboniferous, upper Carboniferous–Lower Triassic, Jurassic, and Cretaceous (Vaz et al., 2007).

In a broader context, the genesis of the deposits of the Cretaceous supersequence, that correspond from base to top to the early Aptian–Albian Grajaú, Codó and Itapecuru formations, was associated with tectonic movements or to the process of separation of the South American and African continents, manifesting the history of the Atlantic Ocean in this region (Rossetti et al., 2001a). In the Parnaíba Basin, the Itapecuru Formation is restricted to late Aptian times (Ferreira et al., 2020, 2021), although in the São Luís Basin the deposition range is Aptian-Cenomanian (Carvalho and Pedrão, 1998).

The late Aptian Codó Formation, subject of the present study, was originally defined by Rossetti et al. (2001a) to encompass the section of dark shales, limestones and evaporites. Mendes (2007) also included it in an essentially terrigenous post-evaporitic. Strontium isotopic ratios in the Codó Formation evaporites indicated a continental environment (Paz et al., 2005). This evidence is corroborated by the presence of typically lacustrine ostracods (Ramos et al., 2006), in addition to the predominance of calcite over dolomite in carbonate facies (Rossetti et al., 2004).

Mendes (2007) reported the presence of dinoflagellates above the main evaporitic succession, indicating marine contribution (lagoon) only at the end of the deposition of the Codó Formation. This marine-influenced interval is deposited unconformably over the evaporites, marking a sequence limit within the Codó Formation.

The age of the Codó Formation was earlier considered as Aptian–Albian (Andar Alagoas Stage) based on the paleoicthyofauna (Santos, 1974; Silva-Santos and Valença, 1968), although palynological data pointed to a late Aptian age (Lima, 1982). Subsequent studies attributed an Aptian age to the Codó Formation in the Parnaíba Basin and in the neighboring basins on the equatorial margin where it also occurs (Antonioli, 2001; Mendes, 2007; Paz et al., 2005; Ramos et al., 2006; Rossetti and Góes, 2000; Rossetti et al., 2001a, 2004; Soares et al., 2007; Zalán and Silva, 2007).

The fossil record of the Codó Formation includes fishes, crustaceans, insects, arthropods and gastropods (Cardoso, 1962; Lima and Leite, 1978; Lisboa, 1914; Pinto and Ornellas, 1974), but the ichthyofauna is the most common fossil group and has allowed for correlation with the fossil fishes from the Santana Formation in the Araripe Basin and Riachuelo Formation in the Sergipe/Alagoas Basin (Brito et al., 2016; Lindoso, 2016; Lindoso and Carvalho, 2012; Lindoso et al., 2011, 2013a, 2013b, 2016; Santos and Carvalho, 2009 and citations therein).

Plant fossils are uncommon, and the presence of angiosperm woods associated with indeterminate leaves and roots were reported by Borges (1937), Duarte (1959) and Moraes Rego (1923). Duarte and Santos (1993) identified in this unit *Nymphaeites choffati* (= *Klitzschophyllites choffati* (Saporta sensu Teixeira) emend. Gomez, Coiffard, Sender, Martín-Closas, Villanueva-Amadoz et Ferrer), the first known fossil angiosperm for the equatorial area. Lindoso et al. (2018) described a taphoflora from Brejo municipality (state of Maranhão) composed of Gnetales (?*Drewria*), conifers (*Cupressinocladus* and *Brachyphyllum*), and basal angiosperms (Nympheales, Magnoliids, and basal Eudicots), which support a late Aptian–?Albian age.

The material analyzed here comes from a 1.5 m thick interval of the 2-CO-1-MA core drilled in the city of Coroatá (Maranhão State,

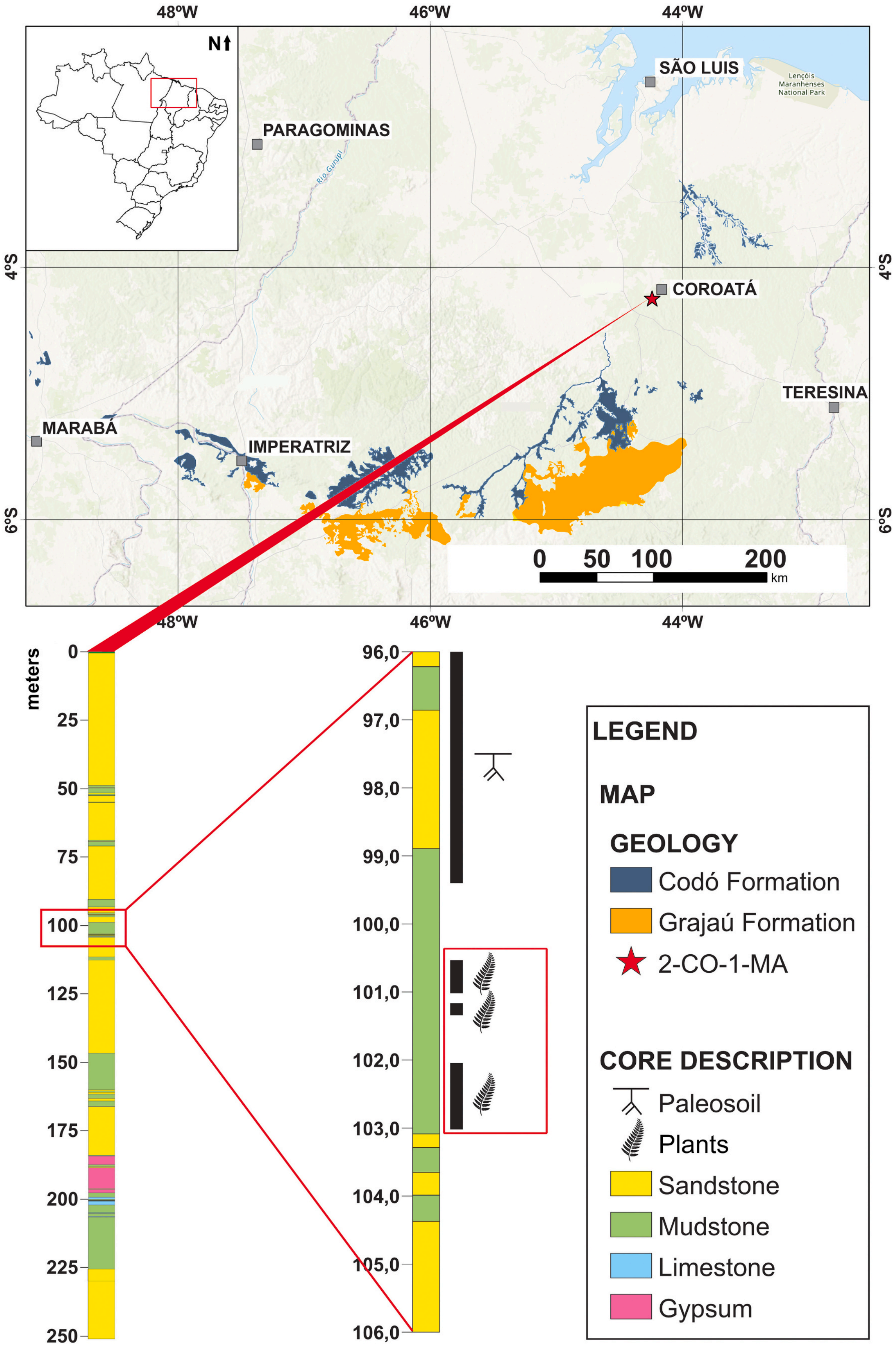

Fig. 1. Location map of the core drilling and position of the analyzed interval in the 2-CO-1-MA core sample from the Codó Formation.

northeastern Brazil), composed of dark shale containing organic matter and pyrite, lying above evaporite and gypsum levels, interspaced between underlying heterolytic sandstones of fluvial origin and overlying paleosols (Fig. 1), in a continental context of deposition.

3. Material and methods

Macrofossil, palynological and palynofacies analyses were conducted in four samples (102.75 m; 101.75 m; 101.35 m; 101.20 m) from a 1.5 m thick interval of a drill core (2-CO-1-MA) from to the Codó Formation (Fig. 1). The plant material was mostly horizontally oriented on the surface of the core slices, sometimes cross cutting the bedding plane. Most of the plant remains were adpression fragments of fern pinnae of *Weichselia*. Remains of delicate, small, elongated, branched shoots densely covered by linear leaves of presumed mosses were also common.

The macroscopic plant material was analyzed and documented under a Zeiss binocular stereomicroscope, model StereoDiscovery v12, motorized with Sycop control and equipped with a Zeiss AxioCam camera. All measurements were taken from calibrated images with the aid of the AxioVision 4.8.2 software package.

Four samples from the same levels where macro-remains were observed were prepared for palynological and palynofacies analyses following non-oxidative extraction techniques (Mendonça Filho et al., 2010, 2012, 2017; Oliveira et al., 2004, 2006) and then sieving the residues using 10/ mm nylon sieves. Thereafter, the samples were mounted on glass slides using Entellan Merck. A minimum of 200 palynomorphs were counted for each sample and the relative abundances of taxa were calculated. England Finder (EF) coordinates were used to record the location of the identified taxa.

The organic matter characterization was based on the quantitative examination of particulate organic matter using microscopy techniques. A total of 300 particles were counted for each sample and normalized in percentiles according to the criteria of Tyson (1995 modified by Mendonça Filho et al., 2012, 2017).

To support the microscopic interpretation of the adpressions, petrographic analysis was carried out in polished blocks under oil (Immersol 518 F) The blocks were also analyzed to obtain reflectance data as a proxy for estimating the degree of coalification (e.g., McParland et al., 2009).

Three fossil-bearing lutite samples were collected at the 101.20-, 101.35-, and 101.75-m depths of the core sample and processed following Salgado-Campos et al. (2021), in which oriented glass slides were produced following Moore and Reynolds (1997). Diffractograms were obtained in a Bruker D8 Advance ECO diffractometer with CuKα (λ = 1.5406 Å) radiation and operated at 40 kV and 25 mA. The range analyzed was from 1 to 40° (2θ) with a pass of 0.01° (2θ) per 0.5 s. Clay-sized fractions were randomly mounted for d_{060} reflection analyses in the back-loading method and acquired in the range from 4 to 70° (2 θ) with a pass of 0.02° (2 θ) per sec. The method of Biscaye (1965) was applied for quantitative clay mineral analyses and the Warr (2020)'s name abbreviations for clay minerals were used.

Processing techniques for palynofacies and organic petrography were performed through a 50× objective using an AxioSkop 2 Plus Zeiss microscope calibrated with a Sapphire standard (0.595%Ro) and equipped with spectrophotometer J&M (MSP200) at the Palynofacies and Organic Facies Laboratory (LAFO), Department of Geology/UFRJ. Clay mineral analysis was conducted in the Centro de Tecnologia Mineral, Coordenação de Análises Minerais, Setor de Caracterização Mineralógica – CETEM/UFRJ.

Macrofloral remains are housed in the Macrofossil Collection, Department of Geology of the Instituto de Geociências, Universidade Federal do Rio de Janeiro (IG/UFRJ) under the acronyms UFRJ-DG 2849 a/b Pb (101.75 m), 2850 a/b Pb (101.20 m), 2851 Pb (101.35 m), 2852 Pb (101.35 m). Palynological and palynofacies slides and polished blocks are stored at LAFO/UFRJ.

4. Results

4.1. Paleobotanical descriptions and comparisons

4.1.1. Weichselia remains

Among the abundant pinnae fragments occurring in the analyzed interval, the four best preserved specimens were selected for detailed observation and description. The vegetative and fertile fragments of the pinnae were highly fractured and limited to a drill core of 8 cm in diameter. Attempts of observing epidermal details by pinnule maceration were unsuccessful.

The fern remains correspond to secondary vegetative pinna fragments with broken ends and associated fertile sporocarps (Figs. 2 and 3). The fragments of the isolated pinnae are up to 8 cm long (Fig. 2A–D). The apical part of the frond was not preserved. The secondary rachis is 0.4–1.00 mm wide, smooth, straight, or slightly sinuous. Pinnules are attached to the rachis in opposite to sub-opposite disposition. They are heteromorphous, typically lingulate to triangular, sessile (pinnules attached to pinna rachis by their entire base), 2.4–5.3 mm long, 1.9–3.7 mm wide, attached to the rachis at oblique to straight angles (60°–90°). When lingulate, pinnule apices are rounded, and slightly acute when triangular (Fig. 2B).

The pinnule heteromorphy (Fig. 2) is a common feature in modern members of the extant leptosporiangiate Matoniaceae family (Kato and Setoguchi, 1998). This morphologic peculiarity can indicate affinity of Mesozoic fossil fronds with Matoniaceae (Taylor et al., 2009). The Matoniaceae family was apparently represented by a relatively small number of species throughout the Mesozoic (Berry, 1919). Currently it has a very narrow distribution and is restricted to southeastern Asia (Lindsay et al., 2003).

Pinnule venation is reticulate, with a thick prominent midrib that is distally forked and slightly curved just before the apex. The secondary venation is characterized by very dense anastomoses, clearly visible in the pinnule surfaces (Fig. 2E and F, 3A). Adaxially, the secondary venation forms polygonal, rhombic or rectangular areoles arising from the midrib. The areoles are mostly isometric (up to 390 μm wide), becoming narrower and rectangular toward the margin (down to 170 μm wide x up to 390 μm long) (Fig. 2F).

This general venation pattern, characterized by a dense reticulate and thick net, is relatively distinct from other Mesozoic matoniacean genera such as *Matonidium* Schenk and *Phlebopteris* Brongniart (e.g., Nagalingum and Cantrill, 2006), but is in accordance with the description of *Weichselia* Stiehler by different authors (e.g., Alvin, 1971; Barale, 1979).

Petrographic analysis in polished blocks allowed for identification of stomata confined to the lower pinnule surface, irregularly oriented within the areoles of lateral veins, with elliptical guard cells, each pair measuring 26–29 μm long and 14–18 μm wide (Fig. 3B). The stomatal pattern resembles that of both *Weichselia reticulata* (Stokes et Webb) Fontaine (Alvin, 1974) and *W. negevensis* Silantieva et Krassilov (2006).

The associated fertile structures are clustered spheroids (synangia) about 1 mm in diameter (Fig. 3C and D). A small impression fragment of a probable reniform pinnule with flabellate venation associated to a cluster of spheroids is also present (Fig. 3C). These synangia are similar to those described for the reproductive structure of *W. negevensis* (Silantieva and Krassilov, 2006). Additionally, two parallel secondary rachis fragments showing putative truncated bases of last order rachis (Fig. 3E) are similar to the ones described by Sender et al. (2015) for the rachises bearing spherical globular soral clusters in *W. reticulata*. The occurrence of these structures suggests that both species could have been present in the plant assemblage studied here. Fragments of sporogenous tissue containing spores occur nearby the fragments of secondary rachises (Fig. 3F).

The putative organization of the reproductive structures in non-laminar fertile pinnules also seems to be in accordance with the diagnosis for *Weichselia*. It contrasts with other Mesozoic matoniaceous

Fig. 2. Adpression remains of *Weichselia* pinnae. A-C) Typical secondary pinnae bearing lingulate pinnules with rounded apices in sub-opposite disposition (UFRJ-DG 2849a/b Pb, 101.75 m, UFRJ-DG 2852 Pb, 101.35 m); D) arrow points to cracks on the primary rachis not filled with sediment (UFRJ-DG 2850a Pb, 101.2 m); E) arrow points to oblique, triangular pinnule (UFRJ-DG 2849 b Pb, 101.75 m); F) counterpart of (C) showing detail of venation pattern (UFRJ-DG 2850 b Pb, 101.2 m). Scale bars = 5 mm.

ferns, i.e., *Matonidium* and *Phlebopteris*, characterized by superficial sori which are radiate with a single ring of large sporangia (Nagalingum and Cantrill, 2006). Nevertheless, the preservation of the macroremains restricted to isolated sterile and fertile pinnae precludes the identification to the species level.

Besides the identification of *Weichselia* with Matoniaceae, affinity of the genus with the Marattiaceae family was proposed by Edwards (1933) and Koeniguer (1966, 1975) based on the sporangial structures and anatomical features, whereas Alvin (1971) assigned the genus to a monotypic family Weichseliaceae. Despite its similarities with the Marattiaceae on account of the synangia, Silantieva and Krassilov (2006) considered that the sporocarp morphology pointed to the Marsileaceae family. Based on the stem anatomy and external morphology, Blanco-Moreno et al. (2020) ratified the Marattiaceae (and Psaroniaceae) affinity, contradicting current acceptation of Matoniaceae affinity based on frond architecture (Sender et al., 2015).

4.1.2. Bryophyte remains

Twelve specimens of isolated and one of clustered bryophyte shoots were found in the same fossiliferous levels as the *Weichselia* pinnae. In tuft the growth pattern is orthotropic, presenting a bundle of equally long, radiating gametophyte axes connected to a dense filamentous mass (Fig. 4A). Shoots are up to 5.62 mm long and 1.32 mm wide. Isolated shoots are sparsely branching in wide angles and in dichotomous arrangement (Fig. 4B–D). The shoots are densely covered with sessile and erect leaves (Fig. 4E and F). Anatomical and morphological features including the potential leaf costa could not be observed.

The compressed leaves are linear, narrow-lanceolate to slightly curved (0.18–1.9 mm long) with acute apex, decurrent base and entire margins. Multiple round leaf scars (23–54.5 μm in diameter) on the surface of a clavate stem where leaves are missing indicate that the phyllotaxy might have been spiral and that the leaves could have been attached to the stem only by the costa (if present) or were terete (Fig. 4D).

Apical leaves are longer and more erect than the proximal ones, sometimes originating an apical rosette (1.7 mm long x 0.7 mm wide), whereas basal leaves are more spaced and smaller than the distal ones (Fig. 4E and F).

In addition to the vegetative shoots, a compression of a capsule-bearing sporophyte, with no visible organic connection with the

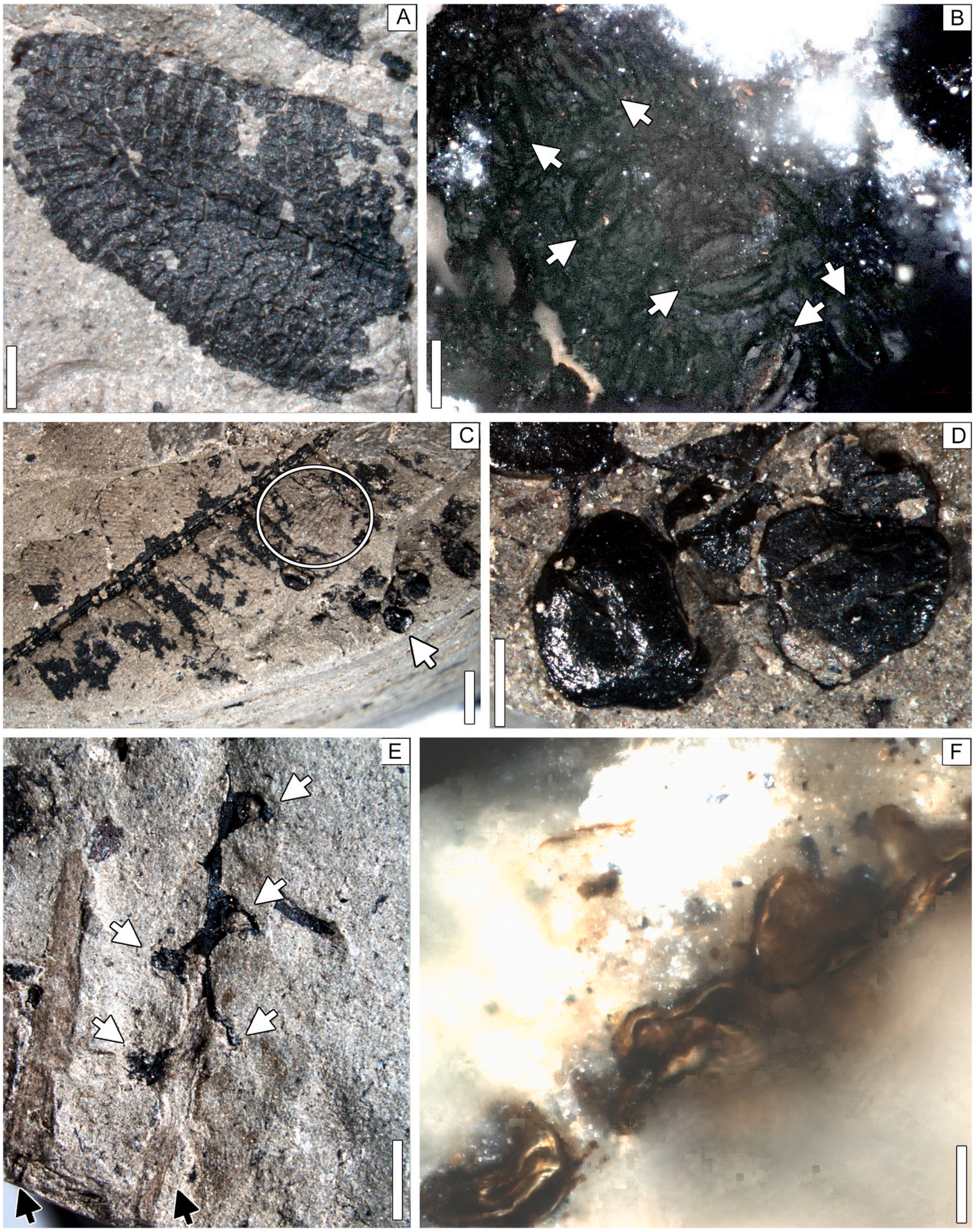

Fig. 3. Epidermal details of *Weichselia* and associated reproductive structures. A) Close-up of the upper surface of a pinnule (102.75 m); B) lower epidermis included in polished block under reflected white light, arrows point to polar end of each pair of guard cells (UFRJ-DG 2852 Pb, 101.35 m); C) Cluster of spheroidal synangia (arrow) and impression of a flabellate pinnule (circle); D) detail of (C); E) two parallel secondary rachises (black arrows) bearing truncated bases of last order rachis (white arrows); F) polished block under reflected white light showing several sectioned spores (UFRJ-DG 2852 Pb, 101.35 m). Scale bars = A, D) 500 μm; B, F) 20 μm; C, E) 2 mm.

gametophytes, was also preserved (Fig. 4F). The capsule is erect, ovoid (0.7 mm long x 0.4 mm wide), resting over an orthotropous seta.

The general organization of the gametophyte resembles that of the morphogenus *Muscites* Brongniart (Class Bryopsida sensu lato according to Moisan et al., 2012; Passalia, 2007; Puebla et al., 2012), which corresponds to a generalized description of extant mosses including brief characterizations of both gametophyte and sporophyte morphology.

This morphogenus has been reported since the late Carboniferous and was spread worldwide in the Cretaceous with several species (e.g., *Muscites antarcticus* Cantrill; *M. cretaceous* Oostendorp; *M. gracilis* Mays et Cantrill; *M. ingodensis* Srebrodolskaya; *M. kujiensis* Katagiri. , Mukai et Yamaguchi; *M. ostracodiferus* Krassilov; *M. tenellus* Wu) and also registered as *Muscites* sp. when specific diagnostic characteristics were absent (Ignatov and Shcherbakov, 2011; Kvaček and Vodrážka, 2016; Passalia, 2007; Puebla et al., 2012, Tomescu et al., 2018).

The main morphological features of the gametophyte assemblage, such as dichotomous branching arrangement, spiral to helicoidal leaf disposition and linear to lanceolate leaves, and absence of leaf costa are comparable with fossil bryophytes identified as *Muscites* sp. from the Triassic Madygen Lagerstätte by Moisan et al. (2012). Based on the gametophyte characteristics, the specimens from the Codó Formation are provisionally and informally assigned to *Muscites*. However, the

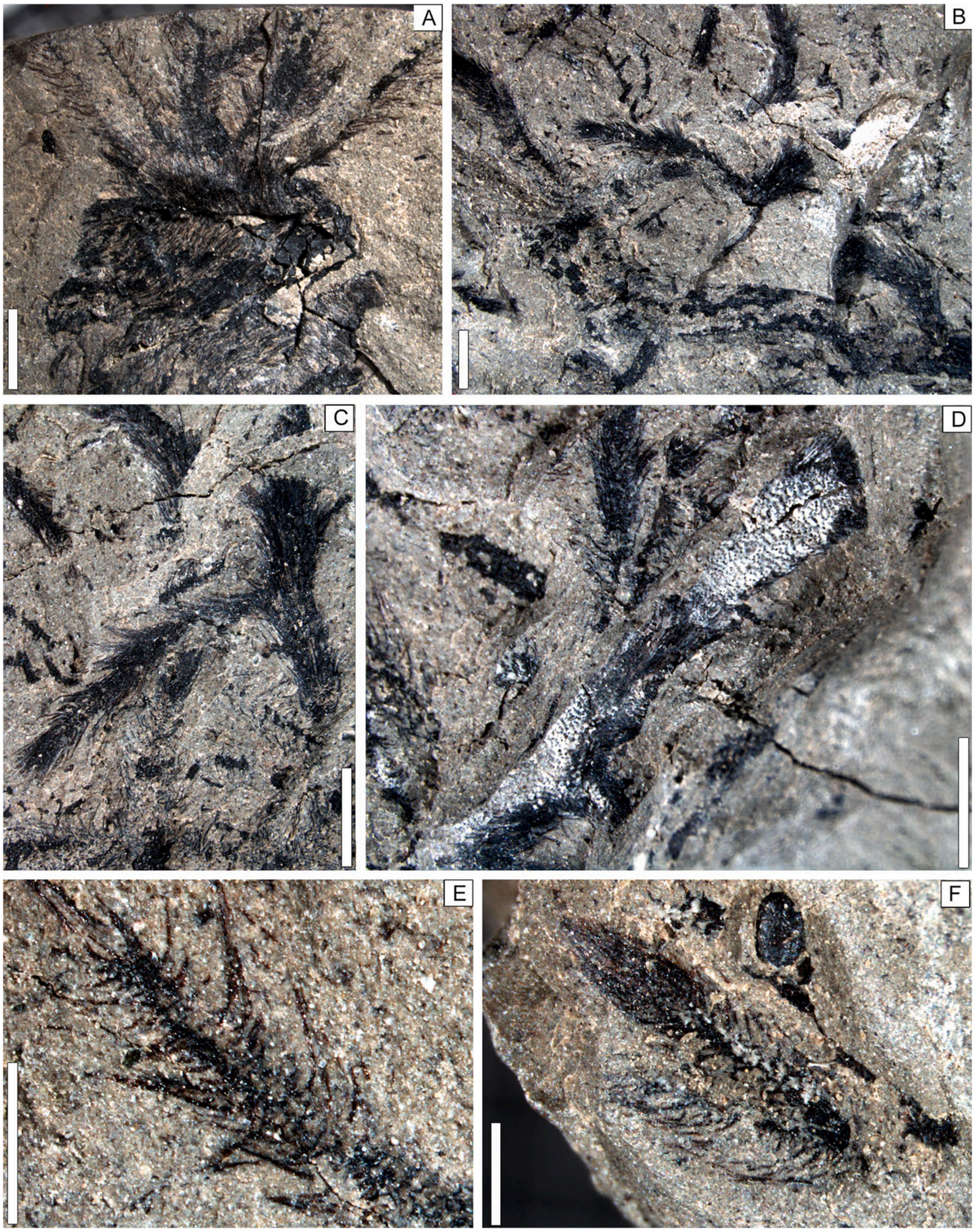

Fig. 4. Bryophyte remains (?*Muscites*). A) Tuft with several shoots connected to a dense filamentous mass (UFRJ-DG 2852 Pb, 101.35 m); B) isolated, ramified shoots (UFRJ-DG 2849 b Pb, 101.75 m); C) detail of shoot ramification; D) round leaf scars on the shoot surface; E) isolated shoot with linear leaves (UFRJ-DG 2852 Pb, 101.35 m); F) isolated shoot with apical rosette and associated capsule and seta (UFRJ-DG 2849 b Pb, 101.75 m). Scale bars = A-D) 2 mm; E, F) 1 mm.

presence of an erect capsula, resting over an orthotropous seta (organic connection to the gametophyte was not visible) points to diagnostic features that would enable its attribution to a better-defined genus, which will be presented elsewhere.

4.2. Palynofacies

The particulate organic matter (POM) from the four samples was composed by phytoclasts (PHY), corresponding to 84.56–89.35%, and palynomorphs (PAL) representing 10.64–14.88%of the association. The amorphous group (AOM) was recorded only in a very low percentage (0.56%) (Fig. 5, Table 1).

PHY is the main component and non-opaque phytoclasts (NOP) represented 77.68–84.19% of the association, with higher occurrence of biostructured phytoclasts in the samples 101.20 m (42.70%) and 101.35 m (40.98%), whereas the dominance of non-bioestructured phytoclasts was identified in sample 101.75 m (49.23%) and 102.75 m (50.76%). Opaque phytoclasts (OP) occurred in insignificant amounts along the four samples (0.62–4.60%), as well as cuticles and membranes (1.69–4.86%).

PAL is scarcely represented and sporomorphs are represented mainly by trilete fern spores with the highest percentage values (7.60–11.08%) over pollen grains and tetrads of *Classopollis* (1.83–3.37%). Freshwater microplankton (*Pediastrum* and *Scenedesmus*) occurred with average relative abundances not exceeding 1%. The occasional presence of *Botryococcus* was identified in the sample 101.35 m. Lastly, it is worth

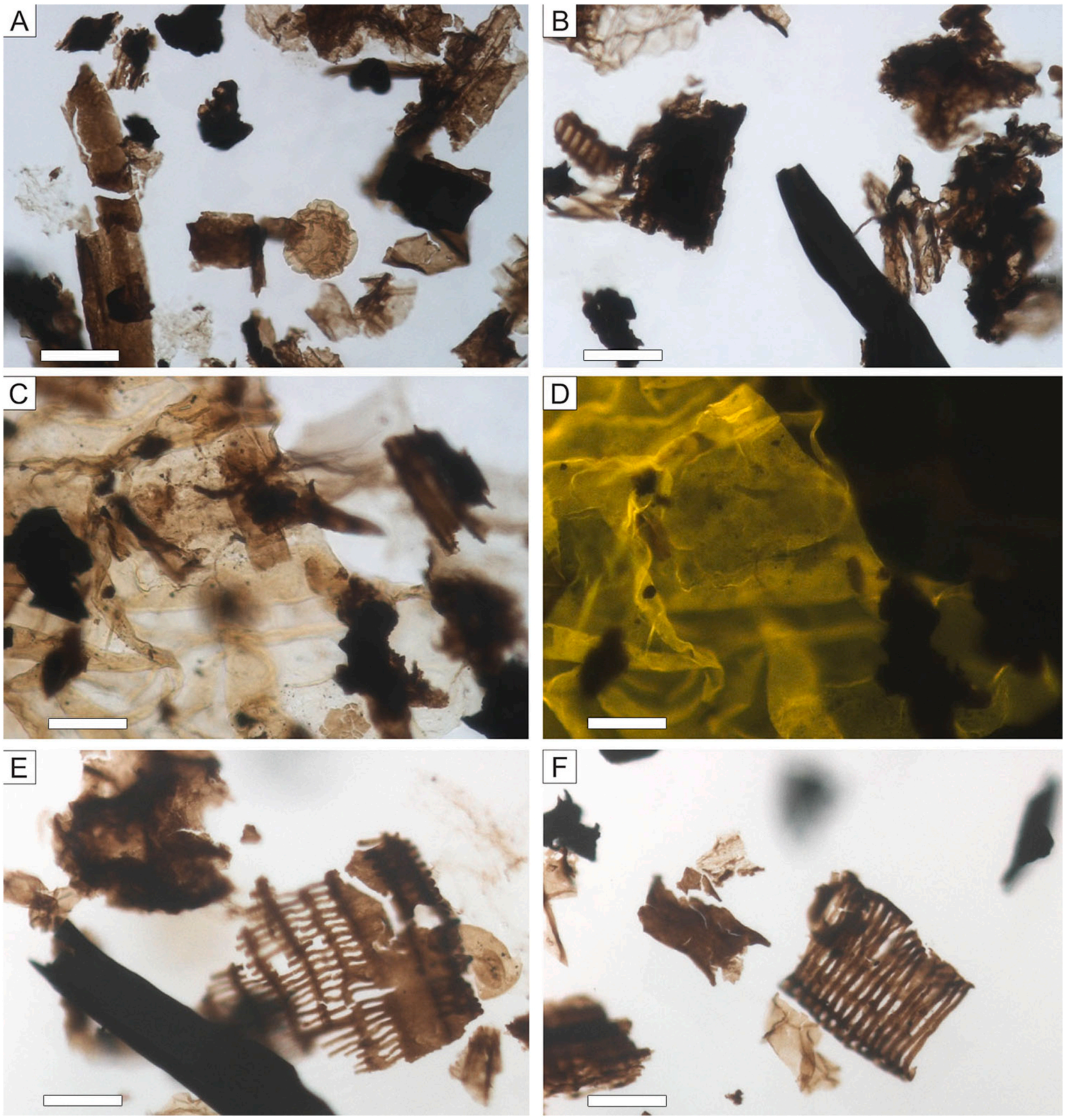

Fig. 5. Selected particulate organic matter. (A–C, E, F) = transmitted white light; (D) = fluorescence mode. A) Non-opaque Phytoclasts. B) Opaque and Non-opaque Phytoclasts. C) Membrane. D) Unidentified membrane. E) Opaque and Non-opaque Phytoclasts-Biostructured: Pitted. F) Non-opaque Phytoclasts-Biostructured: Pitted. Scale bars = 50 μm.

Table 1
Palynofacies results.

Samples Depth (m)	AOM	PHYTOCLAST					PALYNOMORPH				
		Opaque	Non-Opaque		Cut. + Memb.	TOTAL	Sporomorph		Freshwater	Marine	TOTAL
			Biostruc.	N. Biostruc.			Spore	P. Grain			
101.20	0.56	2.25	42.70	37.92	1.69	84.56	10.67	3.37	0.56	0.28	14.88
101.35	0.00	4.60	40.98	36.70	6.44	88.72	8.56	1.83	0.61	0.31	11.31
101.75	0.00	0.62	33.54	49.23	2.46	85.85	11.08	2.46	0.62	0.00	14.16
102.75	0.00	0.30	33.43	50.76	4.86	89.35	7.60	2.13	0.30	0.61	10.64

AOM = Amorphous Organic Matter.
Biostruc. = Biostructured.
N. Biostruc. = Non-Biostructured.
Cut. + **Memb.** = Cuticles + Membranes.

noting the occurrence of dinoflagellate cysts in the samples 101.20 m (0.28%), 101.35 m (0.31%) and 102.75 m (0.61%).

4.3. Palynology

The palynological content of the four selected samples covering the 1.5 m studied interval was qualitatively and quantitatively analyzed (Figs. 6 and 7, Tables 2 and 3).

Aquatic components (4%) correspond to green micro algae represented by members of the families Hydrodictyaceae (*Pediastrum* spp.) Botryococcaceae (*Botryoccocus* spp.), Scenedesmiales (*Scenedesmus* spp.) and Zygnemataceae (*Ovoidites* spp.). The autochthonous aquatic

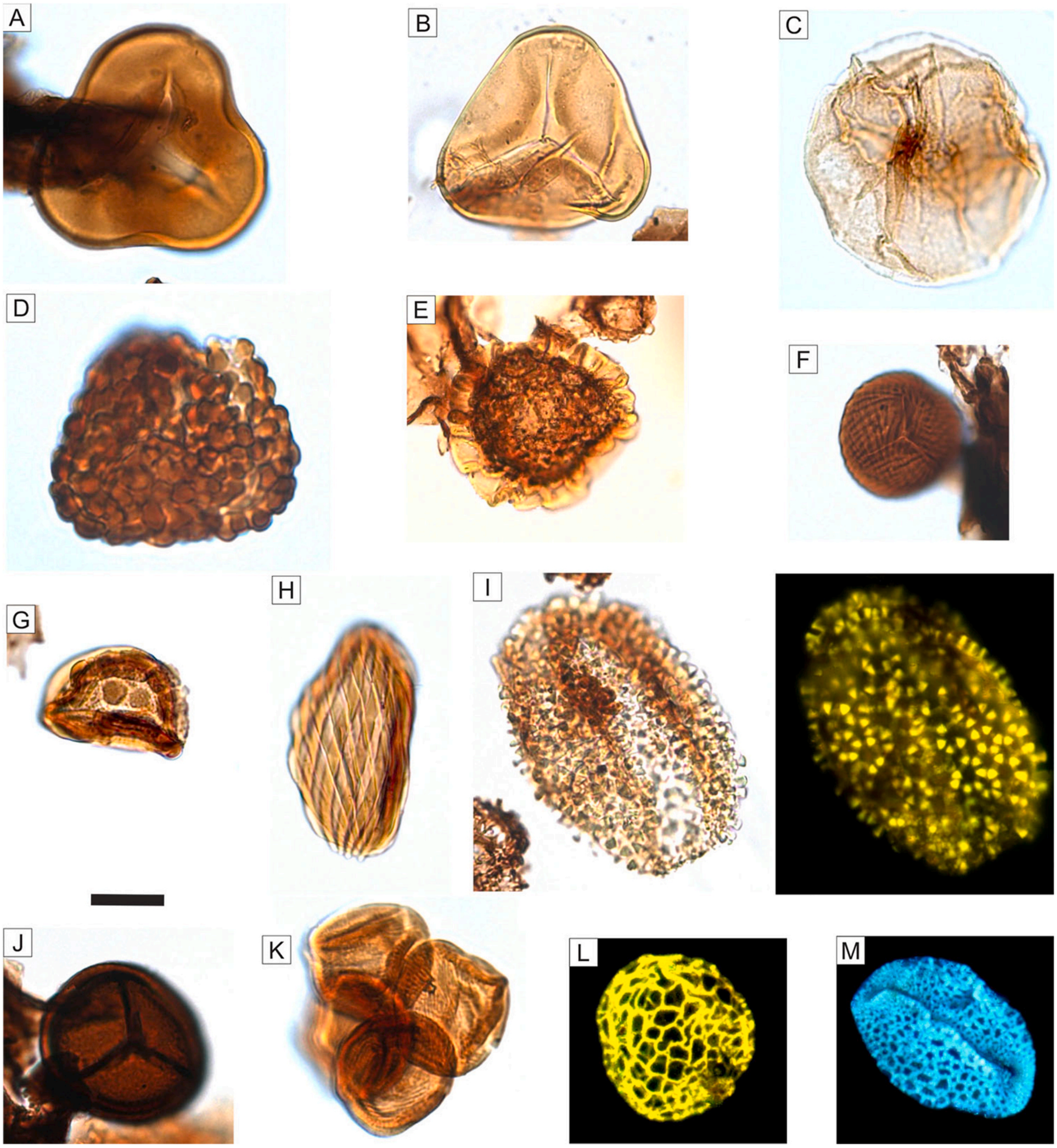

Fig. 6. Selected terrestrial palynomorphs from the Codó Formation. Sample depth followed by the England Finder coordinate. (A–K) = transmitted white light; (I, L, M) = fluorescence mode. A) *Cyathidites australis*, sample 102.75 m, K13/4; B) *Deltoidospora hallii*, sample 101.35 m, V13/); C) *Araucariacites australis*, sample 101.2 m, C25; D) *Leptolepidites verrucatus*, sample 101.75 m, W24/4; E) *Callialasporites dampieri*, sample 102.75 m, S21/3; F) *Cicatricosisporites* sp., sample 102.75 m, M14; G) *Sergipea variverrucata*, sample 101.75 m, C29; H) *Gnetaceaepollenites* sp., sample 101.35 m, S27/3; I) *Stellatopollis barghoornii*, sample 102.75 m, W32; J) *Birestisporites* sp., sample 101.75 m, O15/3; K) *Classopollis classoides*, sample 102.75 m, D23; L) *Afropollis jardinus*, sample 101.75 m, U29/1; M) *Retimonocopites* sp., sample 102.75 m, V13/2. Scale bar = 20 μm.

association does not show peaks and remains homogeneous throughout the studied interval. Dinoflagellate cysts were recorded at minimum values (1%) in the levels 101.20 m, 101.35 m and 102.75 m.

The terrestrial palynoflora (95%) includes various types of spores and gymnosperm pollen, and scarce angiosperm pollen. The assemblage is dominated by trilete spores (mainly *Deltoidospora* spp. and *Cicatricosisporites* spp.) which display a high distribution pattern from the base to the top of the succession (up to 55%).

The gymnospermous assemblage is dominated by *Classopollis* spp. and *Araucariacites* spp. pollen grains, representing 33% of the terrestrial forms. Other gymnosperm pollen types (*Inaperturopollenites* spp., *Callialasporites* spp., *Equisetosporites* spp. and *Gnetaceaepollenites* spp.) are of subordinate importance, whereas some pollen types (*Exesipollenites* spp., *Cycadopites* spp.) occur only rarely and account together for less than 2%.

Pollen grains assignable to angiosperms (*Afropollis* spp., *Stellatopollis* spp. and *Retimonocolpites* spp.) show a very low value along the studied interval (around 5%).

4.4. Degree of coalification

Vitrinite reflectance analysis on the compressed pinnae (Ro = 0.40%) showed a low degree of coalification, implying a low rank material.

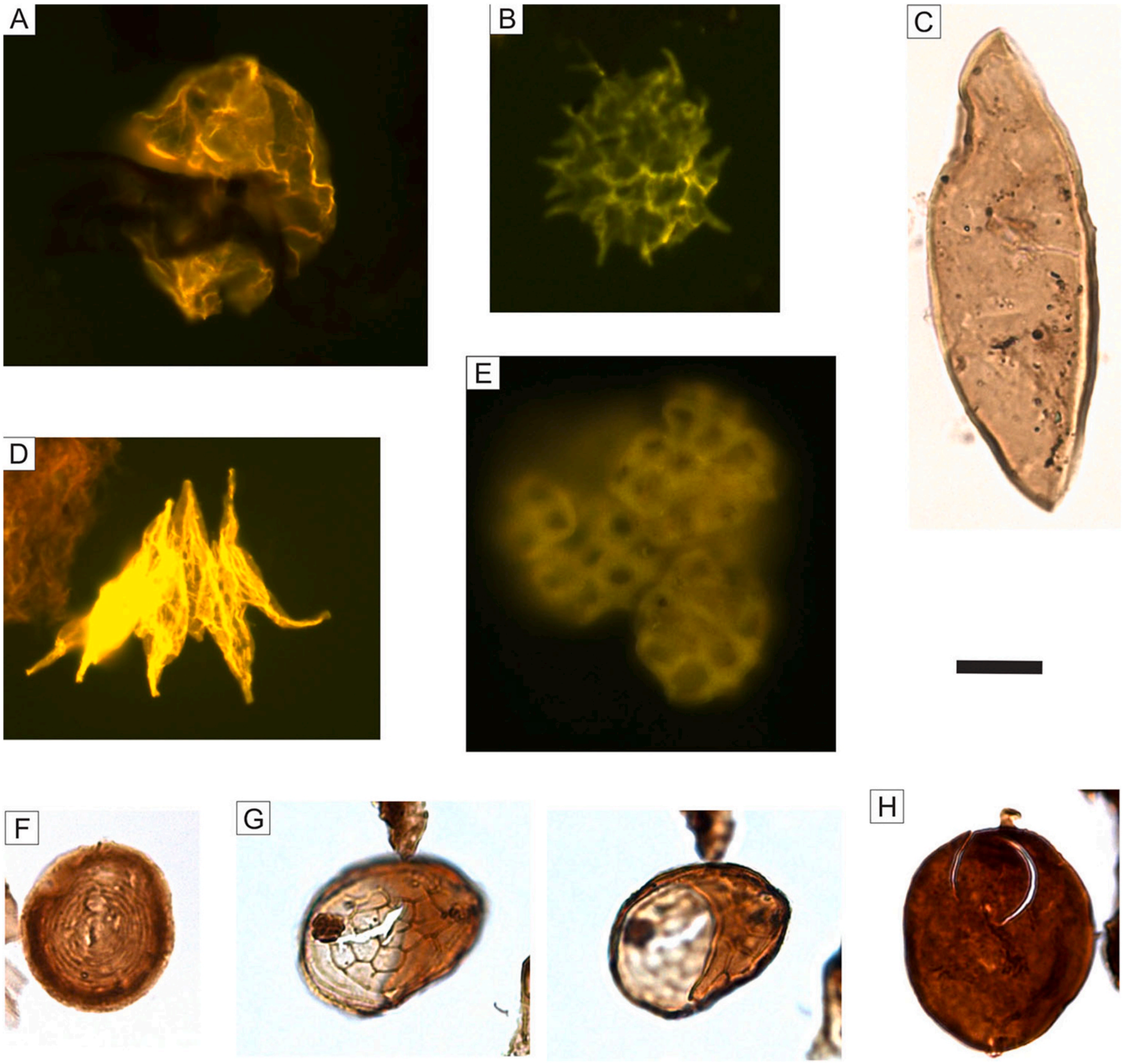

Fig. 7. Selected aquatic palynomorphs and other organic microfossils from the Codó Formation. Sample depth followed by the England Finder coordinate. (A, B, D, E) = fluorescence mode; (C, F–H) = transmitted white light. A) *Subtilisphaera* sp., sample 102.75 m, Z29/2; B) *Pediastrum* sp., sample 101.75 m, J23/3; C) *Ovoidites* sp., sample 101.75 m, B30; D) *Scenedesmus* sp., sample 102.75 m, Z29/2; E) *Botryococcus* sp., sample 101.2 m, S31; F) *Chomotriletes almegrensis*, sample 101.75 m, S13/2; G) *Mystheria oleopotrix*, sample 102.75 m, V22/4; H) Fungal spore, sample 101.2 m, G33/3. Scale bar = 20 μm.

Table 2
Palynology results.

DEPTH	AQUATIC PLANCTONIC						TERRESTRIAL					
	Botryoc	Zygnem	Dinocyst	Scened	Pediastr	Ovoidites	Ferns	Other pterid.	Cheirolep	Arauc	Other gymn.	Angiosp
101.20	1%	1%	1%			1%	44%	4%	13%	17%	10%	8%
101.35		1%	1%				53%	2%	15%	20%	5%	3%
101.75		1%			1%		58%	1%	14%	13%	5%	7%
102.75			1%	1%		1%	43%	2%	12%	20%	11%	9%

4.5. *Clay mineralogy*

Smectite was identified by d_{001} reflections at 15 Å varying from 31.9 to 45.6%, which expanded to 17 Å after ethylene-glycol solvation and collapsed to 10 Å after heating at 550 °C (Fig. 8, Table 4). Montmorillonite was determined as the smectite species by d_{060} reflections at 1.50 Å. Illite was identified by reflection at 10 Å ranging from 12.7 to 17.5%, which did not undergo alteration after treatment with ethylene-glycol and heating at 550 °C. Kaolinite was identified by reflections at 7 Å varying from 41.6 to 50.6%, which did not change after treatment with ethylene-glycol and collapsed after heating at 550 °C.

The relative abundances of clay minerals were plotted in a ternary graph based on Barshad (1966) (Fig. 9), suggesting that annual paleoprecipitation values were between 367 and 429 mm.

Kln – Kaolinite; Ilt – Illite; Mnt – Montmorillonite.

5. Discussion

Our plotted data for the Aptian–Albian interval (Fig. 10, Table 5) do not support the claim by Blanco-Moreno et al. (2018) of apparent vanishing of Weichseliaceae in South America before the Aptian. The depositional environments dominated by *Weichselia* in South America,

Table 3
Botanical affinities identified by palynological analysis (after Carvalho et al., 2017; Dino, 1992; Gary et al., 2009; Kujau et al., 2013; Lima and Boltenhagen, 1981; Regali et al., 1974; Tryon and Lugardon, 1991).

Taxon	Botanical affinity
Afropollis jardinus	Gunneraceae
Araucariacites australis	Araucariaceae
Bennettitaepollenites regalii	Bennettitales
Biretisporites sp.	Matoniaceae
Botryococcus sp.	Botryococcaceae
Callialasporites dampieri	Araucariaceae
Callialasporites trilobatus	Araucariaceae
Chomotriletes almegrensis	Incertae sedis
Cicatricosisporites sp.	Schizaeaceae
Cingutriletes sp.	Bryophyta
Classopollis alexi	Cheirolepidiaceae
Classopollis classoides	Cheirolepidiaceae
Crybelosporites pannuceus	Marsilliaceae
Cyathidites australis	Cyatheaceae
Cycadopites sp.	Cycadaceae
Deltoidospora hallii	Cyatheaceae
Deltoidospora juncta	Cyatheaceae
Deltoidospora sp.	Cyatheaceae
Equisetosporites sp.	Ephedraceae/Gnetaceae
Eucommiidites sp.	Ephedraceae/Gnetaceae
Exesipollenites tumulus	Bennettitales
Inaperturopollenites sp.	Araucariaceae
Klukisporites foveolatus	Schizaeaceae
Klukisporites variegatus	Schizaeaceae
Leptolepidites psarosus	Selaginellaceae
Leptolepidites verrucatus	Selaginellaceae
Matonisporites sp.	Matoniceae
Mystheria oleopotrix	*Incertae sedis*
Ovoidites sp.	Zygnemataceae
Pediastrium sp.	Hydrodictyaceae
Retimonocolpites sp.	Gunneraceae
Scenedesmus sp.	Scenedesmaceae
Sergipea variverrucata	Ephedraceae/Gnetaceae
Stellatopollis barghoornii	Liliaceae
Stellatopollis sp.	Liliaceae
Stereisporites sp.	Bryophyta
Subtilisphaera sp.	Peridiniaceae
Trisectoris reticulatus	Angiospermae
Verrucosisporites sp.	Osmundaceae

previously considered as restricted to coastal marine, are now also linked to continental deposition.

Aiming to better characterize the paleobiogeography of *Weichselia* in South American basins (based on the synthesis by Blanco-Moreno et al., 2018), in this study we included *Paradoxopteris* (Albian Itapecuru Formation) from the neighboring São Luís Basin in our database. Additionally, the occurrence of *Weichselia* in the upper Aptian and lower Albian strata of Colombia (El Ocal, Caballos, and Yaví–Alpujarra formations) reported by Moreno (1994) has also been incorporated to our paleobiogeographic map.

The physical properties shown by the pinna compressions such as black color, lustrous sheen and checkered fractures in rachises and pinnulae (Fig. 2D) led to preliminary identification of potential macrocharcoal fragments as per Scott (2000, 2010), a preservation type frequently reported for *Weichselia* remains (e.g., Abu Hamad et al., 2016; Alvin, 1974; Blanco-Moreno et al., 2019; Harris, 1981). However, organic petrography analysis on the material showed low reflectance (Ro = 0.40%), withdrawing the affinity with charcoal and consequently the occurrence of fire events. Given that the expressive superficial cracks would lead to the fractionation of the pinnae if transported prior to deposition, it can be assumed that the shrinkage was not produced by desiccation prior to the burial. The fact that the numerous radial and tangential cracks on the rachises and pinnule surface were not filled with sediment seems to ratify this inference (Fig. 2D).

The preservation of secondary pinnae of *Weichselia* with pinnules and reproductive structures still attached, showing little or no sign of mechanical fragmentation, is an indication that they have not been transported far before being deposited, suggesting a hypauthochthonous origin from an original habitat near to the site of deposition.

Weichselia is a pioneer taxon from terrestrial habitats constantly influenced by flooding (Blanco-Moreno, 2021; Coiffard et al., 2007) that could be defined as a tropophyte. According to Schimper (1898), the term 'tropophyte' rather than "xerophyte" refers to plants adapted to an alternation of dryness and moisture like *Weichselia.*

The occurrence of shales with thin rhizoliths overlying the fossiliferous interval (Fig. 1) could correspond to a floodplain paleoenvironment close to channels as characterized by Sender et al. (2005) for the middle Albian Escucha Formation (Spain) with impressions/compressions of *Weichselia* isolated pinnae associated to immature paleosols.

The delicate impressions/compressions of ramified gametophyte shoots of bryophytes found together with the *Weichselia* pinnae are good paleoecological markers, indicating humid environments near fresh water and coastal wetland areas. However, these plants cannot survive in strong salt-water influenced environments (Puebla et al., 2012). Mosses are poikilohydric and can grow within the diffuse boundary layer of substrates (Huttunen et al., 2018). They depend directly on immediate environmental conditions and respond quickly to environmental change, which makes them good bioindicators (Gabriel et al., 2019). Nevertheless, desiccation-tolerant mechanisms allow these plants to survive to occasional or intermittent periods of stressed conditions (Wood, 2007).

Bryophytes inhabit environments at the terrestrial-aquatic interface, meaning that they are easily buried even under just thin layers of clastic deposits (Krassilov and Schuster, 1984). As highlighted by Tomescu et al. (2018), bryophytes require a relatively narrow window of mild hydrodynamic conditions to ultimately settle on the bottom and become buried, because an extended time window for exposure to oxidation would promote biological decay and mechanical fragmentation and abrasion.

The macrofloral association reported here, composed by vegetative and fertile fragments of the fern *Weichselia* and bryophytes (*Muscites* sp.), is a good environmental indicator. Considering the continental source of the dark shales where the macroremains were included, it is possible to infer a source environment marginal to freshwater which experienced flooding during periods of discharge. Moisan et al. (2012), in their analysis of fossil bryophytes from the Triassic Madygen Lagerstätte (SW Kyrgyzstan), concluded that *Muscites* were also represented in terrestrial, though probably still very moist habitat.

The dominance of non-opaque components of the Phytoclast Group revealed by palynofacies analysis is conditioned by selective proximal to distal preservation trends and selective sedimentation related to hydrodynamic equivalence of the particulate organic components. The dominance of non-opaque, non-bio-structured over biostructured phytoclasts indicates a proximal trend, i.e., close to the parent flora. However, the gradual decrease from the base to the top of non-biostructured (Table 1), accompanied by a gradual increase in the percentage of biostructured phytoclasts seem to indicate a progressive reversal trend.

Non-opaque phytoclasts are dominant in sediments deposited in estuarine regions or close to the coast lines, with a strong terrestrial influence, often associated with the mouth of rivers, with large inputs from floodplain and upstream sources (Devol and Hedges, 2001; Vannote et al., 1980).

The absence of AOM and low occurrence of cuticles and membranes ratify the inference of a highly oxic, shallow depositional environment, close to a probable intense fluvio-deltaic activity.

In the Palynomorph Group, autochthonous non-marine planktonic algae (*Pediastrum*, *Scenedesmus*, *Ovoidites*, *Zygnema*, and rare *Botryococcus*) suggest favorable conditions for their growth in humid to wet substrates during the vengeance of hydroperiods. Their presence refers to lake, river and lagoon facies, commonly adapted to freshwater, more rarely to brackish conditions (Batten and Grenfell, 1996; Batten et al., 1994; Grenfell, 1995; Phinyo et al., 2017; Worobiec, 2014; Zamaloa and

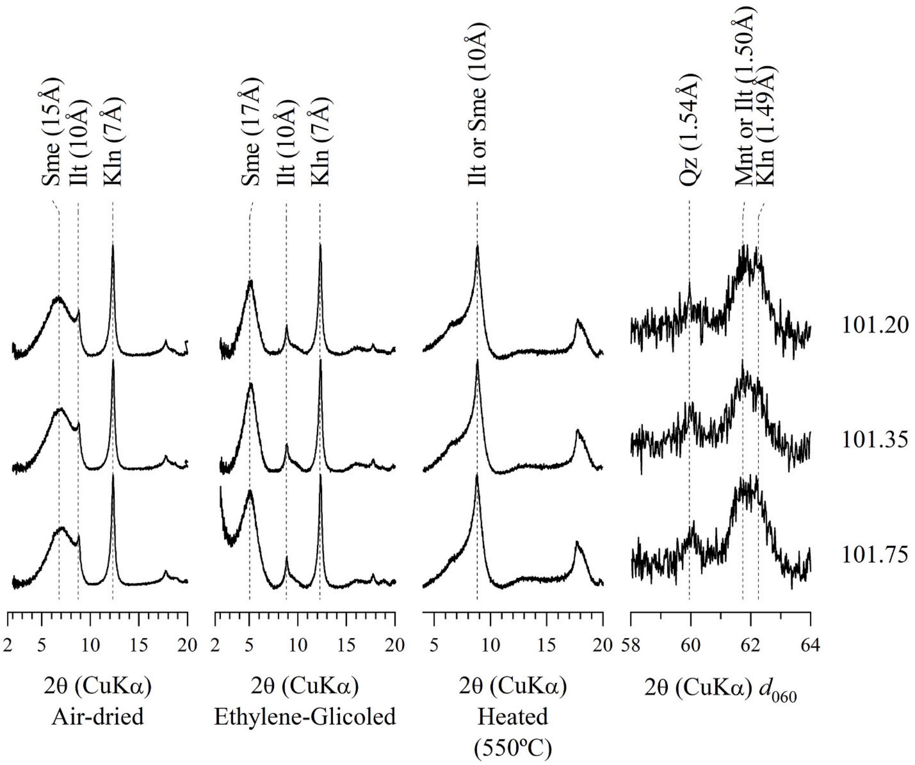

Fig. 8. Background-subtracted and normalized by maximum intensity XRD patterns of the clay-sized fraction of the studied lutites.

Table 4
Quantitative mineral analysis (wt.%) (Biscaye, 1965) of the clay-sized fractions of the studied lutites.

Clay mineralogy (wt%)	101.20 m	101.35 m	101.75 m
Montmorillonite	31.9	35.5	45.6
Illite	17.5	15.4	12.7
Kaolinite	50.6	49.1	41.6
Total	100.0	100.0	100.0

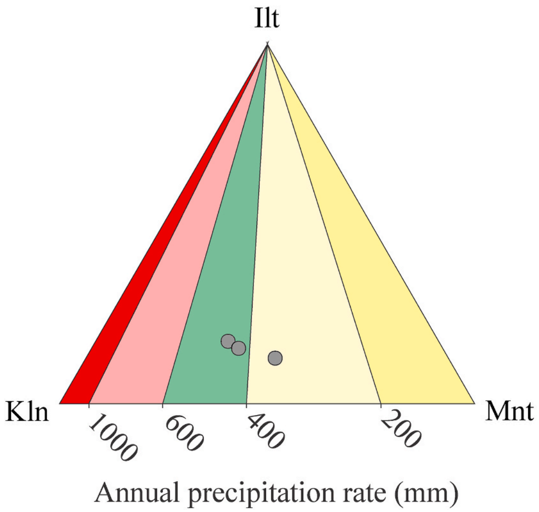

Fig. 9. Ternary graph with the correlation between relative abundance of kaolinite and montmorillonite and annual precipitation rates (Felsic rocks graph; Barshad, 1966). (200 mm = 23% Kln) (400 mm = 55% Kln) (600 mm = 75% Kln) (1000 mm = 93% Kln).

Tell, 2005). A possible floating transport from regions of fluvial inputs to coastal regions, which sometimes occur in extant assemblages and is inferred for fossil ones (Zavattieri et al., 2017) cannot be established in the present study based on the good preservation of cenobia, because their delicate sporopollenin layer would be damaged if extensively transported.

The very low influx of microplankton from the Palynomorph Group along the analyzed interval, with average relative abundances lower than 1% (Table 1), was certainly related to physicochemical controlling patterns of the ecosystem. The qualitative and quantitative data support a source environment for water systems linked to stagnant marginal environments of river systems, estuarine channels or floodplain lakes in riverine systems. In addition, the very low occurrence (below 1%) of dinoflagellate cysts (*Subtilisphaera*), which are sensitive to environmental factors such as light, water temperature, salinity, nutrient levels, and circulation currents (Batten, 1996), suggests a very restricted marine influence of unstable environments probably on coastal margins or in channels in estuarine systems. The ocurrence of *Subtilisphaera* in three out of four levels, even though very scarce (Table 2) places the studied interval in the *Subtilisphaera* Ecozone, registered for the equatorial and interior basins of northeastern Brazil and points to the to the very initial phase of the important transgression that took place during the Aptian as indicated by Arai (2009, 2014).

Within the terrestrial sporomorphs, the large dominance of spores with pteridophytic affinities (9.5% on average) over pollen grains (2.8% on average), and the botanical affinities identified by palynological analysis (Tables 2 and 3) supported additional paleoenvironmental inferences. The high representation of spores of Schizeaceae (Collinson, 2002; Regali and Gonzaga, 1985), Cyatheaceae (Tryon and Tryon, 1982), Osmundaceae (Collinson, 2002), and Marsileaceae (Portela et al., 2014) suggests the existence of humid vegetation (Portela et al., 2014; Van Konijnenburg-Van Cittert, 2002). The hypothesis of an environment under humid conditions is directly related to the importance of humidity on the reproductive cycle of modern pteridophytes (Doyle et al., 1982; Lima, 1982). Although ferns have been considered by Vakhrameev

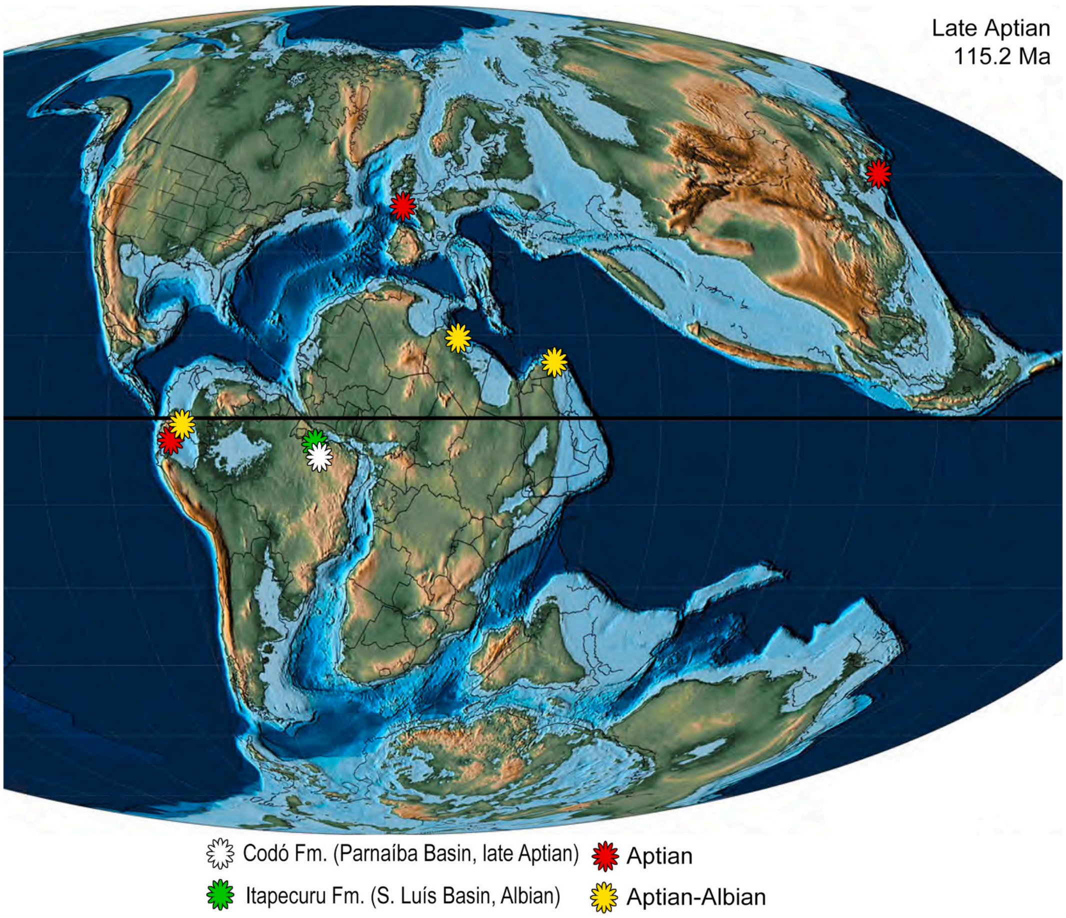

Fig. 10. Paleobiogeography of *Weichselia* during the Aptian–Albian (modified from Scotese, 2014). See Table 5 for details on the plotted data.

Table 5
Aptian–Albian data of *Weichselia* occurrences (Fig. 10).

Species	Origin	Age	Depositional environment	Authors
Weichselia reticulata and *W. negevensis*	Makhtesh Hathira, Makhtesh Qatan, Makhtesh Ramon, Israel,	Aptian–Albian	marginal marine, delta and intertidal zone	Blanco-Moreno et al., (2018); Silantieva and Krassilov (2006); Krassilov and Schrank (2011)
W. reticulata	Bir el Karma and Foum el Hassen, Tunisia	Aptian–Albian	Mangroove swamp	Barale and Ouaja (2001)
W. reticulata	Caballos (ex-Alpujarra) and El Ocal formations, Colombia	Aptian–Albian	Unknown	Moreno (1994)
W. reticulata	Villavicencio, Colombia	Aptian	Delta	Pons (1988)
W. reticulata	Abu Ballas Formation, Egypt	Aptian	Freshwater or slightly brackish	Schrank (1999)
W. reticulata	Isle of Wight, Lower Greensand Formation, England	Aptian	Estuary	Blanco-Moreno et al. (2018)
W. reticulata	Nehden (Sauerland), Germany	Aptian	Lacustrine	Kampmann (1983)
W. reticulata	Todai Formation, Japan	Aptian	Unknown	Kimura and Aiba (1985)
Paradoxopteris sp.	Itapecuru Formation, São Luís Basin, NE Brazil	Albian		Mussa et al. (2000)
Weichselia spp.	Codó Formation, Parnaíba Basin, NE Brazil	Late Aptian		**Present study**

(1991) as moisture-loving plants in Mesozoic environments, Van Konijnenburg-Van Cittert (2002) showed that this picture was too general, given that some ferns like the Matoniaceae grew under stress-related circumstances, especially during the Jurassic and early Cretaceous greenhouse intervals. The presence of spores of Matoniaceae has also been associated to an eventually unstable water table (Sender et al., 2005).

In spite the very low representation of gymnosperm pollen grains (1.8–3.4%), as demonstrated by the palynofacies analysis (Table 1), the identification via palynology of Cheirolepidiaceae and Araucariaceae as clearly dominant over other gymnospermous pollen grains (Table 2) points to ecological differentiation (Doyle et al., 1982). While the Araucariaceae would preferably occupy fluvial-deltaic floodplains with ephemeral humidity, the typical habitat of the Cheirolepidiaceae was linked to well-drained soils or saline influence of variable intensity. Deaf (2009) attributed the presence of Araucariaceae at low latitudes in the early Cretaceous to local humid conditions surrounded by dominant arid to semi-arid conditions in a paleoenvironmental context of relatively dry conifer vegetation.

The absence of quantitative peaks along the analyzed interval

(Tables 1 and 2) indicates the prevalence of similar environmental conditions throughout the restricted interval of 1.55 m. Thus, the presence of fern-dominant spore assemblages over Araucariaceae/Cheirolepidiaceae pollen grains in the palynological spectrum, associated to macroremains and palynofacies analysis reflect proximal environments such as opened ponds recruiting parautochthonous and/or allochthonous elements. Based on this evidence, the terrestrial vegetation surrounding the water system was inferred as divided into two niches, a marginal/proximal "wetland" zone and a very distal, probably lowland "dry" zone. The very low contribution from of pollen grains attributable to angiosperms (3–9%), mostly linked to terrestrial habits, suggests that this plant group would be component of ecotones away from the site of deposition.

The presence of humid conditions in restricted environments during the deposition of the Codó Formation agrees with the results obtained from clay mineralogy in the studied interval, located above the evaporite bed, when the abundances of detrital kaolinite over montmorillonite suggest the dominance of a climatic humidification process and a less expressive semiarid climate in a regional context (Fig. 9). The inferences point to conditions distinct of those suggested by Rossetti et al. (2001b) and Gonçalves et al. (2006) for lutites located below the evaporite bed in the Codó Formation which were composed of higher relative proportions of montmorillonite in relation to kaolinite, indicating drier conditions.

The dominance of araucariacean over cheiroleipidiacean pollen grains in the gymnosperm spectrum of the studied interval (Table 2) was also observed by Heimhofer and Hochuli (2010) and Varejão et al. (2021) in the Araripe Basin at the top of the Romualdo Member, and in the Sergipe Basin by Carvalho et al. (2017, 2019). This palynological evidence reflects the beginning of environmental change from arid to humid conditions, indicating an increase in moisture following the Intertropical Convergence Zone displacement coinciding with the Aptian opening of the Atlantic Equatorial Atlantic Ocean.

The general climatic inferences suggested for the studied interval imply the occurrence of distinct environmental conditions prevailing simultaneously in humid and dry-xerophytic areas of a wider Aptian paleoenvironment included in the Tropical-Equatorial Hot Arid Belt of Chumakov et al. (l995). The presence of "humidity windows" was indicated by Santos et al. (2020) for the periequatorial Aptian Crato Konservat-Lagerstätte from the neighboring Araripe Basin, also included in the Tropical-Equatorial Hot Arid Belt, based on analysis of fungus/-plant interactions associated with climatic signatures of growth ring patterns in araucarian woods. Later, Ribeiro et al. (2021) presented an alternative hypothesis concerning the paleoecological and paleoenvironmental depositional conditions of the Crato Konservat-Lagerstätte based in multiproxies (i.e., vascular plants, arthropods, fishes, and tetrapods) indicating a seasonal, semi-arid, shallow lacustrine wetland where aquatic zones were surrounded by periodically flooded mesophytic ecotones and outer xeric habitats. Moreover, 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 would be deposited in wetter conditions.

Additionally, the depositional interval of the Codó Formation (Parnaíba Basin) could be related to the early stages of the Equatorial Humid Belt, associated to the opening of the Equatorial Atlantic Ocean at the Aptian–Albian boundary (Chumakov et al., 1995; Hay and Floegel, 2012). According to Scotese et al. (2021), the thermal peak at ~120 Ma in the early Aptian was followed by a "cold snap" in the late Aptian – early Albian as a consequence of the Carswell impact (115 Ma), although this cool interval is still speculative.

Further integrated investigation in other similar dark shale levels along the 2-CO-1-MA drill core (Fig. 1) will give insights about recurrence or change of the environmental conditions during the ample depositional interval currently inferred as fluvial-influenced for the intermediate portion of the Codó Formation.

The composition of the palynological spectrum of the studied interval is ecologically very distinct from that recorded for the uppermost levels of the Codó Formation, related to a restricted marine coastal setting and characterized by the impressive occurrence of marine elements (dinocysts). The angiosperm group was reflected in these levels by a great diversity of monocolpate and tricolpate forms (Antonioli and Arai, 2002; Antonioli and Dino, 2007; Lima, 1978, 1982). The restrict association of plant macroremains composed by vegetative and fertile fragments of *Weichselia* and bryophytes (*Muscites* sp.) is not recorded for the upper level of the carbonate succession of the Codó Formation described by Lindoso et al. (2018) from Brejo municipality, which includes Gnetales (?*Drewria*), conifers (*Cupressinocladus* and *Brachyphyllum*), and basal angiosperms (Nympheales, Magnoliids, and basal Eudicots).

6. Conclusions

The presence of vegetative and fertile organs of *Weichselia* in the Aptian Codó Formation from the Parnaíba Basin amplified the paleobiogeographic distribution of this fern genus and points to a periequatorial distribution belt for South America and Africa during the Aptian.

The remains of both *Weichselia* and terrestrial bryophytes (*Muscites* sp.) in a restricted dark shale depositional interval pointed to marginal areas of freshwater bodies subjected to frequent flooding, in a general fluvio-deltaic scenario for an intermediary package of the Codó Formation within the context of the basin succession. The organic matter content restricted the depositional conditions to a shallow water body of marginal areas in fluvial systems in river outlets, channel margins in estuarine systems, and/or shallow floodplain lakes connected/opened to fluvial canals, under very limited influence of unstable environments on coastal margins or channels in estuarine systems.

The integration of paleobotanical, palynofacies, palynological and clay mineral analyses revealed a proximal "wetland zone" that promoted the proliferation of fern communities, and very distal outer xeric habitats dominated by araucariacean/cheirolepidiacean gymnosperms. The integrated analyses led to the inference that distinct environmental conditions prevailed simultaneously in humid and dry-xerophytic areas of a wider paleoenvironment included in the Aptian Equatorial Hot Arid belt. An alternative hypothesis would relate the studied interval to the early stages of the Equatorial Humid belt, associated to the opening of the Equatorial Atlantic Ocean at the Aptian–Albian boundary.

Author contributions

M. Guerra-Sommer: Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Writing - original draft, Writing - review & editing, Project administration I. Degani-Schmidt: Formal analysis, Investigation, Visualization, Writing - original draft, Writing - review & editing J.O. Mendonça: Formal analysis, Investigation, Resources, Methodology, Writing - original draft J.G. Mendonça Filho: Formal analysis, Investigation, Methodology, Writing - original draft F. D.S. Lopes: Formal analysis, Investigation, Writing - original draft V.M.J. Salgado-Campos: Formal analysis, Investigation, Methodology, Writing - original draft B. Araújo: Resources, Writing - original draft I.S. Carvalho: Resources, Writing - original draft, Funding acquisition.

Funding

This study was conducted in association with the ongoing Research & Development project "Correlação estratigráfica, evolução paleoambiental e paleogeográfica e perspectivas exploratórias do Andar Alagoas, which is registered as ANP 20.219–2 and sponsored by Shell Brasil under the ANP R&D levy as "Compromisso de Investimentos com pesquisa e Desenvolvimento". M.G.S., I.S.C. (303596/2016-3), J.G.M.F. acknowledge the financial support of CNPq. I.D.S. acknowledges the financial support of COPPETEC/UFRJ n° 20758. I.S.C. also acknowledges COPPETEC/UFRJ (nº 20758) and FAPERJ (E-26/202.910/2017).

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.

Acknowledgements

The authors are grateful to Candela Blanco-Moreno and Camila Monje Dussán for kindly providing hard to find literature, to Ighor Dienes Mendes for the photographs under the stereoscopic microscope and to the editor and two anonymous referees who greatly helped to improve the manuscript.

References

Abu Hamad, A.M., Amireh, B., El Atfy, H., Jasper, A., Uhl, D., 2016. Fire in a *Weichselia*-dominated coastal ecosystem from the Lower Cretaceous (Barremian) of the Kurnub Group in NW Jordan. Cretac. Res. 66, 82–93.

Alvin, K.L., 1971. *Weichselia reticulata* (Stokes et Webb) Fontaine from the Wealden of Belgium. Mémoire de l'Institut Royal des Sciences Naturelles de Belgique 166, 3–33.

Alvin, K.L., 1974. Leaf anatomy of *Weichselia* based on fusainised material. Palaeontology 17, 587–598.

Antonioli, L., 2001. Estudo palinocronoestratigráfico da Formação Codó - Cretáceo Inferior do Nordeste Brasileiro (Unpubl. PhD thesis). Universidade Federal do Rio de Janeiro 265.

Antonioli, L., Arai, M., 2002. O registro da Ecozona *Subtilisphaera* na Formação Codó (Cretáceo Inferior da Bacia do Parnaíba, Nordeste do Brasil): seu significado paleoecológico. In: VI Simpósio sobre o Cretáceo do Brasil/II Simposio sobre el Cretacico de América del Sur. Rio Claro 25–30.

Antonioli, L., Dino, R., 2007. Análise palinoestratigráfica da Formação Codó - Cretáceo Inferior da Bacia do Parnaíba, NE do Brasil. In: Proceedings of XX Congresso Brasileiro de Paleontologia. Búzios, 36–36.

Arai, M., 2009. Paleogeografia do Atlântico Sul no Aptiano: um novo modelo a partir de dados micropaleontológicos recentes. Bol. Geociencias Petrobras 17, 331–351.

Arai, M., 2014. Aptian-Albian (Early Cretaceous) paleogeography of the South Atlantic: A paleontological perspective. Braz. J. Genet. 44, 339–350.

Barale, G., 1979. Découverte de *Weichselia reticulata* (Stokes & Webb) Fontaine emend. Alvin, filicinée leptosporangiée, dans le Crétace Inférieur de la province de Lérida (Espagne): implications stratigraphiques et paléoécologiques. Geobios 12, 313–319.

Barale, G., Ouaja, M., 2001. Découverte de nouvelles flores avec des restes à affinites angiospermiennes dans le Crétacé inférieur du Sud Tunisien. Cretac. Res. 22, 131–143.

Barshad, I., 1966. The effect of a variation in precipitation on the nature of clay mineral formation in soils from acid and basic igneous rocks. In: Heller, L., Weiss, A. (Eds.), Proceedings of the International Clay Conference, Jerusalem, pp. 167–173. Vol. vol. 2.

Batten, D.J., 1996. Colonial chlorococcales. In: Jansonius, J., McGregor, D.C. (Eds.), Palynology: Principles and Applications. American Association of Stratigraphic Palynologists Foundation, vol. 1, pp. 191–203.

Batten, D.J., Grenfell, H.R., 1996. *Botryococcus*. In: Jansonius, J., McGregor, D.C. (Eds.), Palynology: Principles and Applications., 1 American Association of Stratigraphic Palynologists Foundation, pp. 205–214.

Batten, D.J., Koppelhus, E.B., Nielsen, L.H., 1994. Uppermost Triassic to Middle Jurassic palynofacies and palynomiscellenea in the Danish Basin and Fennoscandian border zone. Cah. Micropaleontol. 9 (2), 21–45.

Berry, E.W., 1922. The Mesozoic Flora of Peru. John Hopkins University Studies in Geology 4, pp. 45–70.

Berry, E.W., 1937. On the presence of the fern *Weichselia* in Colombia, South America. J. Wash. Acad. Sci. 27, 458–461.

Biscaye, P.E., 1965. Mineralogy and sedimentation of recent deep-sea clay in the Atlantic Ocean and adjacent seas and oceans. Geol. Soc. Am. Bull. 76 (7), 803–832.

Blanco-Moreno, C., 2021. Preparation protocols for SEM visualization of charred fossil plants: the case of *Weichselia reticulata* pinnule anatomy. Spanish Journal of Palaeontology 36 (2), 1–14. https://doi.org/10.7203/sjp.36.2.21300.

Blanco-Moreno, C., Decombeix, A.L., Prestianni, C., 2020. New insights into the affinities, autoecology, and habit of the Mesozoic fern Weichselia reticulata based on the revision of stems from Bernissart (Mons Basin, Belgium). Papers in Palaeontology, 1–22.

Blanco-Moreno, C., Gomez, B., Buscalioni, Á.D., 2018. Palaeobiogeographic analysis of the mesozoic fern *Weichselia*. Geobios 51, 571–578.

Blanco-Moreno, C., Gomez, B., Marugán-Lobón, J., Daviero-Gomez, V., Buscalioni, Á.D., 2019. A novel approach for the metric analysis of fern fronds: growth and architecture of the Mesozoic fern *Weichselia reticulata* in the light of modern ferns. Plos One 14 (6) e0219192.

Borges, J., 1937. Estudos geológicos nos estados do Maranhão e Piauhy. Relatorio Annual. Serviço Geológico e Mineralógico, Rio de Janeiro.

Brito, P.M., Lindoso, R.M., Carvalho, I.S., Machado, G.P., 2016. Discovery of †Obaichthyidae gars (Holostei, Ginglymodi, Lepisosteiformes) in the aptian Codó Formation of the Parnaíba Basin: remarks on paleobiogeographical and temporal range. Cretac. Res. 59, 10–17.

Cardoso, R.N., 1962. Alguns conchostráceos mesozóicos do Brasil. Boletim Soc. Bras. Geol. 11, 21–32.

Carvalho, M.A., Bengtson, P., Lana, C.C., Sá, N.P., Santiago, G., Giannerini, M.C.S., 2019. Late Aptian (Early Cretaceous) dry–wet cycles and their effects on vegetation in the South Atlantic: palynological evidence. Cretac. Res. 100, 172–183.

Carvalho, M.A., Lana, C.C., Bengtson, P., Sá, N.P., 2017. Late Aptian (Cretaceous) climate changes in northeastern Brazil: a reconstruction based on indicator species analysis (IndVal). Palaeogeography, Palaeoclimatology,. Palaeoecology 485, 543–560.

Carvalho, I.S., Pedrão, E., 1998. Brazilian theropods from the Equatorial Atlantic margin: behavior and environmental setting. Gaia 15, 369–378.

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.

Coiffard, C., Gomez, B., Thévenard, F., 2007. Early Cretaceous angiosperm invasion of western Europe and major environmental changes. Ann. Bot. 100 (3), 545–553.

Collinson, M.E., 2002. The ecology of Cainozoic ferns. Rev. Palaeobot. Palynol. 119 (1–2), 51–68.

Daber, R., 1953. Paläobotanische untersuchungen in der Unterkreide von Quedlinburg. Geologie 2, 401–416.

Daber, R., 1968. A *Weichselia—Stiehleria*—Matoniaceae community within the Quedlinburg estuary of Lower Cretaceous age. Bot. J. Linn. Soc. 61 (384), 75–85.

Deaf, A.S., 2009. Palynology, Palynofacies and Hydrocarbon Potential of the Cretaceous Rocks of Northern Egypt (Unpubl. PhD Thesis). University of Southampton, p. 348.

Devol, A.H., Hedges, J.I., 2001. Organic matter and nutrients in the mainstem Amazon river. In: McClain, M.E., Victoria, R.L., Richey, J.E. (Eds.), The Biogeochemistry of the Amazon Basin. Oxford University Press, New York, pp. 275–306.

Diéguez, C., Meléndez, N., 2000. Early Cretaceous ferns from lacustrine limestones at Las Hoyas, Cuenca province, Spain. Palaeontology 43 (6), 1113–1141.

Dino, R., 1992. Palinologia, bioestratigrafia e paleoecologia da Formação Alagamar, Cretáceo da Bacia Potiguar, nordeste do Brasil (Unpubl. PhD thesis) 299. Universidade de São Paulo.

Doyle, J.A., Jardine, S., Doerenkamp, A., 1982. *Afropollis*, a new genus of early angiosperm pollen, with notes on the Cretaceous palynostratigraphy and paleoenvironments of Northern Gondwana. Bull. Cent. Rech. Explor.-Prod. Elf-Aquitaine 6, 39–117.

Duarte, L., 1959. Relatório da seção de paleontologia. Relatório Anual do Diretor. DGM/DNPM, Rio de Janeiro, pp. 167–194.

Duarte, L., Santos, R.S., 1993. Plant and fish megafossils of the Codó Formation, Parnaíba Basin, NE Brazil. Cretac. Res. 14, 735–746.

Edwards, W.N., 1933. On the Cretaceous fern *Paradoxopteris* and its connection with *Weichselia*. Ann. Bot. 47, 317–341.

El Atfy, H., Jasper, A., Uhl, D., 2020. A new record of *Paradoxopteris stromeri* Hirmer 1927 (Monilophyta, incertae sedis) from the Cenomanian of Sinai, Egypt. Rev. Palaeobot. Palynol. 273, 104148.

Ferreira, N.N., Ferreira, E.P., Ramos, R.R., Carvalho, I.S., 2020. Terrestrial and marine palynomorphs from deposits of the pull-apart rift of West Gondwana (Parnaíba Basin, northern Brazil): Biostratigraphy and relation to tectonic events. Journal of South American Earth Sciences 101, 102612. https://doi.org/10.1016/j.jsames.2020.102612.

Ferreira, N.N., Ramos, R.R., Ferreira, E.P., Carvalho, I.S., 2021. Lithofaciological analysis of the exposed rocks of the Itapecuru Formation, northeastern Parnaíba Basin, Brazil: paleoenvironmental implications. Journal of South American Earth Sciences 107, 103114. https://doi.org/10.1016/j.jsames.2020.103114.

Gabriel, R., Pimentel, C.M., Claro, D., Brito, M.R., Díaz-Castillo, J., Sérgio, C., Sim-Sim, M., Borges, P.A.V., 2019. Biota of coastal wetlands of Praia da Vitória (Terceira Island, Azores): Part 2-Bryophytes. Biodivers. Data J. 7, e34621.

Gary, A.C., Wakefield, M.I., Johnson, G.W., Ekart, D.D., 2009. Application of fuzzy c-means clustering to paleoenvironmental analysis: example from the Jurassic, Central North Sea, UK. In: Demchuk, T.D., Gary, A.C. (Eds.), Geologic problem solving with microfossils: a volume in honor of Garry D. Jones. SEPM (Soc. Sediment. Geol.) Spec. Publ. 93, 9–20.

Gonçalves, D.F., Rossetti, D.F., Truckenbrodt, W., Mendes, A.C., 2006. Argilominerais da Formação Codó (Aptiano Superior), Bacia de Grajaú, Nordeste do Brasil. Lat. Am. J. Sedimentol. Basin Anal. 13 (1), 59–75.

Grenfell, H.R., 1995. Probable fossil zygnematacean algal spore genera. Rev. Palaeobot. Palynol. 84 (3–4), 201–220.

Harris, T.M., 1981. Burnt ferns from the English Wealden. Proceedings of the Geological Association 92, 47–58.

Hay, W.W., Floegel, S., 2012. New thoughts about the Cretaceous climate and oceans. Earth Sci. Rev. 115, 262–272.

Heimhofer, U., Hochuli, P.A., 2010. Early Cretaceous angiosperm pollen from a low-latitude succession (Araripe Basin, NE Brazil). Rev. Palaeobot. Palynol. 161, 105–126.

Huttunen, S., Bell, N., Hedenäs, L., 2018. The evolutionary diversity of mosses–taxonomic heterogeneity and its ecological drivers. Crit. Rev. Plant Sci. 37 (2–3), 128–174.

Ignatov, M.S., Shcherbakov, D.E., 2011. Lower Cretaceous mosses from Khasurty (Transbaikalia). Arctoa 20, 19–42.

Kampmann, H., 1983. Mikrofossilien, Hölzer, Zapfen und Pflanzenreste aus der unterkretazischen Sauriergrube bei Brilon-Nehden. Beitrag zur Deutung des Vegetationsbildes zur Zeit der Kreidesaurier in Westfalen. Landschaftsverband Westfalen-Lippe, Münster.

Kato, M., Setoguchi, H., 1998. An rbcL-based phylogeny and heteroblastic leaf morphology of Matoniaceae. Systematic Botany 23 (4), 391–400. https://doi.org/10.2307/2419371.

Kimura, T., Aiba, H., 1985. Discovery of *Weichselia reticulata* (Stokes et Webb) from the Lower Cretaceous Todai Formation, in the Outer Zone of Japan. Proceedings of the Japan Academy. Series B 61 (8), 356–358.

Koeniguer, J.C., 1966. Sur de nouveaux échantillons du genre *Paradoxopteris*. Mém. Soc. Géol. France 45 (2), 100–112.

Koeniguer, J.C., 1975. Les genres *Alstaettia, Paradoxopteris, Palmoidopteris*, et *Weichselia* (Dogger – crétacé Inférieur) en Eurafrique. In: Actes du 100 Congres national des Societes savantes, Paris, vol. 2, pp. 93–98.

Krassilov, V.A., 1972. Palaeoecology of Terrestrial Plants. Basic Methods and Principles. Acad. Sci. USSR, Far East Branch, Vladivostok (English Translation 1975, Wiley, New York, Toronto).

Krassilov, V., Schrank, E., 2011. New Albian macro-and palynoflora from the Negev (Israel) with description of a new gymnosperm morphotaxon. Cretac. Res. 32 (1), 13–29.

Krassilov, V.A., Schuster, R.M., 1984. Paleozoic and Mesozoic fossils. New Manual of Bryology 2, 1172–1193.

Kujau, A., Heimhofer, U., Hochuli, P.A., Pauly, S., Morales, C., Adatte, T., Föllmi, K., Ploch, I., Mutterlose, J., 2013. Reconstructing Valanginian (Early Cretaceous) mid-latitude vegetation and climate dynamics based on spore–pollen assemblages. Rev. Palaeobot. Palynol. 197, 50–69.

Kvaček, J., Vodrážka, R., 2016. Late Cretaceous flora of the Hidden Lake Formation, James Ross Island (Antarctica), its biostratigraphy and palaeoecological implications. Cretac. Res. 58, 183–201.

Lima, E.A.A., Leite, J.F., 1978. Projeto Estudo Global dos Recursos Minerais da Bacia Sedimentar do Parnaíba. Integração Geológica-metalogenética. DNPM/CPRM, Recife, p. 437.

Lima, M.R., 1978. Palinologia da Formação Santana (Cretáceo do Nordeste do Brasil). (Unpubl. PhD thesis. University of São Paulo, p. 335.

Lima, M.R., 1982. Palinologia da Formação Codó na região de Codó, Maranhão. Boletim do Instituto de Geociências USP 13, 116–128.

Lima, M.R., Boltenhagen, E., 1981. Estudo comparativo da evolução das microfloras afro-sul-americanas; I. O Cretáceo Inferior. In: Sanguinetti, Y.T. (Ed.). Anais do II Congresso Latino-Americano de Paleontologia, Porto Alegre, pp. 331–341.

Lindoso, R.M., 2016. A biota da Formação Codó (Aptiano da Bacia do Parnaíba), Nordeste do Brasil: aspectos paleoambientais e paleobiogeográficos. (Unpubl. PhD thesis). Universidade Federal do Rio de Janeiro 192.

Lindoso, R.M., Carvalho, I.S., 2012. Crustáceos da Formação Codó (Bacia do Parnaíba, Brasil. In: Lopes, F.C., Andrade, A.I., Henriques, M.H., Quinta-Ferreira, M., Barata, M.T., Pena dos Reis, R. (Eds.), Para entender a Terra: memórias e notícias de geociências no espaço lusófono. Imprensa da Universidade de Coimbra, Cap. Imprensa da Universidade de Coimbra, pp. 171–177.

Lindoso, R.M., Carvalho, I.S., Medeiros, M.A., Mendes, I.D., Marques, N.E., Brito, R., Almeida, C.M., 2013a. A megaflora da Formação Codó (Aptiano, Bacia do Parnaíba), nordeste do Brasil. In: proceedings of XXIII Congresso Brasileiro de Paleontologia, SBP. Gramado 175–176.

Lindoso, R.M., Carvalho, I.S., Medeiros, M.A., Pereira, A.A., Santos, R.A.B., Mendes, I.D., Brito, J.M., Vilas Bôas, I., Araújo, M.N., Ferreira, N.N., 2011. Novos sítios fossilíferos em carbonatos da Formação Codó (Aptiano-Albiano) da Bacia do Parnaíba, Maranhão, Brasil. In: Carvalho, I.S., Srivastava, N.K., Strohschoen Jr, O.S., Lana, C.C. (Eds.), Paleontologia: Cenários de Vida. Interciência, Rio de Janeiro, pp. 819–827.

Lindoso, R.M., Carvalho, I.S., Mendes, I.D., 2013b. An isopod from the Codó Formation (Aptian of the Parnaíba Basin), Northeastern Brazil. Brazilian Journal of Geology 43 (1), 16–21.

Lindoso, R.M., Dutra, T.L., Carvalho, I.S., Medeiros, M.A., 2018. New plant fossils from the Lower Cretaceous of the Parnaíba Basin, northeastern Brazil: southern Laurasia links. Braz. J. Geol. 48 (1), 127–145.

Lindoso, R.M., Maisey, J.G., Carvalho, I.S., 2016. Ichthyofauna from the Codó Formation, Lower Cretaceous (Aptian, Parnaíba Basin), northeastern Brazil and their paleobiogeographical and paleoecological significance. Palaeogeography, Palaeoclimatology, Palaeoecology 447, 53–64.

Lindsay, S., Suddee, S., Middleton, D.J., Pooma, R., 2003. Matoniaceae (Pteridophyta) - a new family record for Thailand. Thai Forest Bulletin (Botany) 31, 47–52.

Lisboa, M.A.R., 1914. The Permian geology of northern Brazil. Am. J. Sci. 37 (221), 425–443.

McParland, L.C., Collinson, M.E., Scott, A.C., Campbell, G., 2009. The use of reflectance values for the interpretation of natural and anthropogenic charcoal assemblages. Archaeological and Anthropological Sciences 1 (4), 249–261.

Mendes, M.S., 2007. Análise estratigráfica do intervalo formacional Grajaú-Codó (Aptiano) da Bacia do Parnaíba, NE do Brasil. (Unpubl. MSc dissertation). Universidade Federal do Rio de Janeiro 214.

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

Mendonça Filho, J.G., Menezes, T.R., Mendonca, J.O., Oliveira, A.D., Silva, T.F., Rondon, N.F., Silva, F.S., 2012. Organic facies: palynofacies and organic Geochemistry approches. In: Panagiotaras, D. (Ed.), Geochemistry Earth's System Processes. InTech, Patras, vol. 1, pp. 211–248. ISBN 978-953-51-0586-2.

Mendonça Filho, J.G., Menezes, T.R., Mendonça, J.O., Oliveira, A.D., Souza, J.T., 2017. 10th ICCP Training Course on Kerogen: Composition and Classification, GFZ. Deutsches GeoForschungsZentrum, Potsdam, p. 276. ISBN 978-84-697-4419-2.

Moisan, P., Voigt, S., Schneider, J.W., Kerp, H., 2012. New fossil bryophytes from the Triassic Madygen Lagerstätte (SW Kyrgyzstan). Rev. Palaeobot. Palynol. 187, 29–37.

Moore, D.M., Reynolds, R.C., 1997. X-ray Diffraction and the Identification and Analysis of Clay Minerals. Oxford University Press, Oxford.

Moraes Rego, L.F., 1923. Reconhecimento Geológico Feito No Estado Do Maranhão. Relatório Anual Do Diretor. Serviço Geológico e Mineralógico, Rio de Janeiro, pp. 74–77.

Moreno, M., 1994. La Paleoflora del Cretácico Inferior de las regiones de San Antonio y Aipe (Huila). In: Etayo-Serna, F. (Ed.), Estudios del Valle Superior del Magdalena. W. Taller Editorial, Bogotá, pp. XIV1–XVI12.

Mussa, D., Carvalho, I.S., Martins, F.J.C., Zuccoloto, M.E., 2000. *Paradoxopteris* Hirmer 1927, o caule de *Weicheselia* Stiehler 1857, presente no Cretáceo da Bacia de São Luís, Estado do Maranhão, Brasil. Revista da Universidade de Guarulhos 5 (6), 60–70.

Nagalingum, N.S., Cantrill, D.J., 2006. Early Cretaceous Gleicheniaceae and Matoniaceae (Gleicheniales) from Alexander Island, Antarctica. Rev. Palaeobot. Palynol. 138 (2), 73–93.

Oliveira, A.D., Mendonça Filho, J.G., Carvalho, M.D.A., Menezes, T.R., Lana, C.C., Brenner, W.W., 2004. Novo método de preparação palinológica para aumentar a recuperação de dinoflagelados. Rev. Bras. Palaontol. 7 (2), 169–175.

Oliveira, A.D., Mendonça Filho, J.G., Sant'Anna, A.J., Souza, J.T., Freitas, A.G., Menezes, T.R., 2006. Inovação no processamento químico para isolamento da Matéria Orgânica Sedimentar. In: proceedings of XLIII Congresso Brasileiro de Geologia. Aracaju, 324–324.

Passalia, M.G., 2007. Nuevos registros para la flora cretácica descripta por Halle (1913) en lago San Martín. Santa Cruz, Argentina. Ameghiniana 44, 565–595.

Paz, J.D., Rossetti, D.F., Macambira, M.J., 2005. An Upper Aptian saline pan/lake system from the Brazilian equatorial margin: integration of facies and isotopes. Sedimentology 52 (6), 1303–1321.

Phinyo, K., Pekkoh, J., Peerapornpisal, Y., 2017. Distribution and ecological habitat of *Scenedesmus* and related genera in some freshwater resources of Northern and North-Eastern Thailand. Biodiversitas Journal of Biological Diversity 18 (3), 1092–1099.

Pinto, I.D., Ornellas, L.P., 1974. New cretaceous Hemiptera (insects) from Codó Formation, northern Brazil. In: Proceedings of XXVIII Congresso Brasileiro de Geologia, Porto Alegre, vol. 2, pp. 289–304.

Pons, D., 1988. Le Mésozoïque de Colombie. Macroflores et Microflores. Muséum National d'Histoire Naturelle, Paris.

Portela, H.A., Antonioli, L., Dino, R., Garcia, M.J., 2014. Caracterização palinoflorística e paleoambiental da Formação Santana (Cretáceo Inferior), poço 4-BO-1-PE, Bacia do Araripe, nordeste do Brasil. Rev. Bras. Palaontol. 17 (3), 363–372.

Puebla, G.G., Mego, N., Prámparo, M.B., 2012. Asociación de briofitas de la Formación La Cantera, Aptiano tardio, Cuenca de San Luis, Argentina. Ameghiniana 49, 217–229.

Ramos, M.I.F., Rossetti, D.F., Paz, J.D.S., 2006. Caracterização e significado paleoambiental da fauna de ostracodes da Formação Codó (Neoaptiano), leste da Bacia de Grajaú, MA, Brasil. Rev. Bras. Palaontol. 9, 339–348.

Regali, M.S.P., Gonzaga, S.M., 1985. Palinocronoestratigrafia da Bacia Potiguar – Rio Grande do Norte, Brasil. Departamento Nacional de Produção Nacional, Coletânea de trabalhos paleontológicos, Série Geologia. Seção Paleontologia e Estratigrafia 27/2 443–460.

Regali, M.S.P., Uesugui, N., Santos, A.S., 1974. Palinologia dos sedimentos meso-cenozoicos do Brasil. II. Boletim Técnico da Petrobras 17 (4), 263–301.

Retallack, G., Dilcher, D.L., 1981. A coastal hypothesis for the dispersal and rise to dominance of flowering plants. In: Niklas, K.J. (Ed.), Paleobotany, Paleoecology, and Evolution 2. Praeger, New York, pp. 27–77.

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.

Rossetti, D.F., Góes, A.M., 2000. Deciphering the sedimentological imprint of paleoseismic events: an example from the Aptian Codó Formation, northern Brazil. Sediment. Geol. 135 (1–4), 137–156.

Rossetti, D.F., Góes, A.M., Arai, M., 2001a. A passagem Aptiano-Albiano na Bacia do Grajaú, MA. In: Rossetti, D.F., Góes, A.M., Truckenbrodt, W. (Eds.), O Cretáceo na Bacia de São Luís-Grajaú. Museu Paraense Emílio Goeldi, Belém, pp. 101–117.

Rossetti, D.F., Truckenbrodt, W., Santos Jr., A.E., 2001b. Clima do Cretáceo no Meio-norte brasileiro. In: Rossetti, D.F., Góes, A.M., Truckenbrodt, W. (Eds.), O Cretáceo na Bacia de São Luís-Grajaú. Museu Paraense Emílio Goeldi, Belém, pp. 67–76.

Rossetti, D.F., Paz, J.D.S., Góes, A.M., 2004. Facies analysis of the Codó Formation (late Aptian) in the Grajaú área, southern São Luís-Grajaú basin. An Acad. Bras Ciências 76 (4), 791–806.

Salgado-Campos, V.M.J., Carvalho, I.S., Bertolino, L.C., Duarte, T.A., Araújo, B.C., Borghi, L., 2021. Clay mineralogy and lithogeochemistry 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, Â.C.S., Guerra-Sommer, M., Degani-Schmidt, I., Siegloch, 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.

Santos, M.E.C.M., Carvalho, M.S.S., 2009. Paleontologia das bacias do Parnaíba, Grajaú e São Luís. CPRM, Rio de Janeiro, p. 215.

Santos, R.S.A., 1974. A paleoictiofáunula da Formação Codó. Anais da Academia Brasileira de Ciências 46(3/4), p. 91.

Schimper, A.F.W., 1898. Pflanzen-geographie auf physiologischer Grundlage, 2. G. Fischer.

Schrank, E., 1999. Mesozoische Floren aus Nordost-Afrika und ihre Beziehungen zum Klima am Paläoäquator. In: deutsche Forschungsgemeinschaft (DFG) (Ed.), Nordost-

Afrika: strukturen und Ressourcen. In: Ergebnisse aus dem Sonderforschungsbereich "Geowissenschaftliche Probleme in ariden und semiariden Gebieten". Wiley-VCH Verlag GmbH & Co. KGaA, Weinheim, pp. 137–166.

Scotese, C.R., 2014. Atlas of Early Cretaceous Paleogeographic Maps, PALEOMAP Atlas for ArcGIS, Volume 2, the Cretaceous, Maps 23–31, Mollweide Projection. PALEOMAP Project, Evanston, IL. https://doi.org/10.13140/2.1.4099.4560.

Scotese, C.R., Song, H., Mills, B.J., van der Meer, D.G., 2021. Phanerozoic paleotemperatures: the Earth's changing climate during the last 540 million years. Earth Sci. Rev. 215, 103503.

Scott, A.C., 2000. The Pre-Quaternary history of fire. Palaeogeography, Palaeoclimatology,. Palaeoecology 164 (1–4), 281–329.

Scott, A.C., 2010. Charcoal recognition, taphonomy and uses in palaeoenvironmental analysis. Palaeogeography, Palaeoclimatology. Palaeoecology 291 (1–2), 11–39.

Sender, L.M., Diez, J.B., Ferrer, J., Pons, D., Rubio, C., 2005. Preliminary data on a new Albian flora from the Valle del Río Martín, Teruel, Spain. Cretac. Res. 26 (6), 898–905.

Sender, L.M., Villanueva-Amadoz, U., Pons, D., Diez, J.B., Ferrer, J., 2015. Singular taphonomic record of a wildfire event from middle Albian deposits of Escucha Formation in northeastern of Spain. Hist. Biol. 27 (3–4), 442–452.

Silantieva, N.A., Krassilov, V., 2006. *Weichselia* Stiehler from Lower Cretaceous of Makhtesh Ramon, Israel: new morphological interpretation and taxonomical affinities. Acta Palaeobot. 46, 119–135.

Silva-Santos, R., Valença, J.G., 1968. A Formação Santana e sua paleoictiofauna. An Acad. Bras Ciências 40 (3), 339–360.

Soares, E.F., Zalán, P.V., Figueiredo, J.J.P., Trosdtorf Jr., I., 2007. Bacia do Pará-Maranhão. Bol. Geociencias Petrobras 15 (2), 321–329.

Taylor, E.L., Taylor, T.N, Krings, M., 2009. Paleobotany: the biology and evolution of fossil plants, 2nd. Academic Press, Burlington.

Tomescu, A.M., Bomfleur, B., Bippus, A.C., Savoretti, A., 2018. Why Are Bryophytes So Rare in the Fossil Record? A Spotlight on Taphonomy and Fossil Preservation. In: Krings, M., Harper, C.J., Cúneo, N.R., Rothwell, G.W. (Eds.), Transformative Paleobotany. Oxford Academic Press, New York, pp. 375–416.

Tryon, A.F., Lugardon, B., 1991. Spores of the Pteridophyta. Springer-Verlag, New York, p. 648.

Tryon, R.M., Tryon, A.F., 1982. Ferns and Allied Plants with Special Reference to Tropical America. Springer Verlag, New York.

Tyson, R.V., 1995. Sedimentary Organic Matter. Springer, Dordrecht, p. 615.

Vakhrameev, V.A., 1991. Jurassic and Cretaceous Floras and Climates of the Earth. Cambridge University Press, Cambridge.

Van Konijnenburg-Van Cittert, J.H.A., 2002. Ecology of some late Triassic to early Cretaceous ferns in Eurasia. Rev. Palaeobot. Palynol. 119 (1–2), 113–124.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37 (1), 130–137.

Varejão, F.G., Warren, L.V., Simões, M.G., Buatois, L.A., Mángano, M.G., Bahniuk, A.M., Assine, M.L., 2021. Mixed siliciclastic-carbonate sedimentation in an evolving epicontinental sea: Aptian record of marginal marine settings in the interior basins of north-eastern Brazil. Sedimentology.

Vaz, P.T., Rezende, N.G.A.M., Wanderley Filho, J.R., Travassos, W.A.S., 2007. Bacia do Parnaíba. Bol. Geociencias Petrobras 15 (2), 253–263.

Warr, L.N., 2020. Recommended abbreviations for the names of clay minerals and associated phases. Clay Miner. 55 (3), 261–264.

Watson, J., Alvin, K.L., 1996. An English Wealden floral list, with comments on possible environmental indicators. Cretac. Res. 17, 5–26.

Wood, A.J., 2007. The nature and distribution of vegetative desiccation-tolerance in hornworts, liverworts and mosses. Bryol. 110 (2), 163–177.

Worobiec, E., 2014. Fossil zygospores of Zygnemataceae and other microremains of freshwater algae from two Miocene palaeosinkholes in the Opole region, SW Poland. Acta Palaeobot. 54 (1), 113–157.

Zalán, P.V., Silva, P.C.R., 2007. Bacia do São francisco. Bol. Geociencias Petrobras 15 (2), 561–571.

Zamaloa, M.D.C., Tell, G., 2005. The fossil record of freshwater micro-algae *Pediastrum* Meyen (Chlorophyceae) in southern South America. J. Paleolimnol. 34 (4), 433–444.

Zavattieri, A.M., Gutiérrez, P.R., Ezpeleta, M., 2017. *Syndesmorion stellatum* (Fijałkowska) Foster et Afonin chlorophycean algae and associated microphytoplankton from lacustrine successions of the La Veteada Formation (late Permian), Paganzo Basin, Argentina. Paleoenvironmental interpretations and stratigraphic implications. Rev. Palaeobot. Palynol. 242, 1–20.

Zeiller, R., 1914. Sur quelques plantes wealdiennes recueillies au Pérou par M. le Capitaine Berthon. Rev. Gen. Bot. 25, 647–674.