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# Late Aptian paleoclimate reconstruction of Brazilian equatorial margin: inferences from palynology

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**Abstract.**

This study conducted high-resolution paleoclimatic analyses based on the identification of palynological groups from the late Aptian age (Biozone *Sergipea veriverrucata*) in the Bragança and Codó formations within the Bragança-Viseu, São Luís, and Parnaíba basins. The analysis comprised 40 palynological samples, with 200 palynomorphs per slide counted when possible. Bioclimatic analysis was mainly supported by the identification of botanical affinities, and ecological and climatic parameters such as wet/arid trend (Fs/X), Shannon-Wiener diversity, and indicator species analysis (IndVal) were used. Statistical analyses such as principal component and cluster analyses were employed to support the paleoclimatic interpretations. The study recognized 69 genera distributed among the main groups of living plants, including bryophytes, ferns, lycophytes, gymnosperms, and angiosperms. It was possible to attribute botanical affinity in 94.2% of the taxa, and nine genera occurred in all sections studied: *Afropollis*, *Araucariacites*, *Callialasporites*, *Cicatricosisporites*, *Classopollis*, *Cyathidites*, *Deltoidospora*, *Equisetosporites*, and *Verrucosisporites*, with *Classopollis*

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Climate of the Past Discussions Open Access EGU

being the most abundant. The stratigraphic distribution of the bioclimatic groups (hydrophytes, hygrophytes, lowland tropical flora, upland flora, and xerophytes) allowed for the identification of climatic phases: pre-evaporitic, evaporites, and post-evaporites. In the pre-evaporitic phase, the most significant abundances were between the hygrophytes and upland flora, indicating a certain level of humidity. Xerophytes were the most abundant in all phases, with a conspicuous increase in the evaporitic phase, reflecting an increase in aridity. In the post-evaporitic phase, there was a significant increase in the upland flora with the return of wetter conditions. This study confirmed an increasing humidity trend in the analyzed sections, probably owing to the influence of the Intertropical Convergence Zone that already operated during the late Aptian.

## 1. Introduction

The palynoflora preserved in the upper Aptian rocks of South America and Africa is typical of hot conditions and is commonly associated with arid climates (Chumakov et al., 1995, Hay and Floegel, 2012). However, because biodiversity tends to be higher in wetter climates, the high diversity observed during the Aptian raises the possibility that this arid phase fluctuated during that period. The palynoflora related to hot and humid climates exhibits a growing trend toward these conditions, even during the Aptian. This trend may be linked to the shifting and strengthening of a humid belt associated with the Intertropical Convergence Zone (ITCZ) (Hay and Floegel, 2012; Scotese, 2016; Carvalho et al., 2022; Santos et al., 2022), as well as to the establishment of the South Atlantic, which affected the marine current system.

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023


Climate of the Past
Discussions
Open Access

Palynology is a valuable tool for inferring paleoclimatic conditions based on palynomorph studies. Late Aptian rocks from Brazilian sedimentary basins, including the Bragança and Codó formations, contain a significant representation of conifers from the family Cheirolepidiaceae and their pollen grains, such as *Classopollis* (Regali et al., 1974; Carvalho et al., 2017, 2019, 2022). *Classopollis* is typically associated with arid conditions, often found in lagoons and coastal areas, and frequently associated with evaporites (Batten, 1975; Vakhrameev, 1970, 1981; Doyle et al., 1982; Hashimoto, 1995; Heimhofer et al., 2008, Carvalho et al., 2019). However, studies of the Sergipe Basin (northwestern Brazil), suggest strong fluctuations in the abundance of *Classopollis* and other xerophytic flora, with a decreasing trend toward the late Aptian accompanied by an increase in fern spores that require water for reproduction (Carvalho et al., 2017, 2019). The geographic extent of these trends remains controversial, and further investigation is required to identify possible climatic oscillations in other sedimentary basins in Brazil. Analysis of the Codó and Bragança formations, located in the Cretaceous section of the São Luís, Bragança-Viseu, and Parnaíba basins near the paleoequator, where the Intertropical Convergence Zone (ITCZ) occurs, has great potential to provide insights into this topic.

The objective of this study was to infer the paleoclimate of the late Aptian ~~period~~ in the Bragança-Viseu, São Luís, and Parnaíba basins, all located in equatorial areas (Fig. 1), by examining the relationships between groups of palynomorphs. Furthermore, this study aimed to investigate how variations in the composition of paleofloras and indicator species are linked to climatic changes such as shifts in humidity and temperature, as well as other paleoenvironmental forcings.

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023


Climate of the Past Discussions

## 2. Geological settings

According to Milani et al. (2007), the three sedimentary basins considered in this study are grouped into large assemblies based mainly on the tectonic context in which they developed: Mesozoic aborted rift basins (Bragança-Viseu and São Luís basins) and Paleozoic Syneclises (Parnaíba Basin).

The Bragança-Viseu, São Luís, and Parnaíba basins show a similar stratigraphic evolution. The Bragança-Viseu and São Luís basins are located on the equatorial margin and the Parnaíba Basin in north-central Brazil (Fig. 1). The basins constitute a rift system (graben and semi-graben) located between the terrains of the folding belt. Together, these cover an area of approximately 645,000 $km^2$. The sedimentary succession of the basins consists of Paleozoic, Mesozoic, and Cenozoic rocks. The Cretaceous strata are represented by the Bragança (Bragança-Viseu and São Luís basins), Grajaú, Codó, and Itapecuru Formations. In the studied sections, the Bragança (EGST-01 and VN-01 wells) and Codó (CI-01, PR-01, PE-01, RL-01 wells) formations were recognized.

The Bragança Formation consists of gray medium- to coarse-grained sandstones and conglomerates supported by conglomerates and greenish siltstones. This formation is interpreted as an alluvial fan deposit.

The Codó Formation is composed of dark shales, anhydrite, and calcilutites, with sandstone intercalations. These deposits were assigned to a lagoonal environment. Marine incursions are indicated by fossil contents and the occurrence of evaporitic deposits.

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023

Climate of the Past
Open Access
Discussions

## 3. Late Aptian climatic evolution

The pre-evaporitic, evaporitic, and post-evaporitic phases are recognized for the late Aptian. These phases occur within the K40-K50 supersequences, and show an average maximum thickness of approximately 650 m in the studied basins. The pre-evaporitic phase is represented by carbonate and siliciclastic deposits formed in fluvial and lacustrine deltaic environments within a large proto-oceanic gulf (Milani et al., 2007). The peak of the evaporitic deposition is recorded in the K50 supersequence, with widespread occurrences in the Brazilian equatorial margin. The origin of these deposits is heat intensification associated with the widening of the Atlantic Ocean. These conditions caused strong evaporation, leading to a wide distribution of evaporites (mainly halite and anhydrite gypsum) in the South Atlantic basins. The post-evaporitic phase is characterized by fully marine conditions, evidenced by the rich assemblages of marine fossils. During this phase, carbonates were deposited, followed by muddy and sandy sediments, in shallow marine to slope environments.

The Bragança and Codó formations are inserted within the K40-K50 Supersequence. However, in the Bragança Formation, only the pre-evaporitic phase is recognized. On the other hand, the Codó Formation has recorded the three climatic phases (pre-evaporitic, evaporitic, and post-evaporitic).

## 4. Material and methods

### 4.1. Studied sections

This study was based on core samples from three basins: Bragança-Viseu and São Luís located in the equatorial margin, and the Parnaíba Basin in north-central Brazil.

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023

Climate of the Past Discussions

The material for this study was derived from the cores of wells EGST-1 and VN-1 from the Bragança-Viseu Basin; PR-1, PE-1, and RL-1 from the São Luís Basin; and CI-1 from the Parnaíba Basin (Table 1), all drilled by Petrobras (the Brazilian oil company) (Fig. 1). Detailed information on the studied sections is presented in Table 1.

The stratigraphic succession studied comprises parts of the Bragança-Viseu, São Luís, and Parnaíba Basins. The Bragança-Viseu Basin includes wells EGST-1 (676-1872.1 m), consisting of sandstones, siltstones, and conglomerates, and VN-1 (1287.6-1317.69 m), consisting only of sandstones (Fig. 2) (Table 1).

Three sections are from the São Luís Basin: PR-1 (1507.6-1513.1 m), composed of sandstones and siltstones, and PE-1 (1562-1776.8 m), which has a lithology similar to that of the previous one, with the addition of calcarenites. RL-1 (1157.3-1240.3 m) is composed of sandstones, siltstones, calcarenites, and anhydrites. The fourth section, CI-1 (768-907.1 m), is from the Parnaíba Basin. CI-1 has a lithology similar to that of RL-1, but the former has a more pronounced package of anhydrites than the latter does (Fig. 2) (Table 1).

The late Aptian age of the samples is based on the *Sergipea variverrucata* Biozone recognized in two studied drill cores (PR-1 and CI-1), which is correlated with part of the upper Aptian *Globigerinelloides algerianus* Zone (Carvalho et al., 2016). In the other four sections (EGST-1, VN-1, PE-1, and RL-1), *Sergipea variverrucata* was not recognized. However, the identified floristic associations (e.g., *Afropollis jardinus*, *Araucariacites australlis*, *Bennettittaepollenites regallie*, *Equisetosporites maculosus*, *Klukisporites foveolatus*, *Sergipea simplex*) are attributed to the late Aptian of Brazil (Regali and Santos, 1999; Carvalho et al., 2017, 2019).

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023


Climate of the Past
Discussions
Open Access

### 4.2. Sample preparation

The samples were prepared at the Research and Development Center of Petrobras (CENPES) in Rio de Janeiro. ~~The method used was~~ the standard Petrobras method of palynological ~~preparation~~ compiled by Uesugui (1979) ~~on the basis of methods developed by~~ Erdtman (1943, 1969) and Faegri et al. (1966). Thus, in this study, most mineral constituents were dissolved by hydrochloric and hydrofluoric acids before heavy-liquid separation, and the remaining organic matter was sieved through a 10 µm mesh before mounting on slides.

### 4.3. Palynological analyses

The samples were analyzed using a transmitted light microscope. Analysis was based on the first 200 palynomorphs counted on each slide. The marine elements (dinoflagellate cysts and microforaminiferal linings) were counted separately. Taxonomic identification was based on the ~~methods of~~ Regali et al. (1974), Lima (1978), Dino (1992, 1994), and Carvalho et al. (2019, 2022).

### 4.4. Bioclimatic analysis

Palynomorphs are useful climatic indicators (bioclimatic groups) because of their botanical affinities. However, identifying the spores and pollen grains of the parent plant classified at the family level is often challenging. This study referred to the literature (e.g., Dino, 1994; Carvalho, 2004; Souza-Lima and Silva, 2018; Jansonius et al., 1976-1996) to identify the botanical affinities of the indicator species.

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023



On the basis of botanical affinities and inferred paleoenvironmental conditions, this study proposes five bioclimatic groups: hydrophytes, hygrophytes, tropical lowland flora, upland flora, and xerophytes. These groups provide valuable insights into the climate and vegetation of the study area.

**4.5. Wet-dry trend**

To support the bioclimatic group distribution, we used the Fs/X (fern spores *versus* xerophytes) ratio. This ratio is based on the co-occurrence of fern spores and xerophytic palynomorphs (*Classopollis* and polyplicate gnetalean pollen); therefore, it can be used as an indicator of dry-wet trends (Carvalho et al., 2019). The ratio of fern spores to xerophytic palynomorphs (Fs/X) was calculated as Fs/X=nFs/(nFs+nX), where n is the number of specimens counted, Fs is the number of fern spores (non-reworked), and X is the number of xerophytic pollen grains. In summary, Fs/X approaching 1 implies high humidity, and that approaching -1 indicates low humidity.

**4.6. Diversity**

Shannon-Weaver diversity indices H (S) were calculated for all samples by using PAST software (Hammer et al., 2001) to provide information for interpreting paleoclimatic trends. Diversity H(S) considers the abundance of each species and is used to characterize the diversity of the assemblages.

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023



### 4.7. Indicator species

To reconstruct the late Aptian vegetation in the studied basins, we employed the indicator species analysis (IndVal) method. This index was applied for the first time in pre-Quaternary samples in the der Sergipe Basin (Carvalho et al., 2017).

The IndVal index determines the taxa strongly associated with particular groups of samples and is assumed to reflect the climatic conditions of those groups. It was calculated using the formula proposed by Dufrêne and Legendre (1997): IndValGroup k, Species j=100 × Ak,j × Bk,j, where Ak,j represents specificity, and Bk,j represents fidelity. We used PAST software (Hammer et al., 2001) to calculate these values.

To ensure that our IndVal analysis fulfilled the criteria of ordination and climate-focused approach, we grouped the samples according to three climatic phases: pre-evaporitic, evaporitic, and post-evaporitic. This allowed us to identify the specific indicator species associated with each climatic phase and gain insights into the vegetation that existed during the late Aptian period.

## 5. Results

Sixty-nine genera were identified in the 40 samples and were distributed into five plant groups: bryophytes (four genera), ferns (17 genera), lycophytes (10 genera), pteridosperms (one genus), gymnosperms (23 genera), and angiosperms (14 genera) (Appendix 1) (Table 2). Twenty indeterminate morphotypes were found in ferns and 10 in angiosperms. Of the 69 genera identified, nine occurred in all the wells studied: *Afropollis, Araucariacites, Callialasporites, Cicatricosisporites, Classopollis, Cyathidites, Deltoidospora, Equisetosporites, Verrucosisporites*.

Climate of the Past Discussions

The recognition of botanical affinities of the 69 genera was based on the literature (e.g., Dino 1992, Balme 1995; Antoniolli, 2001; Carvalho et al., 2017, Carvalho et al., 2019, Carvalho et al., 2022) and the database of *fossilworks.org*. The suggested botanical affinity of the 69 genera was 94.2%. The 5.8% without botanical affinity refers to the group of angiosperms.

All bioclimatic groups were present in the studied sections (Table 3, Appendix 2). In general, the palynological assemblage is predominantly composed of the xerophytic bioclimatic group, characterized by a high abundance of *Classopollis*. The average abundance of xerophytes was 55.7%, ranging from 46.3% to 63.6% in the sections studied (Table 4). In sequence, the upland flora had an overall average abundance of 18.9% (ranging from 7.8% to 26%), with *Araucariacites* being the dominant taxon. The hygrophyte bioclimatic group is characterized by the presence of *Cicatricosisporites*, which had an average abundance of 18.6% (ranging from 11.4% to 28.4%). By contrast, the hydrophyte bioclimatic group is the least abundant, with an overall average of 0.7%, and is dominated by the genus *Crybelosporites*. Regarding diversity, the Shannon-Wiener indices (H') obtained for the 40 samples showed an overall average of H'= 2.0, which ranged from H='1.6 in the VN-1 section to H'= 2 .2 in section PE-1 (Table 4). The values of the wet-dry trend (Fs/X ratio) ranged from 0.19 (dry) in section CI-1 to 0.39 (wet) in EGST-1(wet) (Table 4).

**5.1. Stratigraphic distribution of bioclimatic groups in EGST-1 well**

Although xerophytes are dominant overall, EGST-1 well exhibits a higher abundance of hygrophytes (24.9%) due to moderate to high occurrences of *Cicatricosisporites* and trilete psilate (e.g., *Cyathidites*), especially at the base of the well (Fig. 3). Additionally, the abundance of hygrophytes, tropical lowland flora, and

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023




upland flora increases toward the upper sections, whereas the abundance of xerophytes decreases (Fig. 4). The Shannon-Wiener indices (H') showed an overall average of H'= 2.1, slightly above the general average (H'= 2.0). The Fs/X ratio had the highest value for all sections (0.38), above the overall average (0.28), indicating more humid conditions (Table 4).

**5.2. Stratigraphic distribution of bioclimatic groups in VN-1 well**

Similar to the EGST-1 well, the VN-1 well is composed of four samples from the Bragança Formation, in which xerophytes dominate. However, unlike the former well, hygrophytes exhibit the highest average abundance (28.4%) among all studied wells, primarily because of the abundance of trilete psilate. Despite few samples, an increasing trend of hygrophytes, tropical lowland flora, and upland flora was observed, with a significant peak in hygrophytes (Fig. 4). The average diversity of H'=1.6 is the lowest for the studied basins, below the overall average (H'= 2.0). The Fs/X ratio was 0.31, above the overall average (0.28).

**5.3. Stratigraphic distribution of bioclimatic groups in PR-1 well**

The section comprises four samples from the Codó Formation. Notably, the PR-1 well exhibits the lowest average abundance of xerophytes (46.3%) (Table 4). However, it shows the highest average abundance in the tropical lowland flora group (20.4%) of all the wells studied, driven by the presence of the genus *Afropollis*. In general, an increasing trend toward hygrophytes, upland flora, and mainly tropical lowland flora was observed (Fig. 5). The average diversity was H'= 2.1 in this well. This value is one of the highest values among all the wells studied. This high diversity is mainly

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023


Climate of the Past
Discussions
Open Access
EGU

attributed to the significant number of species belonging to the tropical lowland flora group. The Fs/X ratio was 0.25, slightly below the overall average (0.28) (Table 4).

**5.4. Stratigraphic distribution of bioclimatic groups in PE-1 well**

The PE-1 well shows a clear decreasing trend upward of the xerophytes, which did not exceed 20% (Fig. 6). By contrast, hygrophytes and upland flora show a conspicuous increase. Highlight for the upland flora group show an average of 26% driven by the genus *Araucariacites*. The average diversity of H'=2.2 is the highest for the basins. This average diversity is due to the many species of upland flora and hygrophytes. The Fs/X ratio was 0.28, the same as the overall average (0.28) (Table 4).

**5.5. Stratigraphic distribution of bioclimatic groups in RL-1 well**

The section consists of seven samples from the Codó Formation. The xerophytic bioclimatic group dominated the entire section, with no sudden changes in the abundance curve observed, except at the base of the section, where the hygrophytes, tropical plain flora, and upland flora groups together reached almost 40% (Fig. 7). The average diversity of H’=1.9 is the second lowest for the studied basins. The Fs/X ratio was 0.24, slightly below the overall average (0.28) (Table 4).

**5.6. Stratigraphic distribution of bioclimatic groups in CI-1 well**

The Parnaíba Basin is represented by one well, which comprises 13 samples from the Codó Formation. The palynological assemblage of this section was dominated by the xerophytic bioclimatic group, with a high average of 63.6%, largely because of the abundance of *Classopollis* and *Equisetosporites*. The dendrogram shown in Fig. 8 reveals two intervals: the base with a greater balance between xerophytes and the other

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023



groups, especially the upland flora (15.9%) (Table 4). The Fs/X ratio recorded the lowest value in all sections (0.19), which was below the overall average (0.28), indicating drier conditions (Table 4). However, despite this, the average diversity of H'=2.0 was one of the highest, with the same value as the overall average of 2.0.

**5.7. Climatic phases**

All six sections were individually analyzed for palynology. However, a composite section was constructed (Table 5) based on the stratigraphically evident chronological distribution of the climatic phases in each studied section. The composite section of the Bragança-Viseu, São Luís, and Parnaíba basins consists of 40 samples, with 24 samples from the pre-evaporitic phase, eight from the evaporitic phase, and eight from the post-evaporitic phase (Table 5). In general, the composite section highlights the bioclimatic groups of hygrophytes (18.8%) and tropical lowland flora. The diversity and Fs/X ratio curves showed strong synchrony, indicating a relation between diversity and humidity (Fig. 9). No marine elements were recorded in these sections.

During the pre-evaporitic phase, there is a higher abundance of xerophytes, hygrophytes, and upland flora, but with strong oscillations observed in their respective curves. The dendrogram in Fig. 9 identifies two intervals within this phase: with significant values of xerophytes at the base but with a decreasing trend toward the top. The interval above the xerophyte curve exhibits an upward trend. The diversity and Fs/X ratio curves show synchrony but with a decreasing trend toward the top. The indicator species (IndVal) identified for the pre-evaporitic phase, *Deltoidospora* spp. (Cyatheaceae-Dicksoniaceae) is related to the montane rainforest, suggesting more humid conditions (Table 5).

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023



The evaporitic phase, which corresponds to the gypsum layers of the Codó Formation, is characterized by the highest average of the xerophytic bioclimatic group in the composite section (Table 5). Additionally, the average abundance of the tropical lowland flora group is also high, driven by the genus *Afropollis*. Surprisingly, the mean diversity is high during this phase, but the mean Fs/X ratio is the lowest. The high diversity in arid conditions is due to the great diversity of species in the xerophytic group, such as *Classopollis classoides*, *Equisetosporites maculosus*, and *Gnetaceaepollenites jansonius*. The IndVal for the evaporitic phase is *Afropollis* spp. related to tropical lowland flora (Table 5).

The post-evaporitic phase, which includes part of a section of the Codó Formation, is characterized by a significant decrease in the dominance of the xerophytic bioclimatic group; lower average abundance (47%) in PR-1; and the clear dominance of hygrophyte groups, including tropical lowland flora and upland flora. The dendrogram reveals a break between this phase and the evaporitic phase (Fig. 9). In general, this reflects an inversion in abundance between groups related to humidity (hygrophytes, hydrophytes, tropical flora, and upland flora) and groups related to drier conditions (xerophytes) (Fig. 9). In this phase, the indicator species is *Deltoidospora* spp., suggesting more humid conditions for pre- and pro-evaporitic phases.

## 6. Discussion

The data obtained from these sections provide clear evidence of the dominance of the xerophytic bioclimatic group during the late Aptian in Brazilian sedimentary basins. This information supports that in the literature that suggests an essentially arid climate during this period (e.g., Lima, 1983; Suguio and Barcelos, 1983; Petri, 1983; Rossetti et

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023



al., 2003; Hay and Floegel, 2012, Carvalho et al., 2017, 2019, 2022). These authors attributed this aridity to the predominance of conifers from the Cheirolepidiaceae family and their *Classopollis* pollen grains. However, climatic oscillations were identified during this period, indicated by bioclimatic groups related to the humid conditions: hydrophytes, hygrophytes, tropical lowland flora, and upland flora. A relationship between these groups has been suggested (e.g., Carvalho et al., 2017, 2019, 2022). In this study, principal component analysis (PCA) was conducted between bioclimatic groups that exhibited patterns similar to those observed in the literature (e.g., Carvalho et al., 2017, 2019, 2022). The PCA revealed a positive correlation among hygrophytes, hydrophytes, tropical lowland flora, and upland flora, whereas xerophytes show a negative relationship on the first axis (Component 1) (Fig. 10), explaining more than 70% of the variation. Component 1 characterizes the wet-dry trend.

The sections of the São Luís Basin (PE-1, RL-1, and PR-1) showed the lowest abundance of xerophytic flora, followed by the sections of the Bragança-Viseu Basin (VN-1 and EGST-1) and the CI-1 section (Parnaíba Basin) farther south (Fig. 11A). More humid conditions also were suggested by Santos et al. (2022) for the São Luis Basin. This study utilized palynological data and PCA analysis to propose the existence of a wet phase during the late Aptian in the São Luis Basin. Through the analysis of the abundance of *Araucariacites* and fern spores, as well as the presence of the genus *Classopollis* associated with carbonate sedimentation in two semi-arid intervals, an intermediate humid interval was identified. The authors suggested that the data were sufficient to identify a pre-Albian humid belt, which challenges the view of exclusively arid Gondwana during the Aptian and supports the presence of a wet phase.

As also suggested by Carvalho et al. (2022), we compared the studied sections with sections in the Espírito Santo Basin, located much farther south (at 20°S). We

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023




found that the studied basins had a lower abundance of xerophytic flora than the Espírito Santo Basin did (Fig. 11B-C). The decreasing trend in aridity observed from the southeast (Espírito Santo Basin) to the northeast (Fig. 11B-C) coincides with the location of the hot and humid belt attributed to the ITCZ (Ohba et al., 2010, Chaboureau et al., 2012, 2014; Scotese, 2016). Notably, the approach to the ITCZ belt, where xeric restrictions are milder, reflected even in the most aridity phase, the evaporitic phase, whose indicator species was the *Afropollis* spp. of the lowland tropical flora. This indicates that the ITZC must have had diminished aridity. The genus *Afropollis* has been associated with hot, humid climates. According to Carvalho et al. (2022), this genus exhibits the weakest negative correlation with xerophytic flora (e.g., *Classopollis*).

The ITCZ belt proposed by Scotese (2016) for the Aptian covers the entire African continental paleoequator. However, although very close, it did not reach South America (Fig. 11B). Palynological analyses conducted by Deaf et al. (2020) on the late Aptian material of the Dahab Formation (Mathruh Basin, Egypt) indicated a predominance of fern spores from the hygrophyte bioclimatic group (e.g., *Triplanosporites*, *Cicatricosisporites*) and uplands (e.g. *Deltoidospora*, *Araucariacites*), accounting for approximately 60% on average. This finding suggests that the formation is characterized by humid conditions.

The xerophytic flora (*Classopollis* and *Equisetosporites*) in the Dahab Formation averaged approximately 25%. Considering the climatic belts proposed by Scotese (2016, 2021), this formation occurred “inside” the ITCZ, which is reflected in the prevalence of bioclimatic groups associated with more humid conditions. The abundance of xerophytic flora in the Dahab Formation (Mathruh Basin) was lower than that in the sections studied. This difference was particularly significant when compared

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023



with the Espírito Santo Basin, where the abundance of xerophytic flora was 87.3%, as opposed to 25% in the Dahab Formation (Fig. 11C). Notably, a significant contributor to the humidity in the Dahab Formation was likely a marine influence, which was not present in the sections studied.

**7. Conclusion**

The Aptian sections studied have well-preserved palynological diversity dominated by the genera *Classopollis* (Cheirolepidiaceae) and *Araucariacites* (Araucariaceae). Some genera of ferns are also abundant such as *Cicatricosisporites* (Anemiaceae), *Verrucosisporites* (Osmundaceae), and *Deltoidospora* (Cyatheaceae).

Five bioclimatic groups were identified and proposed for interpretation: hydrophytes, hygrophytes, tropical lowland flora, upland flora, and xerophytes. The bioclimatic groups provide evidence that the climate during the late Aptian was arid. However, when considering the distribution curves of bioclimatic groups, as well as the indicator species (IndVal) and diversity, a clear upward trend toward increased humidity was observed.

The late Aptian period was characterized by three distinct climatic phases: pre-evaporitic, evaporitic, and post-evaporitic. During the pre-evaporitic phase, despite the dominance of xerophytic flora, there were episodes of humidity, evidenced by indicator species such as *Deltoidospora* spp. The evaporitic phase was dominated by xeric elements, although the moderate to high abundance of lowland tropical flora, confirmed by *Afropollis* spp. as an indicator species, indicated some periods of humidity. The post-evaporitic phase was marked by a lower abundance of xerophytic elements and a clear dominance of groups associated with wet conditions, mainly the upland flora, suggesting a wetter climate during this phase.

The climatic variation during the late Aptian is reflected in the palynological assemblages, with the arid phase being dominated by the genus *Classopollis* and other xerophytic bioclimatic group indicators. The wet phase is marked by a significant decrease in xerophytes and a high abundance and diversity of *Araucariacites*, fern spores, and other genera related to highland, hydrophytic, and hygrophytic bioclimatic groups. The "mirror effect" observed in the frequency curves highlights the ecological differences between the arid and humid trend groups.

According to our findings, vegetation dynamics were affected by a combination of the Intertropical Convergence Zone (ITCZ) and the opening of the South Atlantic Ocean during the late Aptian period. The influence of the ITCZ is currently stronger in the north-central region of South America. Notably, climate evolution during the late Aptian in the South Atlantic led to increased humidity, which was closely linked to plant diversity and marine influences.

**Appendices**

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023


Climate of the Past
Discussions

Appendix 1. Eleven plates with the most relevant palynomorphs recorded in the studied wells.

**PLATE 1**

A. *Stereisporites* sp. Pflug, 1953 (RL-1).

B. *Todisporites* sp. Couper, 1958 (RL-1).

C. *Deltoidospora diaphana* Wilson & Webster, 1946 (EGST-1).

D-E. *Deltoidospora minor* (Couper 1953) Pocock 1970[a] (CI-1).

F. *Cyathidites* sp. Couper, 1953 (CI-1).

G. *Cyathidites minor* Couper, 1953 (CI-1).

H. *Biretisporites sp*. Delcourt & Sprumont, 1955 emend. Delcourt, Dettmann & Hughes, 1963 (CI-1).

I. *Biretisporites Pontoniaei* Delcourt & Sprumont, 1955 (RL-1).

J. *Undulatisporites* sp.*?* Thomson & Pflug, 1953 (CI-1).

K. *Granulatosporites* sp. Ibrahim, 1933 (CI-1).

L. *Verrucosisporites* sp. Ibrahim, 1933 *emend.* Potonié & Kremp, 1955 (CI-1).

**PLATE 2**

A. *Leptolepidites psarosus* Norris, 1966 (CI-1).

B. *Leptolepidites verrucatus* Couper, 1953 (CI-1).

C-D. *Uvaesporites* sp. Doring, 1965 (CI-1).

E. *Apiculatisporis* sp. Potonié & Kremp, 1954 (CI-1).

F. *Echinatisporis* sp. Krtuzsch, 1959 (CI-1).

G. *Hamulatisporis* sp. Krtuzsch, 1959 (RL-1).

H. *Cicatricosisporites* sp. Potonié & Gelletch, 1933 (EGST-1).

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023




I. *Cicatricosisporites avnimelechi* Horowitz, 1970 (CI-1).

J-K. *Cicatricosisporites brevilaesuratus* Couper, 1958 (EGST-1).

L. *Cicatricosisporites cf. Cicatricosisporites?* sp.5 Duarte, 2011 (EGST-1).

**PLATE 3**

A - B. *Lycopodiumsporites* sp. Thiegart, 1938 (RL-1).

C. *Klukisporites variegatus* Couper, 1958 (CI-1).

D. *Klukisporites* sp. Couper, 1958 (RL-1).

E. *Klukisporites foveolatus* Pocock, 1964 (EGST-1).

F. *Klukisporites pseudoreticulatus* Couper, 1958 (CI-1).

G. *Foveotriletes* sp. Hammen, 1956 (CI-1).

H. *Gleicheniidites Senonicus* Ross, 1949 (PR-1).

I. *Camarozonaesporites* sp. Pant, 1954 *ex.* Pontonié, 1956 *emend.* Klaus, 1960 (VN-1).

J. *Antulsporites sp.* Archangelsky & Gamerro, 1966 (CI-1).

K. *Cingulatisporites verrucatus* Regali, Uesugui & Santos, 1974 (PE-1)

L. *Distaltriangulisporites* sp. Singh, 1971 (RL-1).

M. *Cingutriletes* Pierce, 196 (PR-1).

**PLATE 4**

A. *Matonisporites silvai* Lima, 1978 (PR-1).

B-C. *Appendicisporites* sp. Weiland & Krieger, 1953; (PR-1).

D. *Aequitriradites* sp. Delcourt & Sprumont, 1955 *emend.* Dettmann, 1963 (RL-1).

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023




E. *Perotrilites* sp. Erdtman, 1947 *ex.* Couper, 1953 (RL-1).

F. *Crybelosporites pannuceus* Brenner,1963 *emend.*Srivastava, 1975 (RL-1)

G. *Paludites mameolatus* Lima, 1978 (PR-1).

H. *Densoisporites* sp. Weyland & Krieger, 1953 (EGST-1).

I. *Triporoletes* sp. Mtchedlishvili, 1960 (RL-1).

J. *Reticulosporis* sp. Krutzsch, 1959 (PR-1).

K. *Reticulosporis foveolatus* Krutzsch, 1959 (EGST-1).

L. *Callialasporites trilobatus* Dev, 1961 (CI-1).

**PLATE 5**

A. *Callialasporites dampiere* Dev, 1961 (CI-1).

B. *Complicatisaccus cearensis* Regali, 1989c (PR-1).

C. *Cedripites* sp. Wodehouse, 1933 (CI-1).

D. *Vitreisporites pustulosus* Regali, 1987 (PR-001-MA); (PE-1).

E. *Vitreisporites microsaccus* Jersey, 1964 (PR-1).

F. *Vitreisporites pallidus* Nilsson, 1958 (PR-1).

G. *Rugubivesiculites bahiasulensis* Pierce, 1961 (RL-1).

H. *Inaperturopollenites* sp. (Pflug, 1952 ex. Thomsom e Pflug, 1953, Pontonié, 1958) Pontonié, 1966 (RL-1).

I. *Araucariacites* sp. Cookson, 1947 ex Coouper, 1953 (CI-1).

J. *Araucariacites australis* Cookson, 1947 (CI-1).

K. *Araucariacites limbatus (*Balme) Habib, 1957 (EGST-1).

L. *Araucariacites pergranulatus* Volkheimer, 1968 (EGST-1).

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Climate of the Past
Discussions
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**PLATE 6**

A. *Araucariacites* sp. S. Cl. 265 A Jardiné & Magloire, 1965 (EGST-1).

B. *Balmeopsis* sp.*?* Archangelsky, 1977 (PE-1).

C. *Balmeopsis limbatus* Archangelsky, 1977 (EGST-1).

D. *Cingulatipollenites* sp.*?* Saad & Ghazaly, 1976 (PE-1).

E. *Cingulatipollenites aegyptiaca* Saad & Ghazaly, 1976 (EGST-1)

F. *Spheripollenites* sp. Couper, 1958 (RL-1).

G. *Spheripollenites scabratus* Couper, 1958 (EGST-1).

H. *Sergipea variverrucata* Regali, Uesugui & Santos, 1974 *emend.* Regali, 1987 (PR-1).

I. *Sergipea simplex* Regali, 1987 (PE-1).

J. *Uesuguipollenites callosus* Dino, 1992 (RL-1).

K. *Classopollis classoides* Pflug, 1953 (CI-1).

L. *Classopollis brasiliensis* Herngreen, 1973 (PE-1).

**PLATE 7**

A. *Equisetosporites aff. elegans* Lima, 1978 (CI-1).

B. *Equisetosporites dudarensis* (Deák, 1964) Lima, 1980 (CI-1).

C. *Equisetosporites ambuguus* Hedlund, 1966 (RL-1).

D. *Equisetosporites consinnus* Singh, 1964 (PR-1).

E. *Equisetosporites leptomatus* Lima, 1978 (CI-1).

F. *Equisetosporites luridus* Lima, 1978 (CI-1).

G. *Equisetosporites lanceolatus* Lima, 1978 (CI-1).

H. *Equisetosporites aff. leptomatus* Lima, 1978 (CI-1).

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023




I. *Elateropollenites bicornis* Regali, 1989e (EGST-1).

J. *Elateropollenites dissimilis* Regali, 1989e (EGST-1).

K. *Classopollis intrareticulatus* Volkheimer, 1972 (PR-1).

L. *Equisetosporites aff. luridus* Lima, 1978 (RL-1).

**PLATE 8**

A. *Equisetosporites maculosus* Dino, 1992 (CI-1).

B. *Equisetosporites minuticostatus* Lima, 1978 (PR-1).

C. *Equisetosporites aff. minuticostatus* Lima, 1978 (CI-1).

D. *Equisetosporites ovatus* (Pierce) Singh, 1961 (CI-1).

E. *Gnetaceaepollenites* sp. Thiegart, 1938 (CI-1).

F. *Gnetaceaepollenites consisus* Regali, 1989c (CI-1).

G. *Gnetaceaepollenites jansonii* Pocock, 1964 (CI-1).

H. *Gnetaceaepollenites uesuguii* Lima, 1978 (CI-1).

I. *Gnetaceaepollenites undulatus* Regali, Uesugui & Santos, 1974 (RL-1).

J. *Steevesipollenites* sp. Stover, 1964 (CI-1)..

K. *Singhia sp.* Srivastava, 1968 (PR-1).

L. *Singhia punctata* Lima, 1978 (EGST-1)

**PLATE 9**

A. *Regalipollenites* sp. Lima, 1978 (PR-1).

B. *Eucommiidites* sp. (Erdtman, 1948) Hugues, 1961 (CI-1).

C. *Eucommiidites troedssonii* (Erdtman, 1948) Hugues, 1961 (RL-1).

D. *Arecipites microfovolatus* Ibrahim, 2002 (CI-1)

E. *Cycadopites* sp. Wilson e Webster, 1946 (PE-1).

F. *Dejaxpollenites foveoreticulatus* Dino, 1992 (EGST-1)

G. *Bennettitaepollenites* sp. Thiegart, 1949 (CI-1)

H. *Cavamonocolpites* sp. Lima, 1978 (RL-1).

I. *Cavamonocolpites* sp.1 Dino, 1992 (CI-1) .

J. *Clavatipollenites* sp. Couper, 1958 (EGST-1).

K. *Clavatipollenites huguesi* Couper, 1958 (PE-1).

L. *Stellatopollis* sp. Doyle, Van Campo e Lugardon, 1975 (VN-1).

**PLATE 10**

A. *Retimonocolpites* sp. Pierce, 1961 (PR-1).

B. *Monocolpopollenites sp.* Thomsom & Pflug, 1953 *emend.* Nichols, Ames & Traverse, 1973 (CI-1).

C. *Brenneripollis reticulatus* Júhasz & Góczan, 1985 (PE-1).

D. *Afropollis jardinus* Doyle, Jardiné e Doeren Kamp, 1982 (CI-1).

E. *Afropollis aff. jardinus* Doyle, Jardiné e Doeren Kamp, 1982 (PR-1).

F. *Psiladicolpites papillatus ?* Regali, 1989c (EGST-1).

G. *Tricolpites* sp. Cookson, 1947 *ex* Couper, 1953 (EGST-1).

H. *Rousea* sp. Srivastava, 1969 (PR-1).

I. *Rousea georgensis* (Brenner, 1963) Dettmann, 1973 (PR-1).

J. *Trisectoris reticulatus* (Regali, Uesugui & Santos, 1974b) Heimhofer & Hochuli, 2010 (EGST-1).

K. *Retiquadricolpites* sp. Regali, 1989 (CI-1).

L. *Exesipollenites tumulus* Balme, 1957 (PR-1).

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Preprint. Discussion started: 5 May 2023


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**PLATE 11**

A. *Cretacaeiporites* sp.*?* Herngreen, 1973 (RL-1).

B. *Schizosporis* sp. Cookson e Dettmann, 1959 (PE-1).

C. *Schizosporis parvus* Cookson e Dettmann, 1959 (RL-1).

D. *Schizosporis spriggi* Cookson e Dettmann, 1959 (EGST-1).

E. Acritarch Evitt 1963 (CI-1).

F. *Cymatiosphera ?* Wetzel, 1933 (CI-1).

G. *Duvernaysphaera sp.* (Staplin, 1961) Deunff, 1964 (CI-1).

H. *Maranhites* sp. Brito, 1965 *emend*. González, 2009 (CI-1).

I. *Tasmanites* sp. Newton, 1875 *emend*. Schopf, Wilson & Bentall, 1944 (CI-1).

J. *Scylaspora* sp. Burgess & Richardson, 1995 (EGST-1).

K. *Raistrickia* sp.? Schopf *etal.*1944 *emend.* Potonié & Kremp, 1954 (VN-1).

L. *Chomotriletes* sp. Naumova, 1937 (VN-1).

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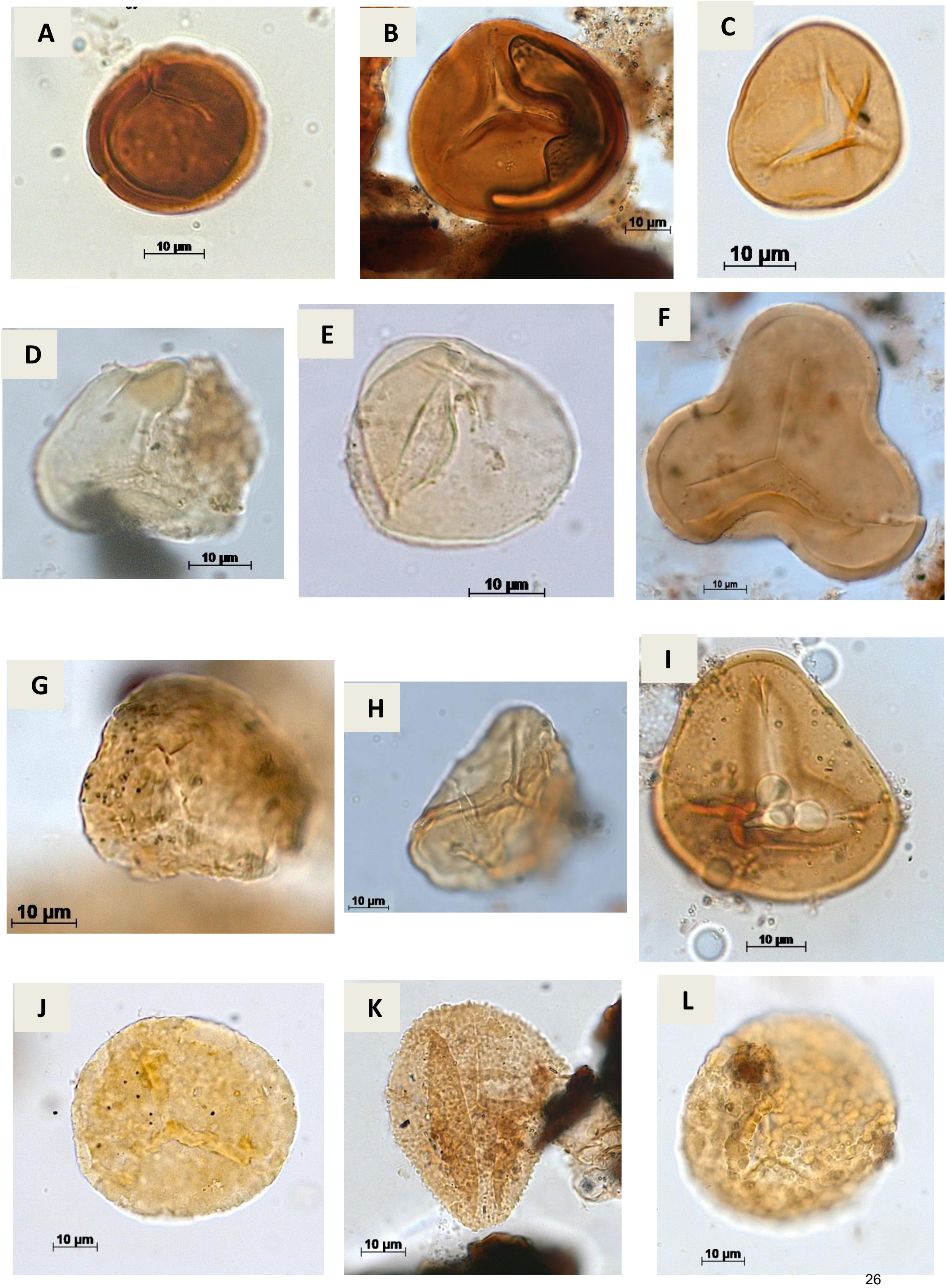
Preprint. Discussion started: 5 May 2023


PLATE 1



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Climate of the Past
Discussions

PLATE 2

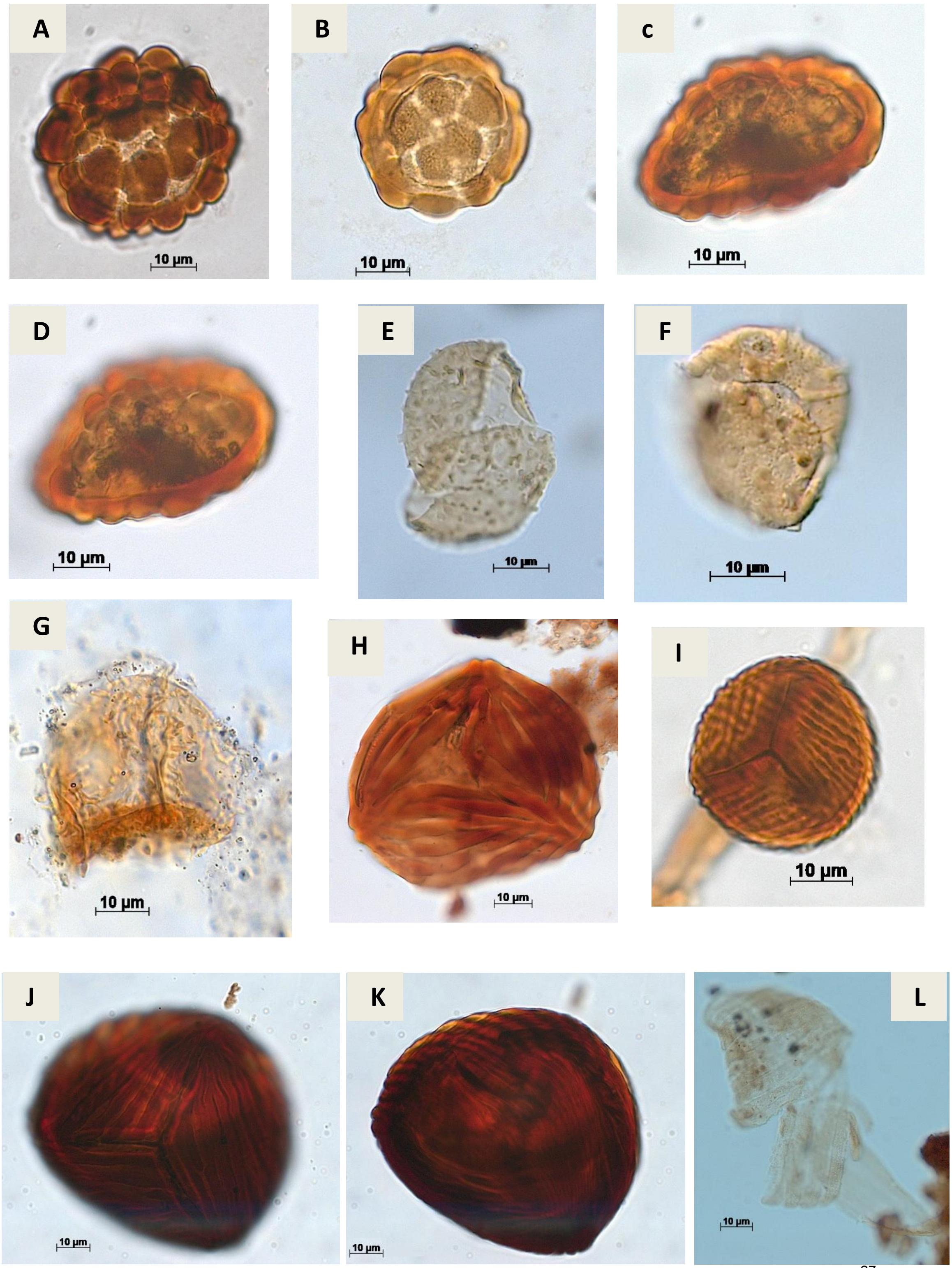

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**PLATE 3**

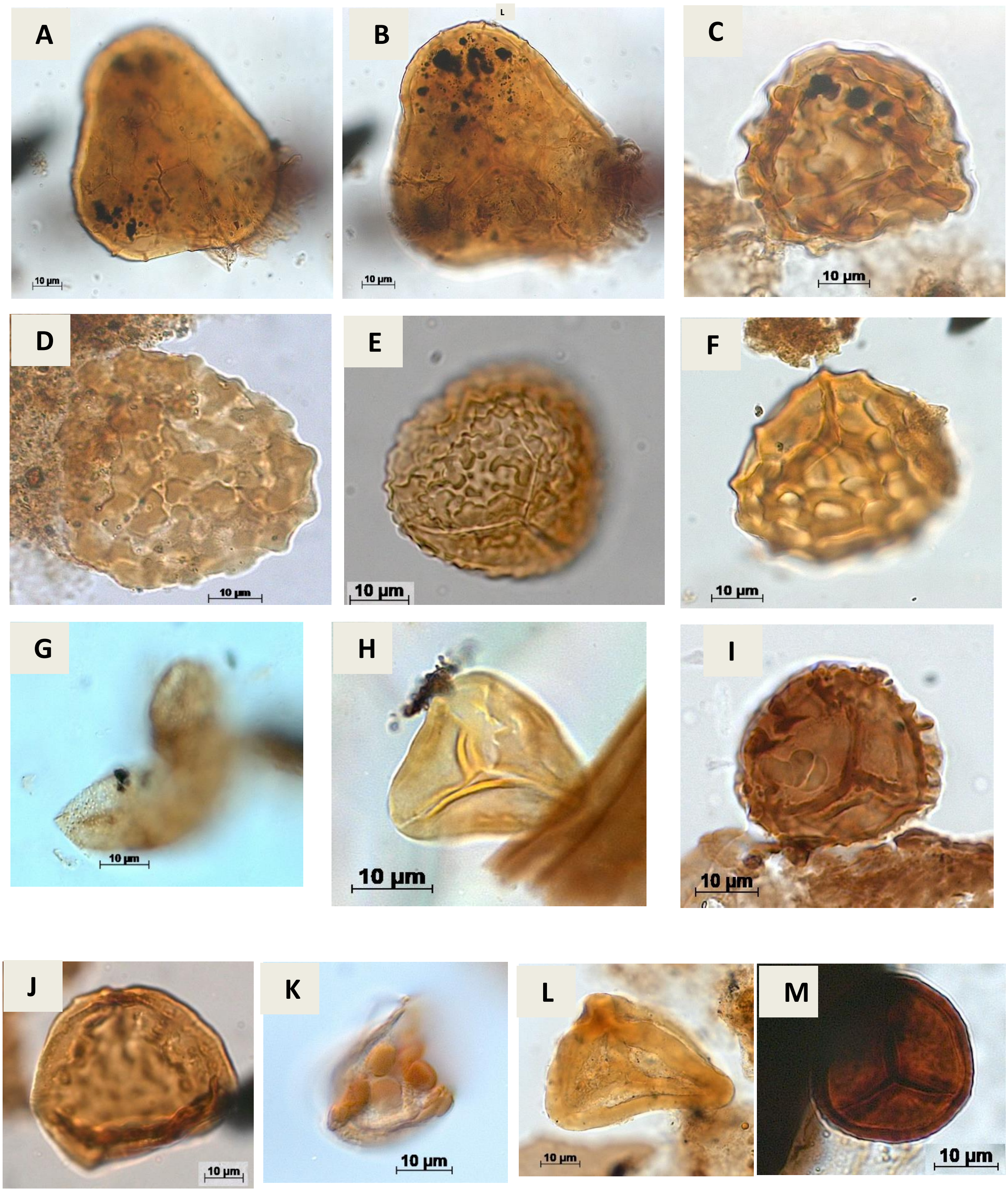

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PLATE 4

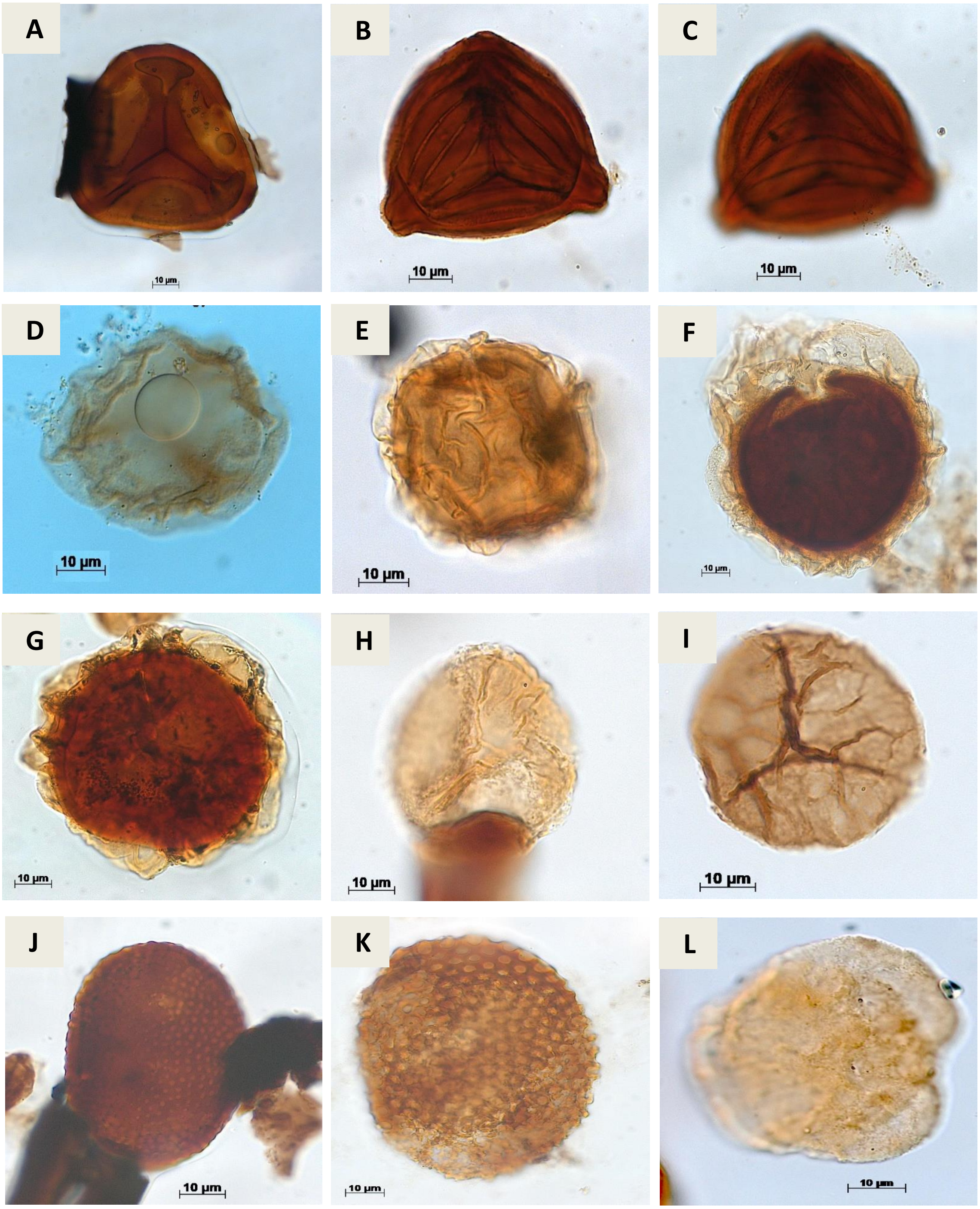

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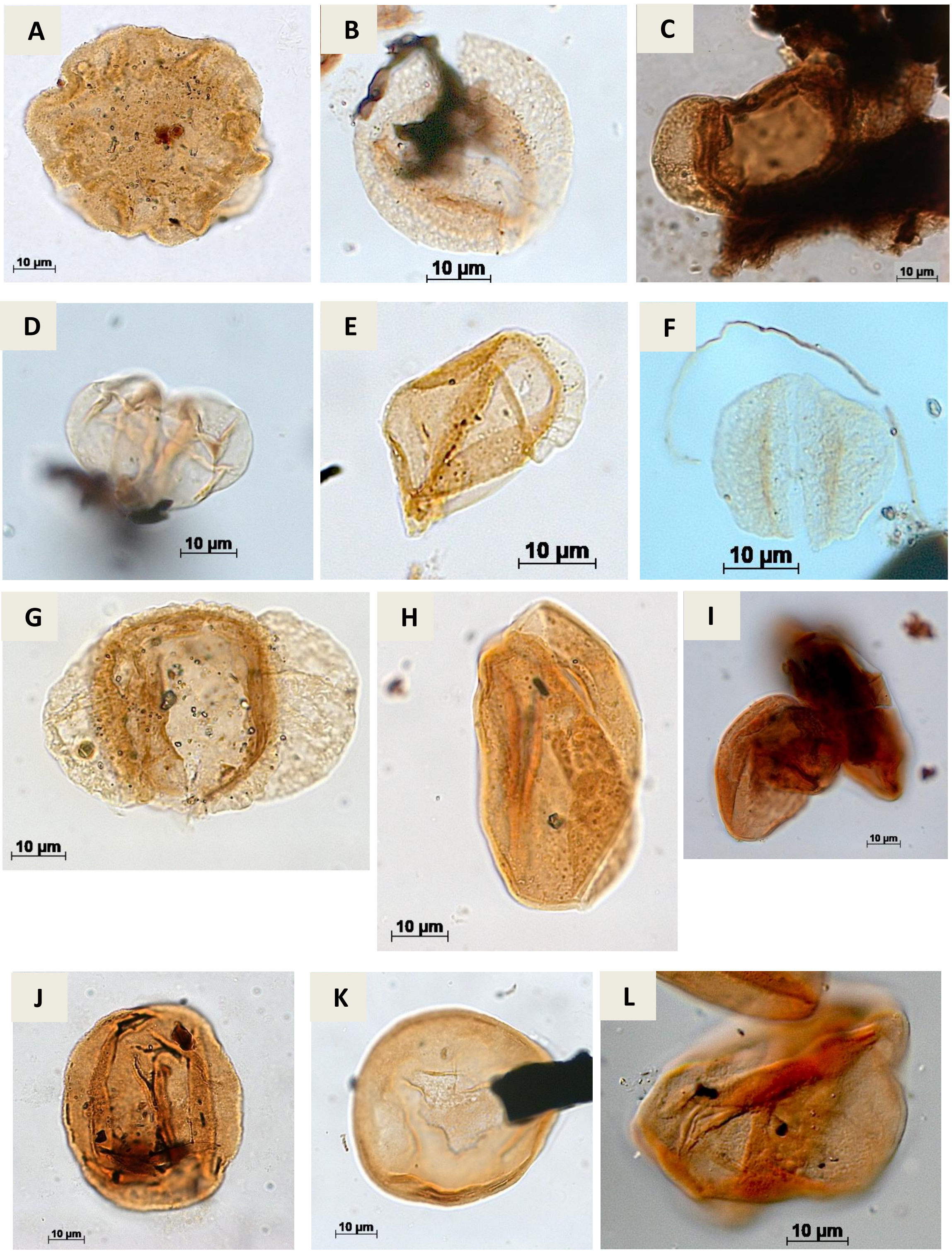
**PLATE 5**



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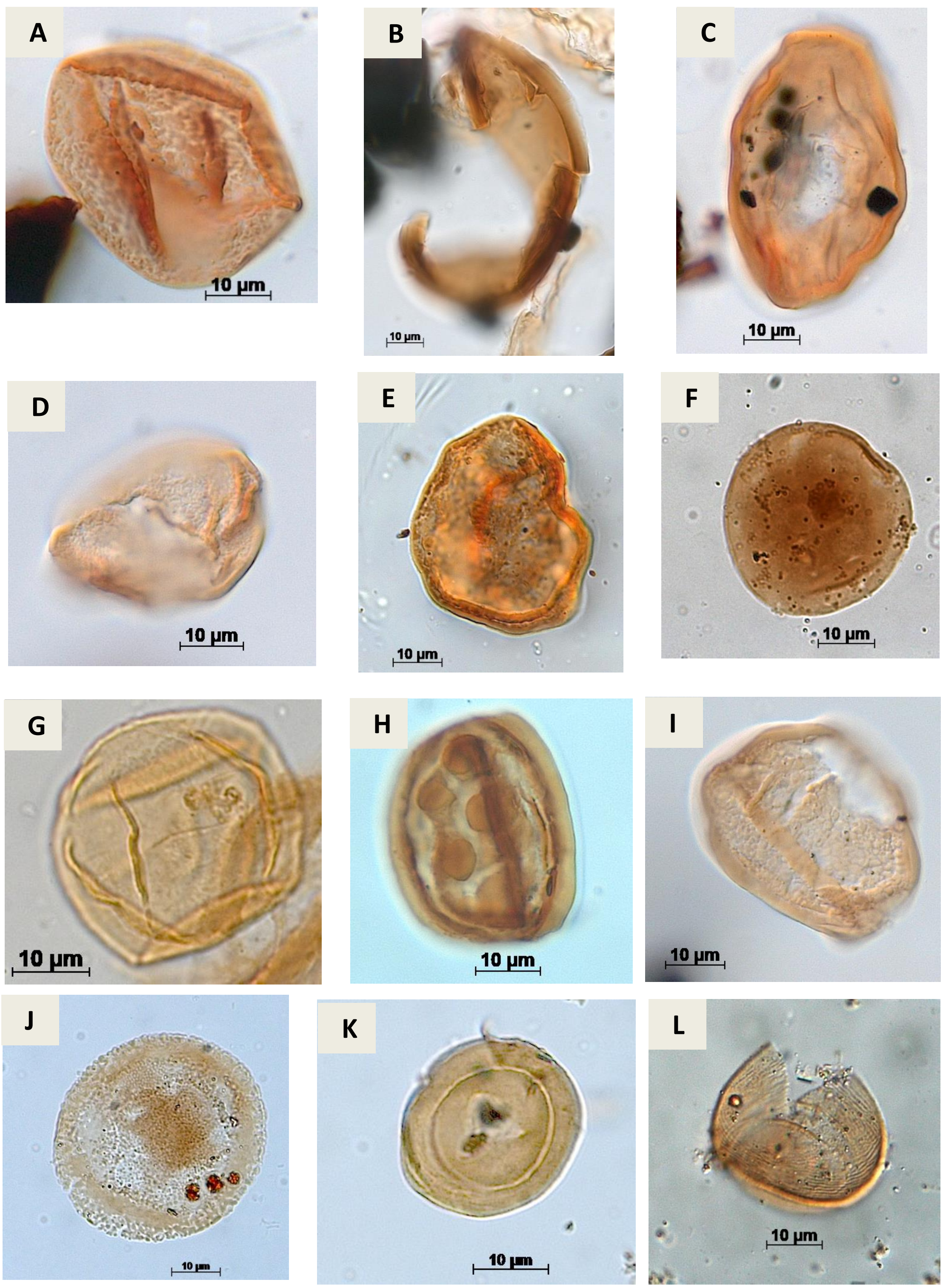
Preprint. Discussion started: 5 May 2023




**PLATE 6**



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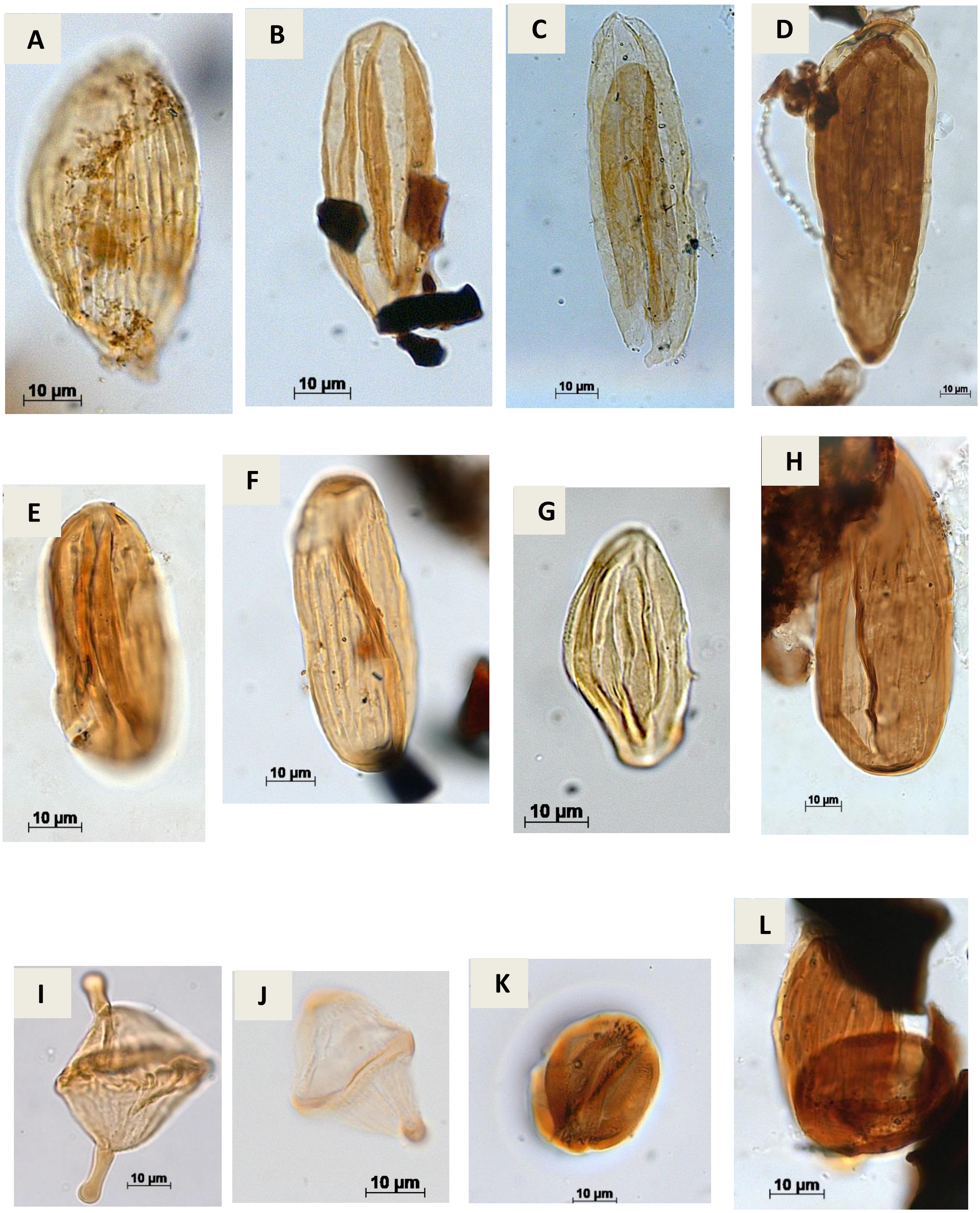
Preprint. Discussion started: 5 May 2023

Climate of the Past
Discussions

PLATE 7



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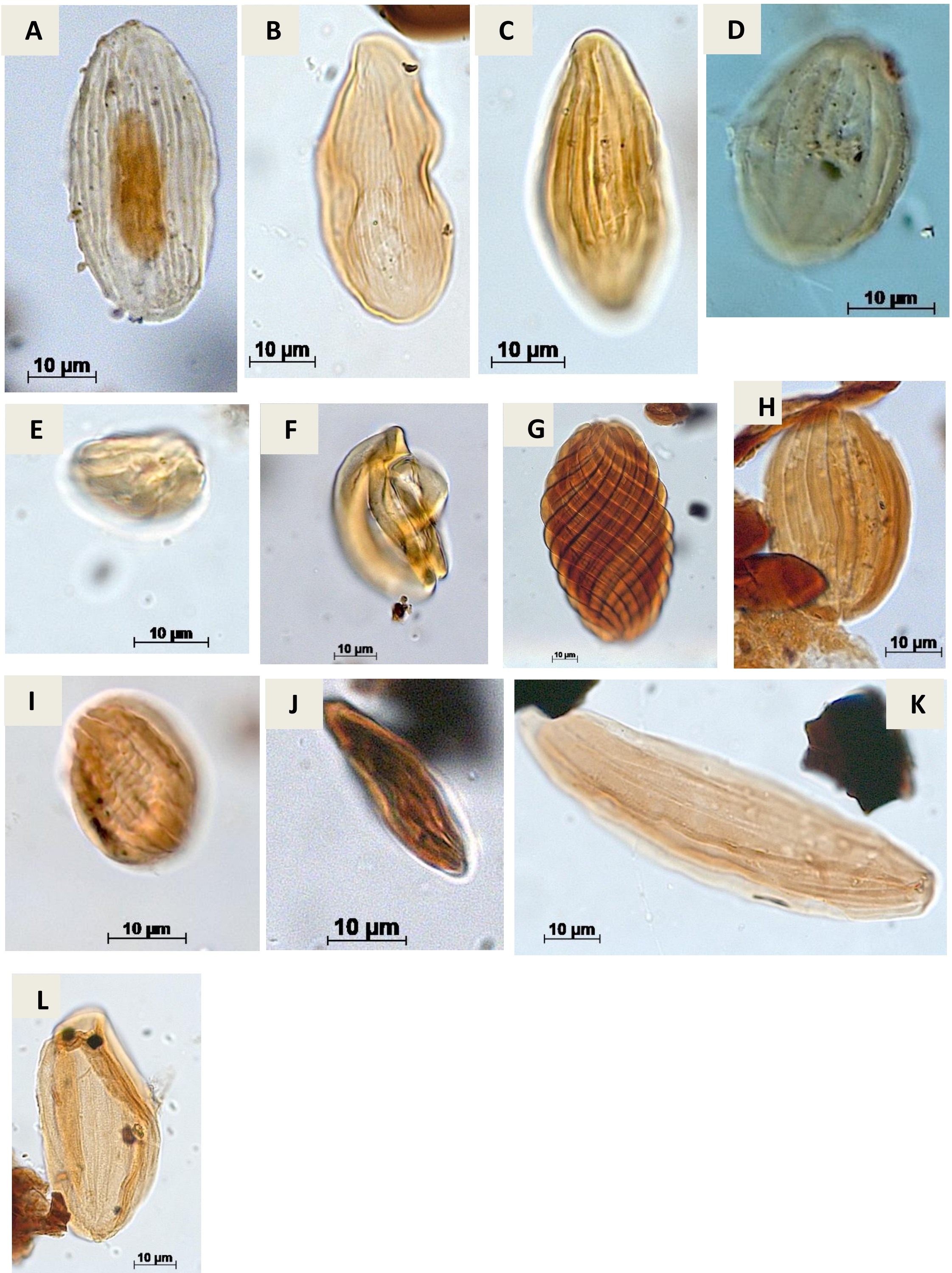
Preprint. Discussion started: 5 May 2023

Climate of the Past
Discussions

**PLATE 8**



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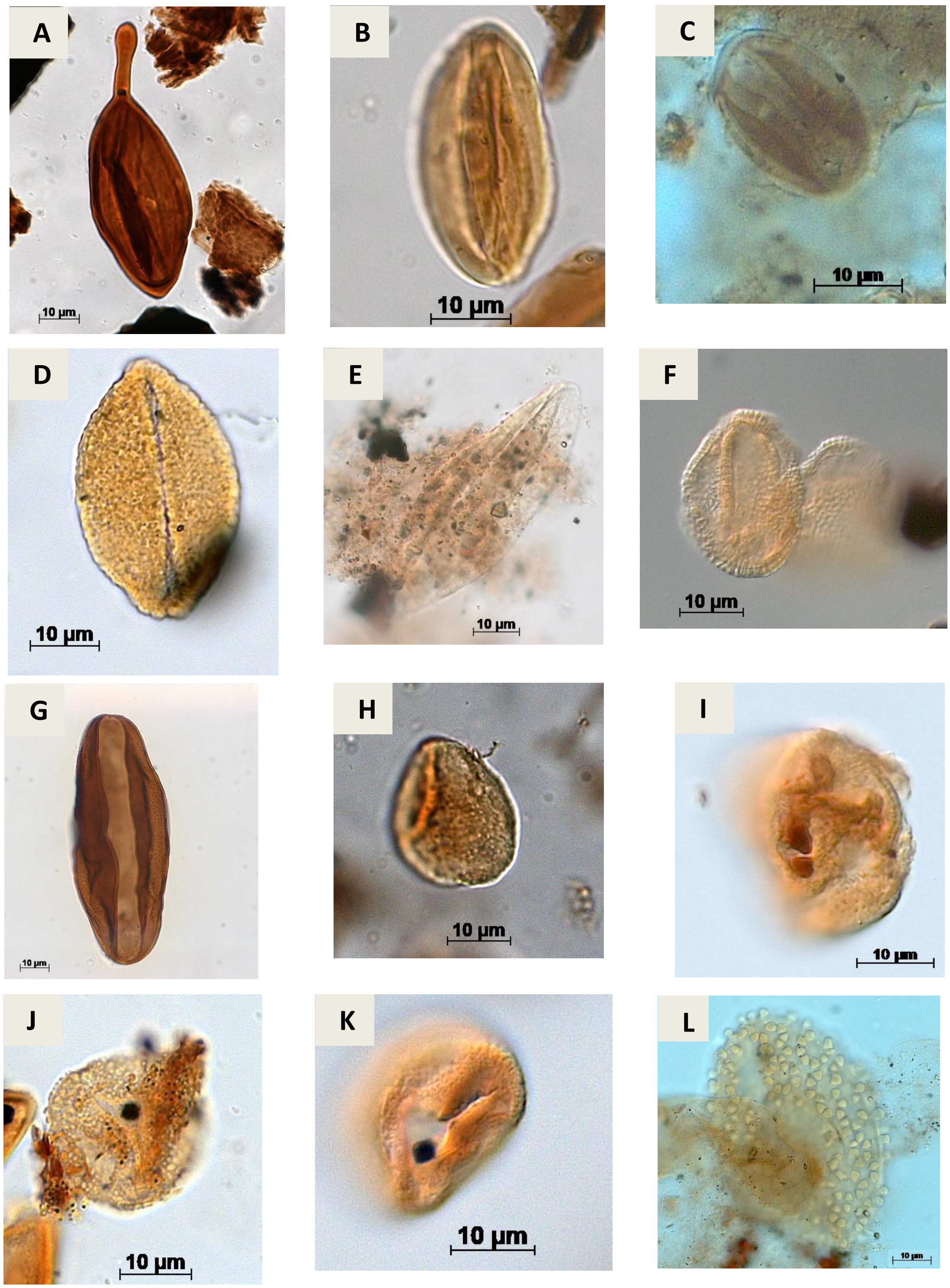
Preprint. Discussion started: 5 May 2023


Climate of the Past
Discussions

PLATE 9



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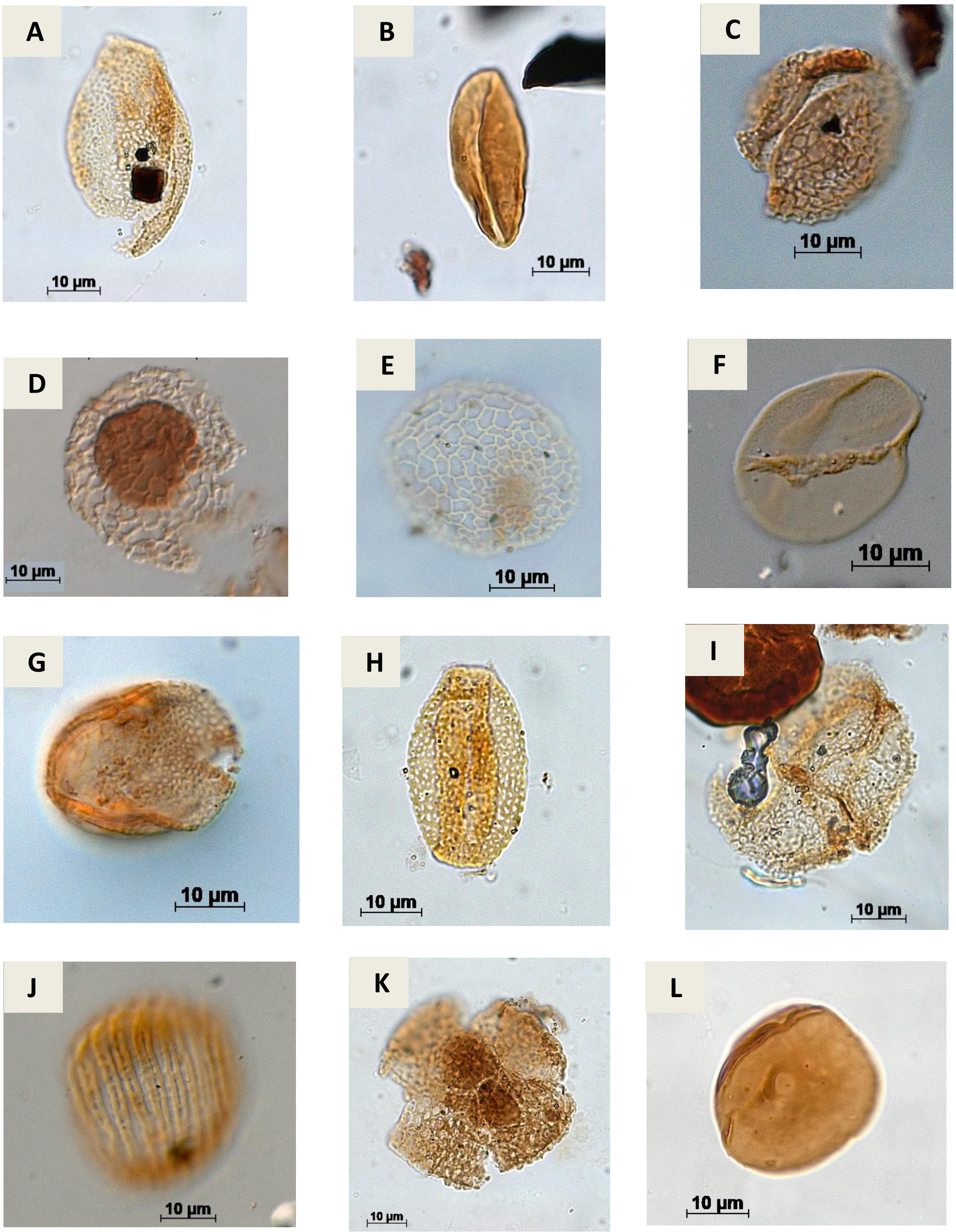
Preprint. Discussion started: 5 May 2023

Climate of the Past
Discussions

PLATE 10



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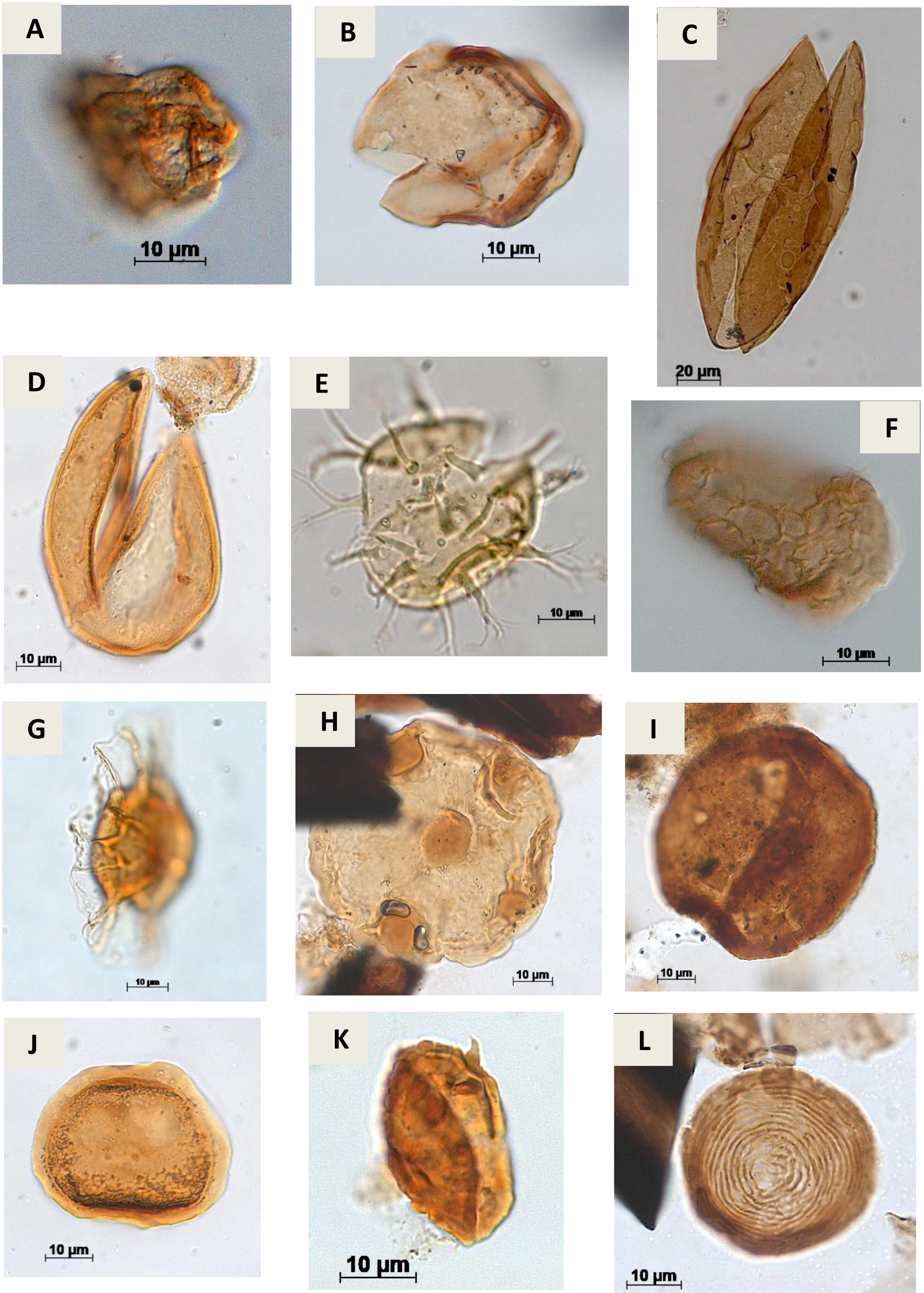
Climate of the Past
Discussions

**PLATE 11**



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Preprint. Discussion started: 5 May 2023




Appendix 2. Bioclimatic groups (percentages) of studied wells. Legend: HG= hygrophytes; HD= hydrophytes; TLF= tropical lowland flora; UF= upland flora; XP= xerophytes; H'= diversity; Fs/X= fern spores/xerophytes.

| Lithostratigraphy | Sections | Depth (m) | HG | HD | TLF | UF | XP | H' | Fs/X | Marine |
|---|---|---|---|---|---|---|---|---|---|---|
| Codó Formation | PR-1 | 1507,6 | 15,7 | 1,5 | 31,0 | 14,2 | 37,6 | 2,26 | 0,31 | 0 |
| | | 1509,7 | 19,6 | 0,5 | 8,2 | 29,4 | 42,3 | 2,19 | 0,32 | 0 |
| | | 1510,6 | 15,4 | 0,0 | 22,0 | 15,4 | 47,3 | 1,88 | 0,25 | 0 |
| | | 1513,1 | 6,6 | 2,0 | 20,2 | 13,1 | 58,1 | 2,04 | 0,13 | 0 |
| | PE-1 | 1562,0 | 44,4 | 0,0 | 8,7 | 33,2 | 13,8 | 2,59 | 0,76 | 0 |
| | | 1566,0 | 14,4 | 0,6 | 2,2 | 30,0 | 52,8 | 2,21 | 0,22 | 0 |
| | | 1568,5 | 4,2 | 0,0 | 20,8 | 16,7 | 58,3 | 1,99 | 0,07 | 0 |
| | | 1570,0 | 4,1 | 0,0 | 2,4 | 24,1 | 69,4 | 1,90 | 0,06 | 0 |
| | RL-1 | 1173,5 | 1,6 | 0,0 | 23,8 | 6,3 | 68,3 | 2,22 | 0,02 | 0 |
| | | 1174,1 | 12,0 | 4,0 | 10,0 | 12,0 | 62,0 | 2,06 | 0,21 | 0 |
| | | 1175,5 | 20,0 | 0,0 | 14,5 | 1,8 | 63,6 | 2,63 | 0,24 | 0 |
| | | 1235,25 | 18,8 | 1,6 | 10,2 | 7,8 | 61,7 | 2,57 | 0,25 | 1 |
| | | 1237,0 | 19,8 | 0,0 | 4,9 | 14,2 | 61,1 | 2,61 | 0,24 | 0 |
| | | 1239,5 | 27,0 | 1,6 | 6,3 | 6,3 | 58,7 | 1,85 | 0,33 | 0 |
| | | 1240,3 | 11,2 | 0,5 | 13,8 | 5,9 | 68,6 | 1,91 | 0,15 | 0 |
| | CI-1 | 820,6 | 6,5 | 0,0 | 15,7 | 0,0 | 77,8 | 1,78 | 0,08 | 0 |
| | | 834,5 | 3,7 | 0,0 | 3,7 | 0,0 | 92,6 | 1,30 | 0,04 | 0 |
| | | 836,0 | 0,0 | 0,0 | 0,0 | 10,2 | 89,8 | 1,66 | 0,00 | 0 |
| | | 837,0 | 14,7 | 2,7 | 6,0 | 48,9 | 27,7 | 2,28 | 0,18 | 0 |
| | | 838,0 | 15,8 | 0,0 | 1,5 | 9,8 | 72,9 | 1,74 | 0,06 | 0 |
| | | 845,0 | 4,8 | 0,0 | 1,4 | 23,3 | 70,5 | 2,07 | 0,33 | 0 |
| | | 855,0 | 5,2 | 0,0 | 5,2 | 5,2 | 84,5 | 1,10 | 0,13 | 0 |
| | | 855,9 | 10,8 | 0,6 | 10,1 | 3,8 | 74,7 | 2,11 | 0,38 | 0 |
| | | 857,6 | 21,6 | 2,6 | 4,2 | 31,6 | 40,0 | 2,64 | 0,10 | 1 |
| | | 866,55 | 8,6 | 0,5 | 5,6 | 6,6 | 78,8 | 2,27 | 0,25 | 1 |
| | | 866,65 | 16,9 | 1,6 | 4,4 | 21,3 | 55,7 | 2,26 | 0,21 | 0 |
| | | 867,8 | 16,0 | 0,0 | 16,6 | 7,1 | 60,4 | 2,83 | 0,39 | 0 |
| | | 888,75 | 19,3 | 0,0 | 12,9 | 22,9 | 45,0 | 2,28 | 0,30 | 0 |
| Bragança Formation | VN-1 | 1287,9 | 55,0 | 0,0 | 0,0 | 5,0 | 40,0 | 1,56 | 0,58 | 0 |
| | | 1289,88 | 18,4 | 0,0 | 5,3 | 18,4 | 57,9 | 1,94 | 0,24 | 0 |
| | | 1315,7 | 6,7 | 0,6 | 1,2 | 15,3 | 76,1 | 1,57 | 0,09 | 0 |
| | | 1317,69 | 33,3 | 0,0 | 0,0 | 0,0 | 66,7 | 1,29 | 0,33 | 0 |
| | EGST-1 | 676,44 | 19,2 | 0,5 | 14,8 | 54,4 | 11,0 | 2,54 | 0,64 | 0 |
| | | 732,3 | 30,1 | 2,4 | 3,0 | 8,4 | 56,0 | 2,65 | 0,37 | 0 |
| | | 733,3 | 8,1 | 0,0 | 4,3 | 7,6 | 80,0 | 1,48 | 0,09 | 0 |
| | | 735,3 | 13,7 | 3,0 | 0,5 | 12,2 | 70,6 | 1,97 | 0,19 | 0 |
| | | 1017,7 | 25,6 | 1,2 | 0,6 | 22,6 | 50,0 | 2,42 | 0,35 | 0 |
| | | 1789,1 | 19,0 | 0,0 | 1,7 | 6,3 | 73,0 | 1,83 | 0,21 | 0 |
| | | 1791,0 | 26,7 | 0,0 | 4,4 | 6,7 | 62,2 | 1,92 | 0,30 | 0 |
| | | 1846,0 | 57,1 | 0,0 | 14,3 | 14,3 | 14,3 | 1,95 | 0,80 | 0 |

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Preprint. Discussion started: 5 May 2023




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**Data availability**

The data and code used in this paper are deposited at CENPES, PETROBRAS, Rio de Janeiro, RJ, Brazil (wells VN-1, EGST-1, RL-1, PE-1, CI-1, and PR-1). Additional information on samples (wells VN-1, EGST-1, RL-1, PE-1, CI-1 and PR-1) can be accessed in www.anp.gov.br.

**Author contributions**

M.C.S.G and M.A.C. led the writing with contributions of all coauthors; M.C.S.G., C.C.L, G.S., N.P.S. and G.C.C. collected the palynological data and M.C.S.G. and M.A.C. carried out the pollen data analysis.

**Competing interests**

The authors declare no competing interests.

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Preprint. Discussion started: 5 May 2023


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Preprint. Discussion started: 5 May 2023


Climate of the Past
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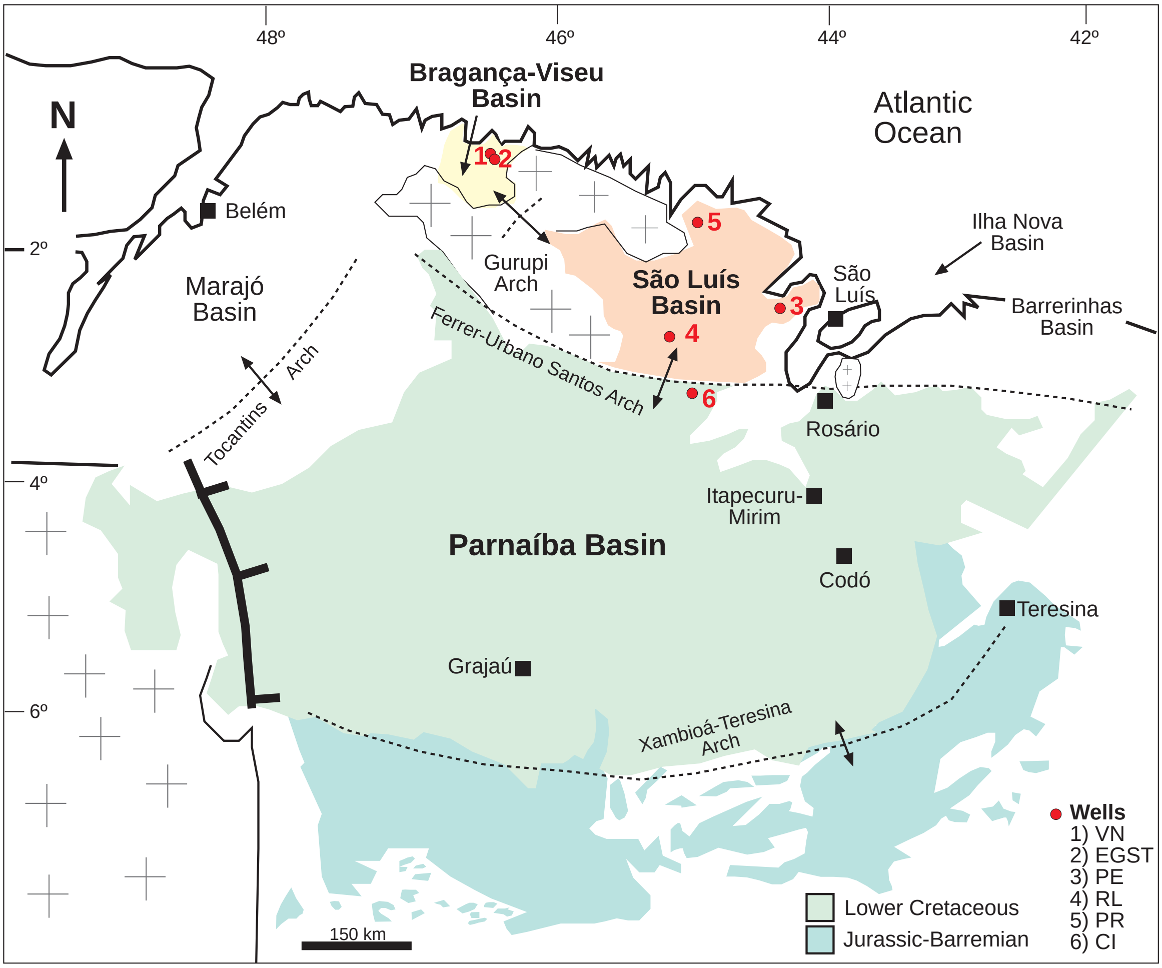


Figure 1. Location of sedimentary basins showing the sites of stratigraphic sections.

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023


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Discussions
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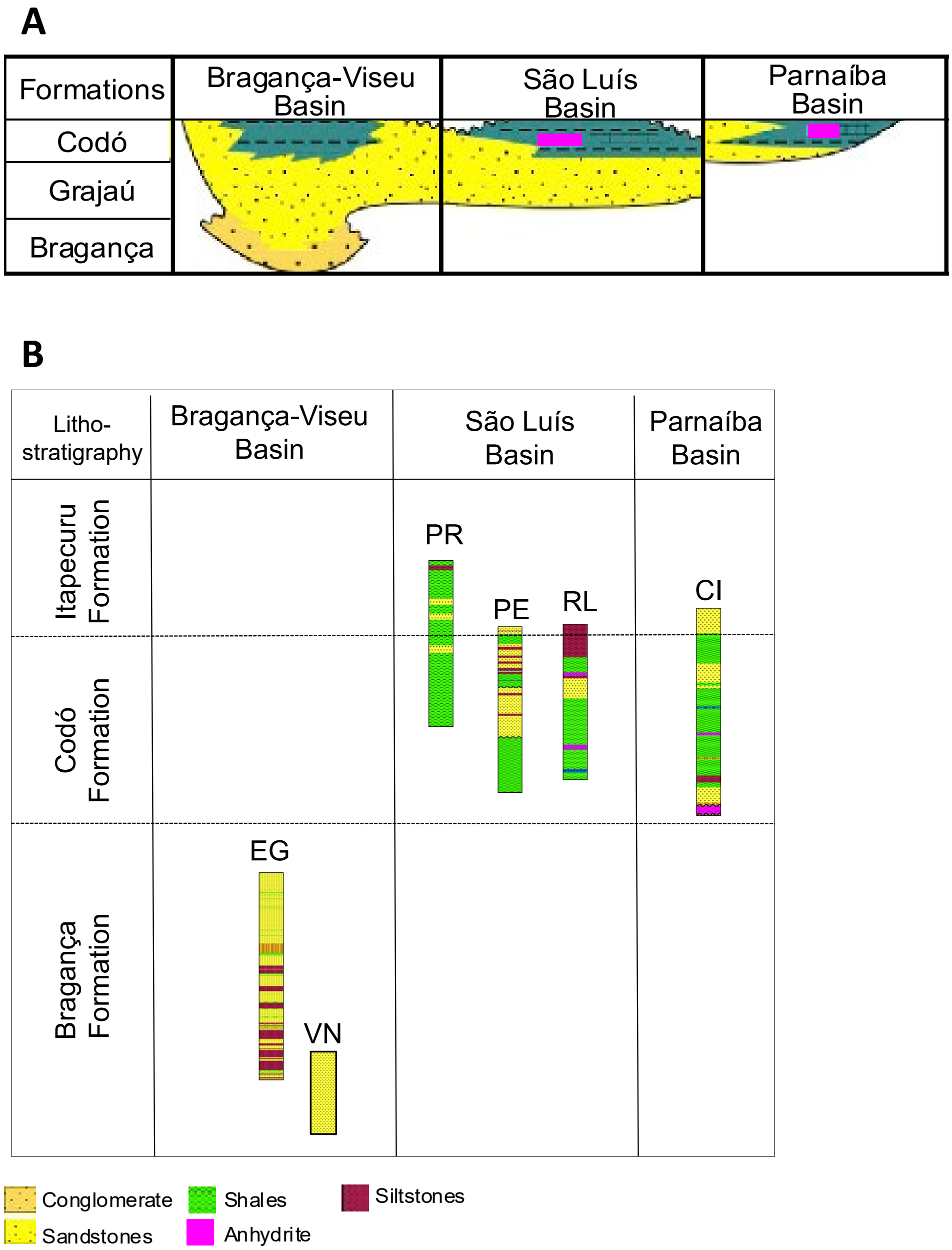


Figure 2. A) Correlation of lithostratigraphic data of the studied basins and; B) the studied wells.

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Preprint. Discussion started: 5 May 2023


Climate of the Past
Discussions

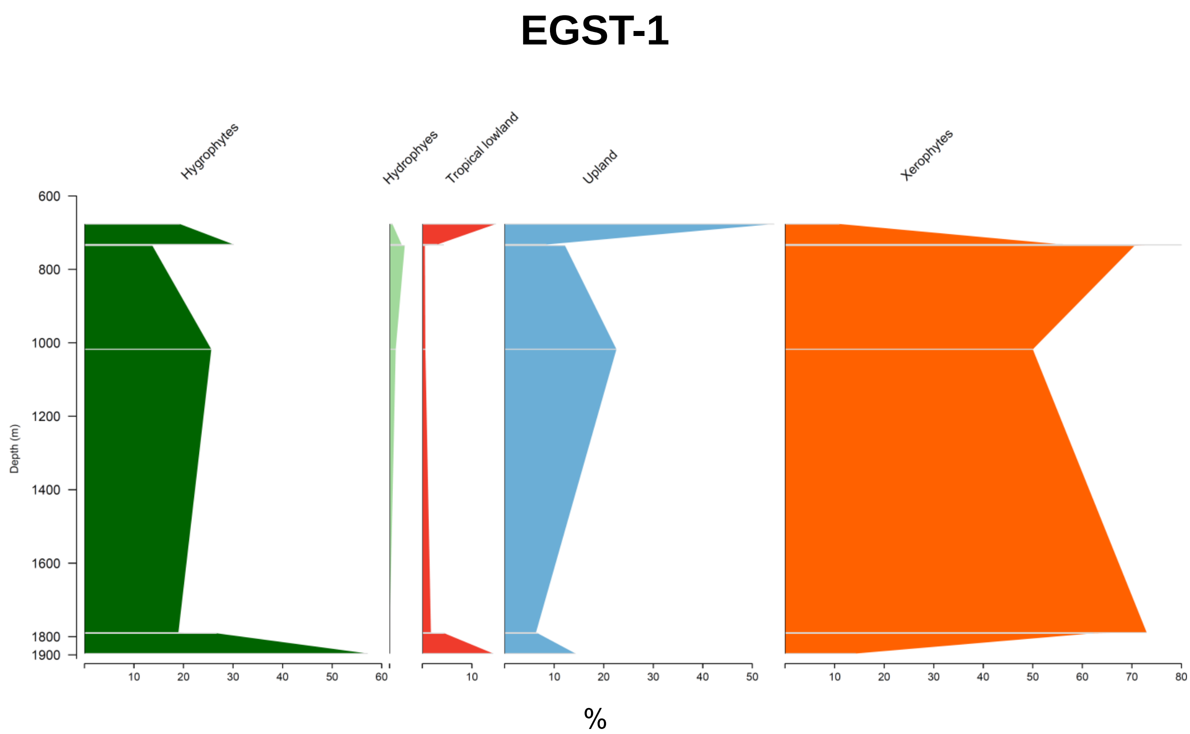


Figure 3. Stratigraphic distribution of bioclimatic groups of well EGST-1 (Bragança-Viseu Basin).

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Preprint. Discussion started: 5 May 2023


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Discussions
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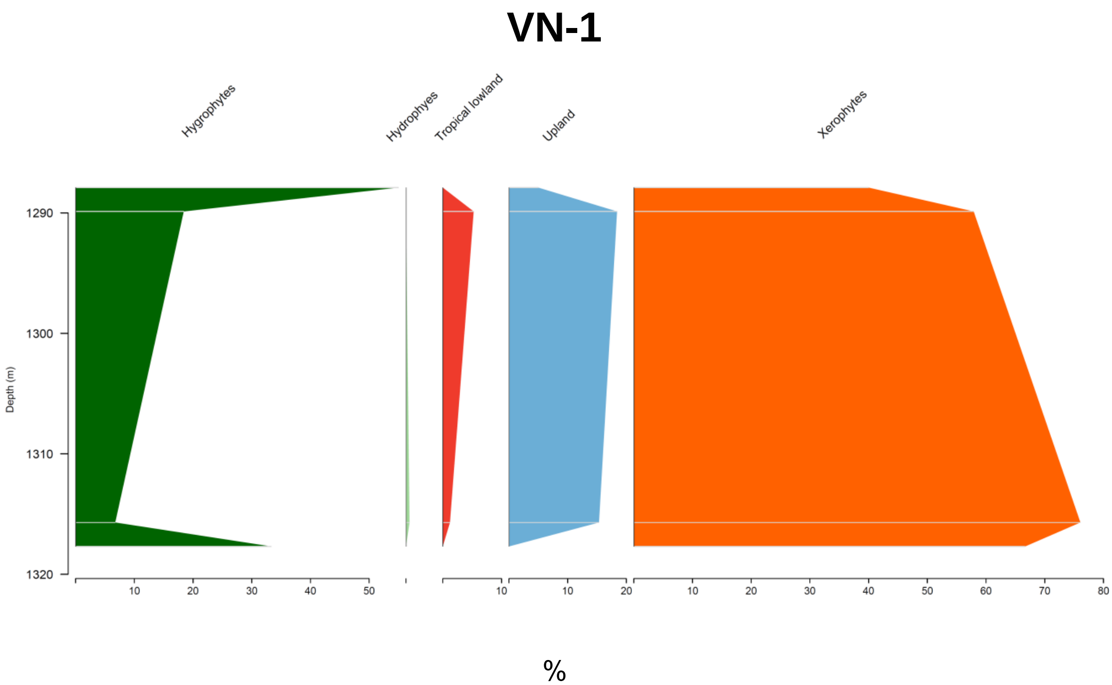


Figure 4. Stratigraphic distribution of bioclimatic groups of well VN-1 (Bragança-Viseu Basin).

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Preprint. Discussion started: 5 May 2023


Climate of the Past
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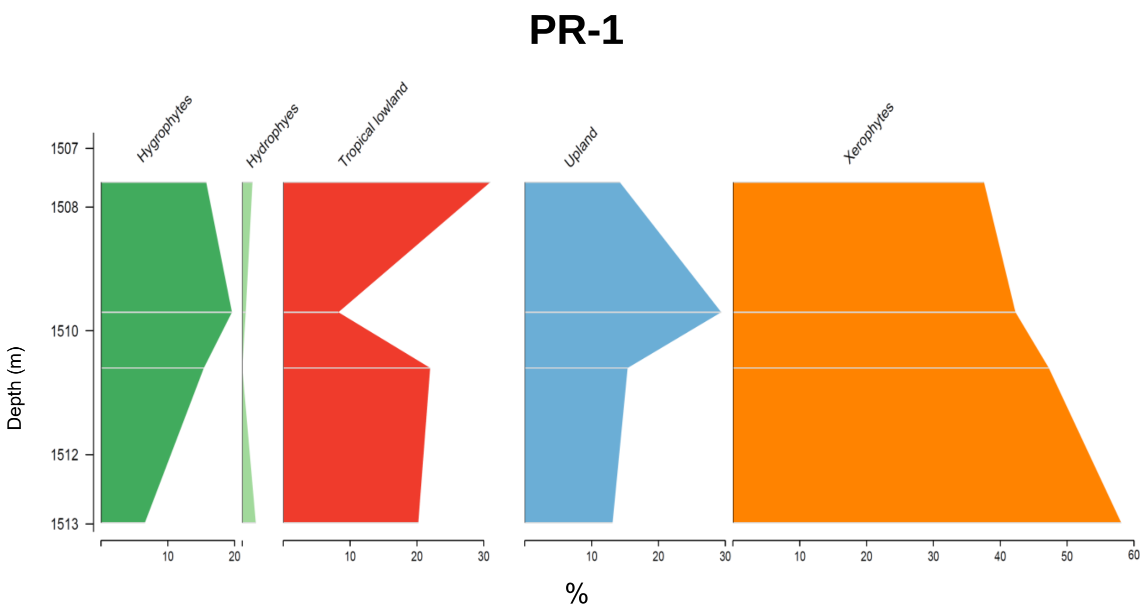


Figure 5. Stratigraphic distribution of bioclimatic groups of well PR-1 (São Luís Basin).

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Preprint. Discussion started: 5 May 2023


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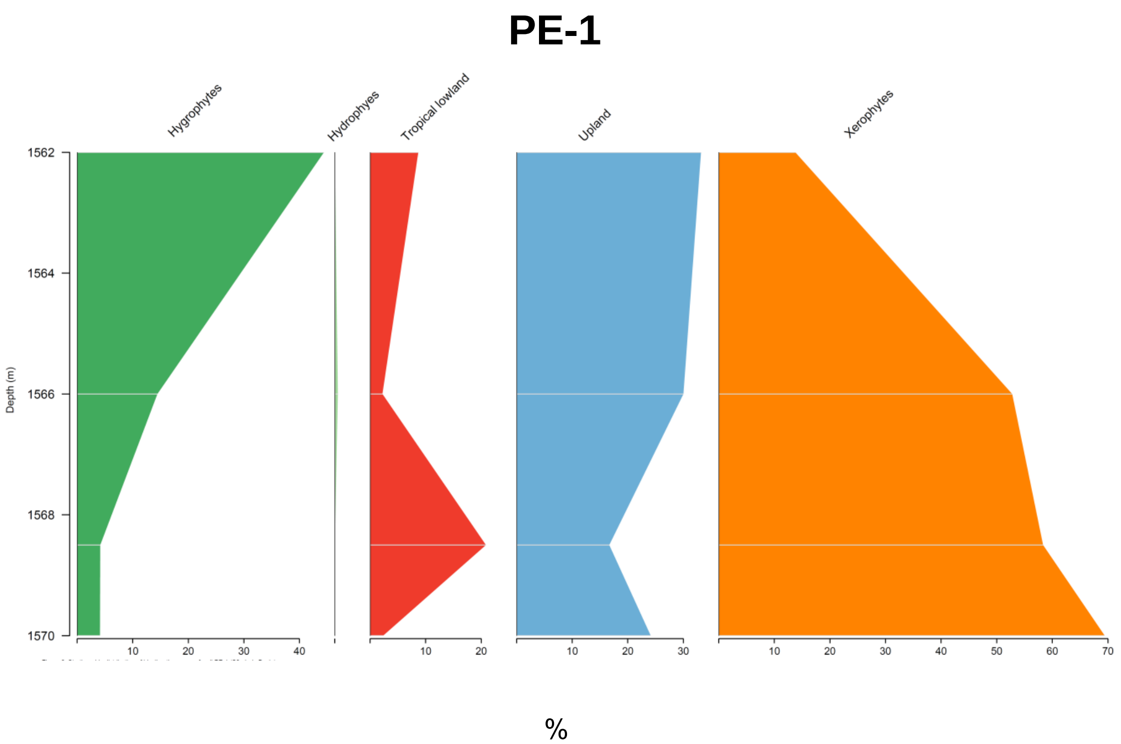


Figure 6. Stratigraphic distribution of bioclimatic groups of well PE-1 (São Luís Basin).

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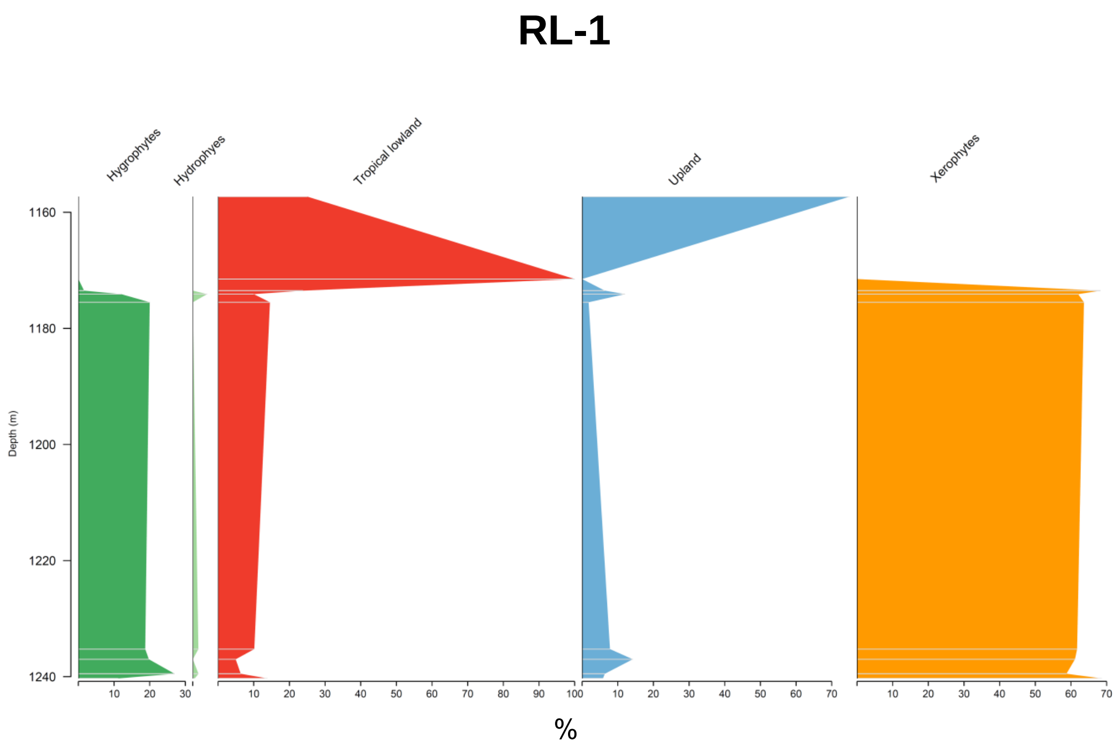


Figure 7. Stratigraphic distribution of bioclimatic groups of well RL-1 (São Luís Basin).

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Preprint. Discussion started: 5 May 2023

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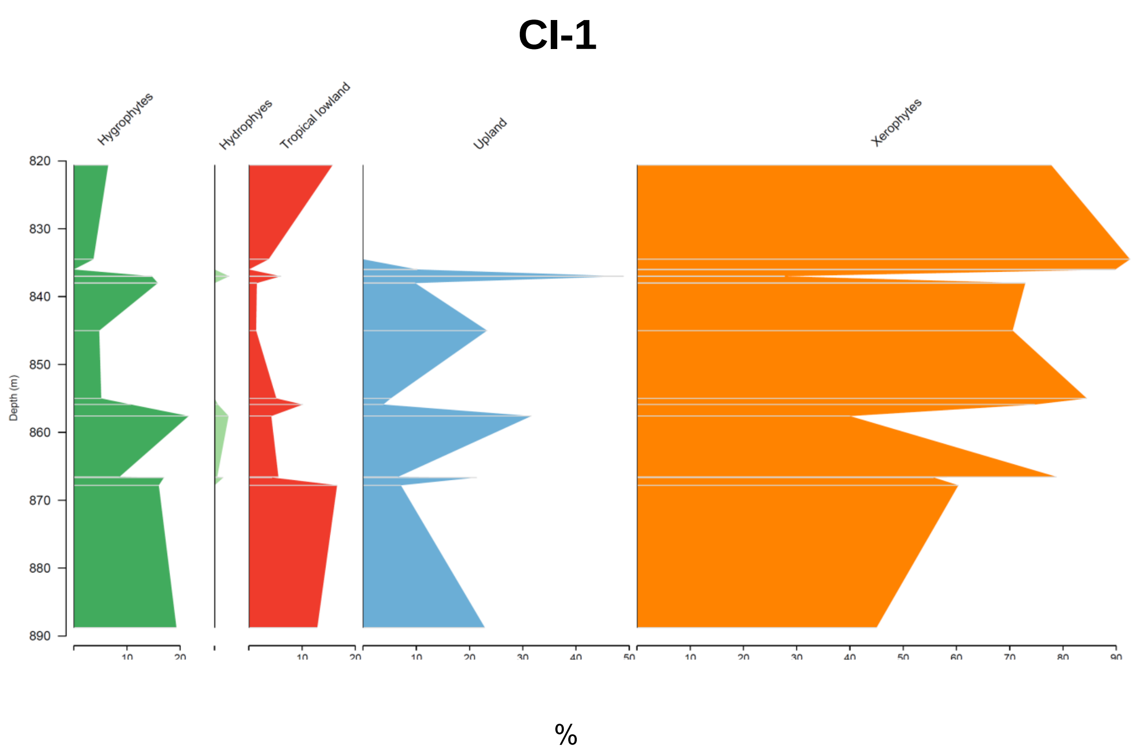


Figure 8. Stratigraphic distribution of bioclimatic groups of well CI-1 (Parnaíba Basin).

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Preprint. Discussion started: 5 May 2023


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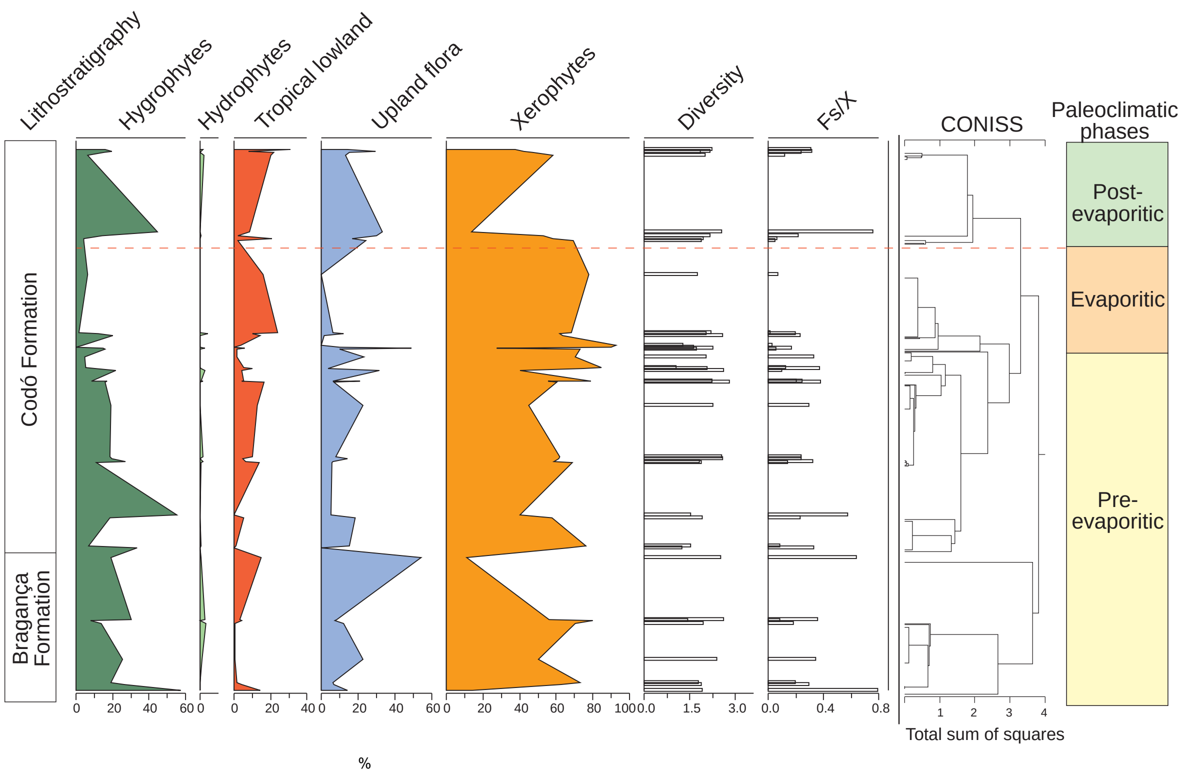


Figure 9. Composite profile showing the stratigraphic distribution of bioclimatic groups, diversity, Fs/X against the paleoclimatic phases. Agglomerative, hierarchical clustering and stratigraphically constrained dendrogram (CONISS) showing the main break (dashed red line).

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023


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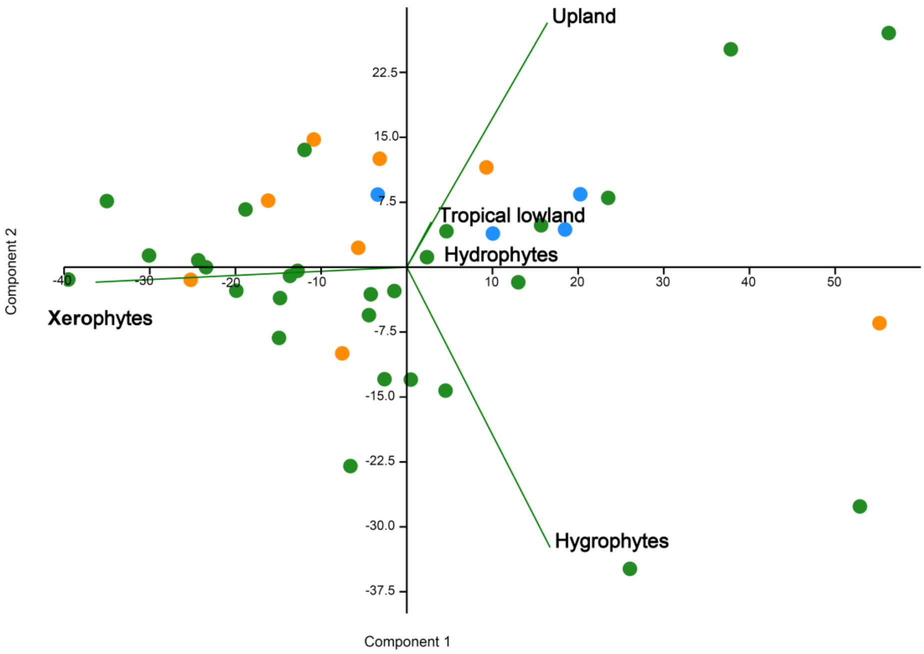


Figure 10. Principal component plot of bioclimatic groups for the pre-evaporitic phase (green dots, N = 28), evaporitic phase (orange dots, N = 8), and post-evaporitic phase (blue dots, N =4).

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023



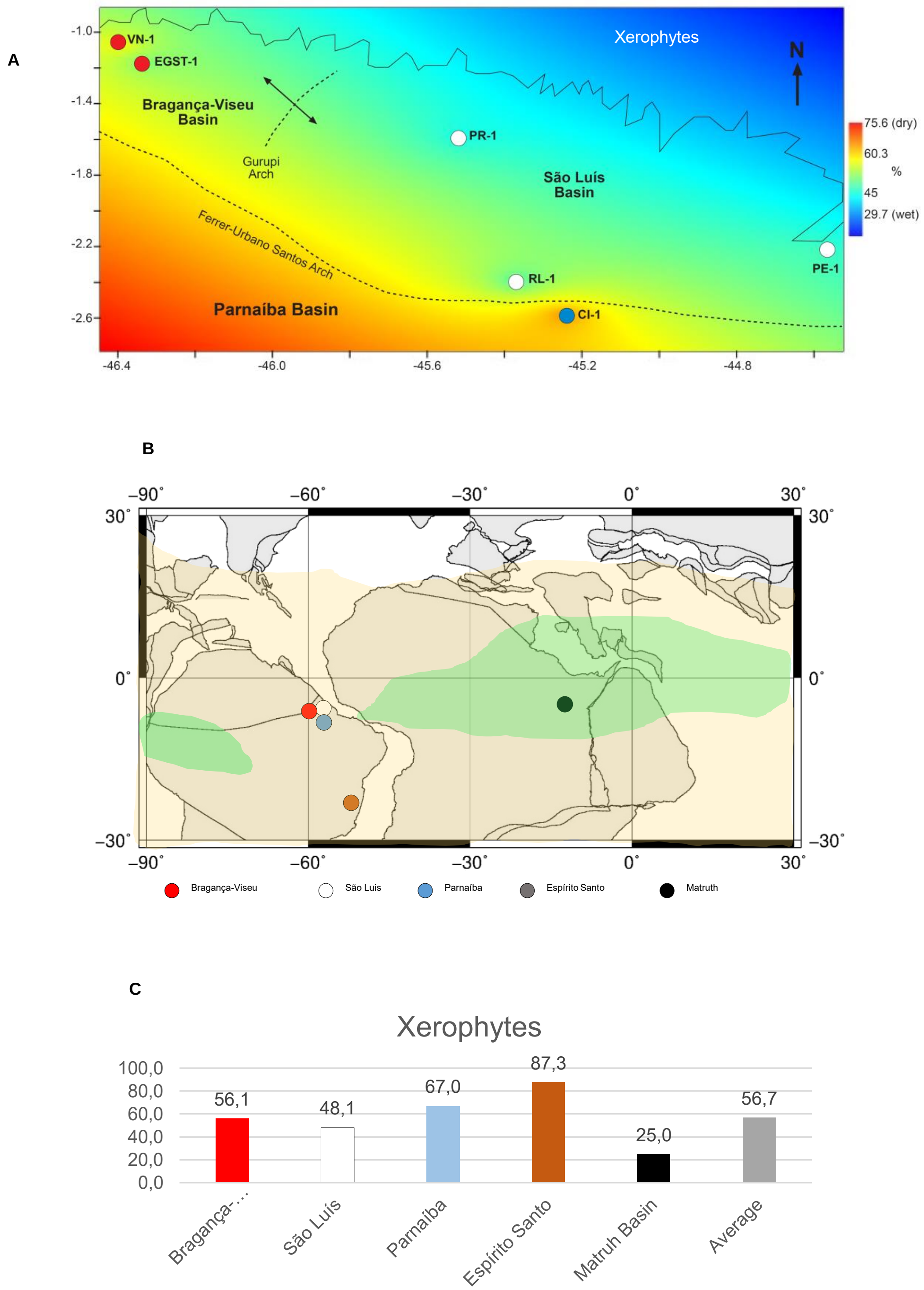


Figure 11. A) Late Aptian latitudinal distribution of the xerophyte bioclimatic group. B) Paleoclimatic belts of the late Aptian in South America (climatic belts modified from Scotese, 2016). Reconstruction map at 116 Ma modified from ODSN Plate Tectonic Reconstruction Service. C) Comparison of the bioclimatic group Xerophytes by basin. Data from the Mathru Basin (Dahab Formation) from Deaf et al. (2020).

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Preprint. Discussion started: 5 May 2023


Climate of the Past
Discussions
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Table 1. Localities, lithostratigraphy of the studied sections and lithologies of studied interval.

| Wells | Basins | Lithostratigraphy (Formation) | Interval (m) | Lat (S) | Long (W) | No. total core samples | Lithology of the studied interval |
|---|---|---|---|---|---|---|---|
| EGST-1 | Bragança-Vizeu | Bragança Fm. | 676-1872.1 | -01:17:55.229 | -46:34:55.683 | 8 | Sandstones, siltstones, conglomerates. |
| VN-1 | Bragança-Vizeu | Bragança Fm. | 1287.6-1317.69 | -01:06:48.216 | -46:40:35.673 | 4 | Sandstones. |
| PE-1 | São Luís | Codó Fm. | 1562-1776.8 | -02:22:09.725 | -44:57:28.505 | 4 | Sandstones, siltstones, calcarenites. |
| RL-1 | São Luís | Codó Fm. | 1157.3-1240.3 | -02:40:21.105 | -45:37:09.065 | 7 | Sandstones, siltstones, calcarenites, anhydrites. |
| PR-1 | São Luís | Codó Fm. | 1507.6-1513.1 | -01:59:59.070 | -45:52:58.477 | 4 | Sandstones, siltstones. |
| CI-1 | Parnaíba | Codó Fm. | 768-907.1 | -02:59:54.215 | -45:24:30.842 | 13 | Sandstones, siltstones, conglomerates, calcarenites, anhydrites |

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023




Table 2. Plant groups, palynomorph taxa, botanical affinities and bioclimatic groups of the material studied.

| Plant Groups | Palynomorph taxa | Botanical affinities | Bioclimatic groups |
|---|---|---|---|
| Bryophytes | *Aequitriradites* | Hepaticae | Hygrophyte |
| | *Cingutriletes* | Sphagnaceae | Hygrophyte |
| | *Stereisporites* | Sphagnaceae | Hygrophyte |
| | *Triporoletes* | Ricciaceae | Hygrophyte |
| Ferns | *Appendicisporites* | Schizaeales (Anemiaceae?) | Hygrophyte |
| | *Biretisporites* | Osmundaceae | Hygrophyte |
| | *Cicatricosisporites* | Schizaeales (Anemiaceae?) | Hygrophyte |
| | *Crybelosporites* | Marsileaceae | Hydrophyte |
| | *Cyathidites* | Cyatheaceae-Dicksoniaceae | Upland flora |
| | *Deltoidospora* | Cyatheaceae-Dicksoniaceae | Upland flora |
| | *Distaltriangulisporites* | Schzaeales (Schizaeaceae?) | Hygrophyte |
| | *Foveotriletes* | Schzaeales (Schizaeaceae?) | Hygrophyte |
| | *Gleicheniidites* | Gleicheniaceae | Hygrophyte |
| | *Granulatusporites* | Pteridaceae | Hygrophyte |
| | *Klukisporites* | Schizaeales (Lygodiaceae?) | Hygrophyte |
| | *Matonisporites* | Matoniaceae | Upland flora |
| | *Paludites* | Marsileaceae | Hydrophyte |
| | *Reticulosporis* | Schzaeales (Schizaeaceae?) | Hygrophyte |
| | *Todisporites* | Osmundaceae | Hygrophyte |
| | *Undulatisporites* | Schzaeales (Schizaeaceae?) | Hygrophyte |
| | *Verrucosisporites* | Osmundaceae (?) | Hygrophyte |
| Lycophytes | *Antulsporites* | Selaginellaceae | Hygrophyte |
| | *Camarozonosporites* | Lycopodiaceae | Hygrophyte |
| | *Cingulatisporites* | Selaginellaceae | Hygrophyte |
| | *Densoisporites* | Selaginellaceae | Hygrophyte |
| | *Echinatisporites* | Selaginellaceae | Hygrophyte |
| | *Hamulatisporis* | Lycopodiaceae | Hygrophyte |
| | *Leptolepidites* | Lycopodiaceae | Hygrophyte |
| | *Lycopodiumsporites* | Lycopodiaceae | Hygrophyte |
| | *Perotrilites* | Selaginellaceae | Hygrophyte |
| | *Uvaesporites* | Selaginellaceae | Hygrophyte |
| Pteridosperms | *Vitreisporites* | Caytoniaceae | Upland flora |
| Gymnosperms | *Araucariacites* | Araucariaceae | Upland flora |
| | *Balmeiopsis* | Araucariacites | Upland flora |
| | *Bennettitaepollenites* | Cycadaceae | Tropical lowland flora |
| | *Callialasporites* | Araucariacites/Podocarpaceae | Upland flora |
| | *Cavamonocolpites* | Cycadaceae | Tropical lowland flora |
| | *Cedripites* | Pinaceae | Upland flora |
| | *Cingulatipollenites* | Araucariaceae | Upland flora |
| | *Classopollis* | Cheirolepidiaceae | Xerophytes |
| | *Complicatisaccus* | Coniferae i. sedis | Upland flora |

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023



| | | | |
|---|---|---|---|
| | *Cycadopites* | Cycadaceae | Tropical lowland flora |
| | *Elateropollenites* | Gnetales (Gnetaceae?) | Xerophytes |
| | *Equisetosporites* | Gnetales (Ephedraceae?) | Xerophytes |
| | *Eucommiidites* | Gnetales? | Xerophytes |
| | *Exesipollenites* | Cupressaceae | Upland flora |
| | *Gnetaceaepollenites* | Gnetales (Gnetaceae?) | Xerophytes |
| | *Inaperturopollenites* | Cupressaceae | Upland flora |
| | *Regalipollenites* | Gnetales (Ephedraceae?) | Xerophytes |
| | *Rugubivesiculites* | Podocarpaceae | Upland flora |
| | *Sergipea* | Gnetales | Xerophytes |
| | *Singhia* | Gnetales (Ephedraceae?) | Xerophytes |
| | *Spheripollenites* | Cupressaceae | Upland flora |
| | *Steevesipollenites* | Gnetales (Gnetaceae?) | Xerophytes |
| | *Uesuguipollenites* | Cupressaceae | Upland flora |
| Angiosperms | *Afropollis* | ? | Tropical lowland flora |
| | *Arecipites* | Monocots (Arecaceae?) | Tropical lowland flora |
| | *Brenneripollis* | Chloranthaceae | Tropical lowland flora |
| | *Clavatipollenites* | Chloranthaceae | Tropical lowland flora |
| | *Cretacaeiporites* | Trimeniaceae? | Tropical lowland flora |
| | *Dejaxpollenites* | ? | Tropical lowland flora |
| | *Monocolpopollenites* | Monocots (Arecaceae?) | Tropical lowland flora |
| | *Psiladicolpites* | Monocots (Liliaceae?) | Tropical lowland flora |
| | *Retimonocolpites* | Monocots (Arecaceae?) | Tropical lowland flora |
| | *Retiquadricolpites* | ? | Tropical lowland flora |
| | *Rousea* | Eudicots (Flacourtiaceae?) | Tropical lowland flora |
| | *Stellatopolis* | ? | Tropical lowland flora |
| | *Tricolpites* | Eudicots | Tropical lowland flora |
| | *Trisectoris* | Illiciaceae | Tropical lowland flora |

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023


Climate of the Past Discussions

Table 3. Description of the bioclimatic groups and their main representatives.

| Bioclimatic groups | Main representatives (sporomoph genera) | Remarks |
|---|---|---|
| Hydrophytes | *Crybellosporites* | Hydrophytes represent aquatic plants that live with a portion of their vegetative parts permanently immersed in water. |
| Hygrophytes | *Cicatricosisporites* | Hygrophyte plants depend on water to reproduce and are therefore generally associated with moist conditions and rarely reported from arid environments. |
| Tropical lowland flora | *Afropollis* | The tropical lowland flora is composed by families related to more humid conditions in lowland areas. All angiosperm genera and morphotypes are included in this flora |
| Upland flora | *Araucariacites, Caliallasporites* | Families assigned to thermophilic, large conifers, formed forests in the highlands from 200 to 1800 m. |
| Xerophytes | *Classopollis, Gnetaceaepollenites* | The group is adapted to xeric or water-stressed environments and therefore associated with arid climates. |

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023

Climate of the Past
Discussions
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Table 4. Average abundance of bioclimatic groups, diversity (H') and Fs/X ratio of the studied wells.

| Basins | Wells | Hydrophytes | Hygrophytes | Tropical lowland flora | Upland flora | Xerophytes | Fs/X | H' |
|---|---|---|---|---|---|---|---|---|
| Bragança-Viseu | EGST-1 | 0.9 | 24.9 | 5.5 | 16.6 | 52.1 | 0.38 | 2.1 |
| Bragança-Viseu | VN-1 | 0.2 | 28.4 | 1.6 | 9.7 | 60.2 | 0.31 | 1.6 |
| São Luís | PR-1 | 1.0 | 14.3 | 20.4 | 18.0 | 46.3 | 0.25 | 2.1 |
| São Luís | PE-1 | 0.1 | 16.8 | 8.5 | 26.0 | 48.6 | 0.28 | 2.2 |
| São Luís | RL-1 | 1.0 | 15.8 | 12.0 | 7.8 | 63.4 | 0.24 | 1.9 |
| Parnaíba | CI-1 | 0.7 | 11.4 | 6.0 | 15.9 | 63.6 | 0.19 | 2.0 |
| *General average* | | *0.7* | *18.6* | *9.0* | *15.7* | *55.7* | *0.28* | *2.0* |

https://doi.org/10.5194/cp-2023-22
Preprint. Discussion started: 5 May 2023


Climate of the Past Discussions
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Table 5. Average abundance of bioclimatic groups, diversity, Fs/X and marine elements of the paleoclimatic phases for the Bragança-Viseu, São Luís and Parnaíba basins. No marine elements.

| Paleoclimatic phases | Hygrophytes | Hydrophytes | Tropical lowland flora | Upland flora | Xerophytes | Diversity (H') | Fs/X | IndVal |
|---|---|---|---|---|---|---|---|---|
| Pre-evaporitic | 18.8 | 0.7 | 5.6 | 14.1 | 60.7 | 2.0 | 0.3 | *Deltoidospora* sp. (80.6%) |
| Evaporitic | 10.0 | 1.0 | 16.0 | 5.0 | 67.9 | 2.2 | 0.1 | *Afropollis* spp. (79.3%) |
| Post-evaporitic | 15.5 | 0.6 | 14.4 | 22.0 | 47.4 | 2.1 | 0.3 | *Deltoidospora* sp. (86.2%) |
| *General average* | *14.8* | *0.8* | *12.0* | *13.7* | *58.7* | *2.1* | *0.2* | |