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**Vegetational composition of the Early Cretaceous Chicalhão flora  
(Lusitanian Basin, western Portugal) based on palynological and  
mesofossil assemblages**

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**Abstract**

A new Early Cretaceous flora is described from the Lusitanian Basin in the Estremadura region (western Portugal) based on a combined study of mesofossils and palynomorphs. The fossil specimens were extracted from samples collected in the Chicalhão clay pit complex, near the village of Juncal from sediments belonging to the Figueira da Foz Formation. The plant bearing sequence is considered to be of Late Aptian-Early Albian age. Palynomorphs and mesofossils are generally well-preserved and include about 63 taxa. The palynoflora is dominated by conifer pollen and fern spores. Angiosperm pollen is also present, but subordinate among the palynomorphs. In contrast, angiosperms completely dominate the mesofossil flora and are mainly represented by fruits and seeds. Four taxa of angiosperm flowers were also identified. The combined palaeobotanical and sedimentological evidence indicates seasonally dry climate and an open vegetation consisting of a mixed conifer forest with an understorey and ground cover of ferns and angiosperms and with patchy occurrences of lycophytes and plants of the Bennettitales-Erdtmanithecales-Gnetales (BEG) group. Angiosperms probably inhabited moister areas bordering rivers and lakes.

**keywords:** Angiosperms; Late Aptian-Early Albian; Figueira da Foz Formation; mesofossils; palynomorphs; palaeobotany.

## 1. Introduction

Early Cretaceous continental deposits of the Lusitanian Basin in western central Portugal include abundant plant remains pivotal for documenting the vegetational context of early angiosperm radiation (for summary see Friis et al., 2010, 2011). The sediments span a time interval from the earliest Cretaceous pre-angiosperm world to the late Early Cretaceous time of emerging angiosperm communities. Classic studies of leaf floras have provided a basic framework for understanding the vegetational composition in the region through the Early Cretaceous (e.g., Heer, 1881; Saporta, 1894; Teixeira 1945, 1946, 1947, 1948, 1950, 1952) and palynological studies have added the time dimension to the changing ecosystems (e.g., Hasenboehler, 1981; Chapman, 1982; Leereveld et al., 1989; Trincão, 1990). The more recent discovery of mesofossil floras with exquisitely preserved flowers, fruits, seeds, dispersed stamens, twigs and other plant organs has considerably expanded the record of plant taxa, added new elements to the known biodiversity, and changed the perception on early angiosperm diversification. The mesofossil floras are particularly important for the understanding systematic diversity and phylogenetic diversification in the Early Cretaceous plant assemblages (Friis et al., 1992, 1997, 1999, 2000, 2001, 2004, 2006, 2007, 2009, 2010, 2011, 2013; Friis and Pedersen, 1996, 2011; Rydin et al., 2006; Pedersen et al., 2007; Mendes et al., 2008a, b; Mendes et al., 2010, 2011).

Typically, mesofossils and palynofloras have been studied separately, partly due to differences in the techniques for extracting and studying the material, partly because of the specialisation required for studying the different kinds of plant organs and partly because of the abundance of new material. It is, however, clear that mesofossil floras and palynological assemblages preserve different fractions of the vegetation due to

complexity in preservational processes as well as fossilisation potential and dispersal patterns of different plant organs (e.g., Friis et al., 2011). This has been demonstrated for the Vale Painho flora where a combined palynological-mesofossil study was carried out (Mendes et al., 2011). While the palynological assemblage of the Vale Painho flora was dominated by ferns and conifers, no fern fragments were observed in the mesofossil flora and conifer remains were rare. Instead the mesofossil flora was dominated by fossils assigned to the Bennettitales-Erdtmanithecates-Gnetales (BEG) group, which in turn were rare in the palynological assemblage. The Vale Painho flora is from the earliest Cretaceous representing a pre-angiosperm vegetation. In this study we perform a combined palynological and mesofossil study of a new Aptian-Albian flora from the same area representing a time slice where angiosperms are well established in the Lusitanian Basin.

The new fossil flora is from the Chicalhão clay pit complex, near the village of Juncal in western Portugal. We focus on a palaeoenvironmental analysis based on vegetation composition and significance of physiological/morphological features. In species composition the palynoflora is clearly dominated by conifers and ferns, but the mesofossil assemblages show that angiosperms were diverse in this plant community during the Aptian-Albian. Probably angiosperms constituted a minor part of the Chicalhão vegetation, but they were phylogenetically diverse. The presence of cheirolepidiaceae conifers and schizaeaceous ferns suggests that the Chicalhão plants formed a relatively open vegetation growing in a warm and seasonally dry climate (Watson and Alvin, 1996, Mendes et al., 2011).

## 2. Material and methods

### 2.1. Sampling and preparation

The fossil specimens described here are from seven sediment samples (96, 97, 98, 125, 126, 127 and 129) collected by M.M. Mendes and J.L. Dinis from the Chicalhão opencast clay pit complex (39° 37' 13.1'' N; 08° 51' 57.2'' W) near the village of Juncal, western central Portugal (Fig. 1).

Samples were collected from a slightly laminated, micaceous, dark-grey mudstone bed of the “Complexos Gresosos da Nazaré e Cós-Juncal” local unit of Early Cretaceous age (1:50.000 geological map; Zbyszewski et al., 1961). This unit is now assigned to the Figueira da Foz Formation defined in the northern sector of the Lusitanian Basin (Dinis, 1999, 2001) and correlative of the Rodízio Formation and the upper member of the Almargem Formation (Dinis et al., 2008) from the southern sector of the Lusitanian Basin. The fossil-bearing level is located at the base of the Famalicão Member, just overlying the conglomerates and sandstone of the Calvaria Member (Fig. 2). Both members can be correlated with the lower transgressive-regressive cycle of the southern onshore sector of the Lusitanian Basin deposits (Dinis et al., 2002). Accordingly, a Late Aptian to Early Albian age can be assigned for the Famalicão Member, using mainly macrofossils and palynology (Teixeira, 1950; Friis et al., 1999, 2010; Heimhofer et al., 2005), as well as correlation with the Atlantic rifting events of Iberia (Rey et al., 2006; Dinis et al., 2002, 2008).

Mesofossils were extracted from ca. 60 kg of sediments, which were air-dried in the laboratory, disaggregated in water and sieved over a 125 µm mesh sieve using a hand shower. Adhering mineral matrix was removed with hydrofluoric (40% HF) and

hydrochloric (10% HCl) acids, thoroughly rinsed in water and dried in air, following standard methods previously described by Friis et al. (1988). The fossils were initially investigated and observed using a Nikon SMZ 800 stereomicroscope. Specimens selected for more detailed study were mounted on polished aluminium stubs, sputter coated with gold for 60 seconds and examined using a Hitachi Field S-4300 scanning electron microscope (FE-SEM) at 2kV at the Swedish Museum of Natural History, Stockholm.

Two specimens (P0093 and P0311) were studied using attenuation-based synchrotron-radiation X-ray tomographic microscopy (SRXTM) at the TOMCAT beamline of the Swiss Light Source of the Paul Scherrer Institut, Switzerland (for preparation and techniques see references in Friis et al., 2013).

Palynomorphs were extracted by maceration of ca. 50 g of sediments from the same samples used for extracting the mesofossils. The samples were treated by HCl (10%) and HF (40%) for 48 hours to dissolve carbonates and silicates and concentrated HNO<sub>3</sub> for oxidation, following standard palynological techniques (Traverse, 2007). The organic residue was washed repeatedly with distilled water until neutral using a 125 µm net mesh nylon sieves in order to remove larger coal fragments from the palynomorphs. All the material passing the nylon sieves was concentrated by centrifuging and preserved in distilled water with a drop of HCl in small glass vials.

For light microscopy (LM) five glycerine jelly microscope permanent slides were mounted for each sample and sealed with nail varnish. Specimens were examined under light microscope and LM images were taken with a Nikon Coolpix 5400 digital camera on a Nikon Eclipse E600 microscope using 60x and 100x objectives and the position of the specimens recorded using an England Finder. The percentage distribution of spores and pollen were made based on counts from the LM microslides.

All specimens in each slide were counted to record species diversity and relative occurrence of the major systematic groups.

Mounts for scanning electron microscopy (SEM) were made following standard techniques. A drop of water with suspended palynomorphs was pipetted to polished aluminium stubs covered with double stick carbon tape, air dried, coated with gold for 60 seconds and studied using a Hitachi S-3700N scanning electron microscope at 5kV, at the University of Évora, Portugal. SEM coordinates were recorded for all figured specimens.

SEM-micrographs were improved using Photoshop software to enhance contrast and remove stain from the background.

All LM microslides, SEM stubs and specimens (P-numbers) used for the present study are housed in the Earth Sciences Department, Technology and Sciences College, New University of Lisbon, Portugal.

## *2.2. Sedimentology and depositional environment of the Chicalhão outcrop*

In the study area, the Famalicão Member is dominated by mudstone overbank deposits with meter-scale thickness, interbedded with a minor proportion of sandy channel architectural elements. Most of the mudstone bodies are sheets of mainly massive facies, rarely laminated, frequently rich in iron oxides and hydroxides, bioturbated (both invertebrates and roots), mottled and without marked soil horizons. Slickensides and desiccation cracks are other observed pedogenic features. The unit includes also lenticular mudstone elements with concave base, clearly formed by settling in depressions, and occasional sandy lenticular bodies interpreted as minor channels, crevasse splays or levee deposits (Miall, 2006). Within the floodplain a



proximal (close to the more active channels) or distal setting can be proposed to the deposits. The proximal ones are characterized by a more complex and amalgamated architecture, including most of the muddy and sandy lenses, whereas distal sediments are tabular mudstone devoid of sand levels and showing more evolved hydromorphic palaeosols (Kraus and Aslan, 1993; Allen and Fielding, 2007). The sampled lenticular body of dark-grey mudstone, slightly laminated, micaceous, with thin fine sand levels, can be interpreted as a rarely preserved pond in a depression close to the channel, reached by occasional overbank flows or crevasse splays. The suboxic to anoxic waters required for preservation of the plant remains together with the scarce bioturbation also points to a low-energy perennial pond, perhaps in an abandoned minor channel.

The channel and proximal overbank lithosomes show sigmoidal surfaces, both internal and between adjacent bodies, probably corresponding to lateral accretion surfaces in point-bars and, when in sand bodies, to side or alternate bars. The overall facies association and the depositional architecture point to a fine-grained to sand-bed, perennial, unconfined meandering river (Smith, 1987; Allen and Fielding, 2007). According to Dinis (1999), palaeocurrents from several outcrops (up to 30 km around, N=132) reveal a W to WNW trend, turning to SW in distal positions (dipmeter of two offshore wells, N=62). This regional pattern can be interpreted as the basin margin drainage from the Iberian hinterland, linked with the axial drainage to SW. The correlative stratigraphic interval in the offshore wells includes frequent carbonates of shallow marine protected platform (Matos and Witt, 1975).

### 2.3. *Climate and regional setting*

Clay minerals in both sandstone and mudstone of the Famalicão Member of the studied region are dominated by kaolinite, frequently with important proportions of illite, especially in mudstone (Grade and Moura, 1992; Dinis, 1999). Goethite and minor hematite are pervasive important components of the mud facies. The same clay and iron minerals assemblage occurs in correlative deposits both south (Rey, 1972; Carvalho et al., 1982; Heimhofer et al., 2012) and north (Soares, 1966; Rocha and Gomes, 1995) in the basin. Formation of kaolinite is usually associated with intense chemical weathering under humid tropical to subtropical conditions (Chamley, 1989).

The illite of a few samples of the studied region (Dinis, 1999) shows an ordered crystalline structure (by the Kubler index) and aluminous to intermediate trend (by the Esquevin index). Probably most of the illite corresponds to detrital mica, and the kaolinite fraction in mostly inherit from the watershed saprolite but also resulting from diagenetic weathering and soil-forming processes. Other identified accessory minerals point to a climate with fluctuating moisture, including alunite (Schwarz and German, 1999) and smectite (Chamley, 1989; Kraus and Aslan, 1993; Retallack, 2001), or to leaching conditions under high mean annual precipitation (illite-vermiculite mixed-layer clays; Folkoff and Meentemeyer, 1987).

The kaolinitic goethite-rich palaeosols can be characterized as hydromorphic ferrasols typical of humid tropical to temperate regions with significant seasonal rainfall changes (Chesworth, 2008). Considering also the overall clay assemblage, the pedogenic features (mottling and slickensides) and the accessory minerals, the palaeosols developed and inherit the hinterland regolith under a wet and warm climate, with important seasonal rainfall changes.

Ferrallitic soils develop in flat topography (Cheswoth, 2008) and correlative distal deposits include abundant siderite concretions, indicative of poorly drained environments (Retallack, 2001). This is consistent with the low-gradient deduced by the depositional architecture and strong lixiviation.

During the Aptian and the Albian, the latitudes of the western Portuguese margin were between 25° and 30° N. Chumakov et al. (1995) and Spicer and Skelton (2003) locates this region just north of the boundary between the Warm Humid and the Hot Arid mid-latitude belts during the Barremian to Albian. This is in accordance with the above interpretations of a dominant warm and humid climatic signature for the study region, while coeval arid to semi-arid conditions in the southward adjacent southern Portuguese margin (Algarve) and Iberian Basin are proved, respectively, by clay minerals and palynomorphs (Prates et al., 1983; Heimhofer et al., 2008), and erg and sabkha deposits (Rodríguez-López et al., 2008). A seasonal northward shift of the arid belt explains the inferred dry season.

### *3.1. The palynoflora*

The palynomorphs are attributed to 38 taxa, some of these perhaps encompassing more than one species (Table 1, Plates I and II).

Most of the taxa were recognised in LM microslides where a total of 173 grains were counted. Almost all taxa observed in the LM microslides were also observed in the SEM preparations. Further eight taxa represented by nine specimens were observed only in the SEM preparations. All spores and pollen represent land plants and show the presence of bryophytes, lycophytes, ferns, conifers and a minor component of other seed plants (Table 1, Plates I and II). Ferns and conifers dominate the palynological

assemblage both quantitatively and qualitatively. About 40% of the palynomorphs are trilete spores assigned to at least 18 fern taxa and 45% of the palynomorphs are pollen grains assigned to at least nine conifer taxa. Distortion of some palynomorphs impeded a more precise assignment of some of the fern spores and conifer pollen and the actual number of species for these two groups may be higher.

Bryophytes are rare, represented by *Taurocosporites segmentatus* (1%).

Lycophytes also constitute a minor component of the palynoflora and are represented by *Ceratosporites* (4%) and *Ptelasporites* (2%). The most abundant fern spores in the Chicalhão flora are related to the Schizaeaceae and assigned to *Cicatricosisporites* and *Costatoperforosporites* which represent about 29% of the palynoflora (Plate I, 3-5). Other relative abundant occurrences are spores of *Plicatella* (3%), also assignable to the Schizaeaceae, the psilate spores of *Deltoidospora* (5%) probably related to the Cyatheaceae or Dicksoniaceae. Other fern spores are assigned to *Acritosporites* (1%), *Contignisporites* (1%), *Ischyosporites* (1%), *Leiotriletes* (1%), *Nodosisporites* (1%), *Tessellatosporis* (1%) and *Todisporites* (1%).

Among conifers the dominant pollen is *Classopollis* (Cheirolepidiaceae) reaching frequencies up to about 38% (Plate II, 1-3). Araucarian pollen is represented by the genus *Araucariacites* which comprises about 4% of the palynoflora and perhaps also by the genus *Inaperturopollenites* (1%). Taxodiaceae pollen is also present in the Chicalhão palynoflora represented by pollen grains assigned to the species *Spheripollenites psilatus* (2%). Bissacate pollen of pinaceous affinity is recorded as a minor constituent in the palynoflora.

A few pollen grains assigned to the genus *Eucommiidites* (2%) were only observed throughout the LM microslides, representing the Erdtmanithecales.

Angiosperm pollen is present but subordinate in the palynoflora. The most common type is semitectate-collumelate monosulcate pollen of *Clavatipollenites* (2%) that may be related to the Chlorantaceae. Other monosulcate pollen grains observed in pollen clusters are two different species of the genus *Retimonocolpites* Pierce (Plate II, 6-7). Eudicot angiosperms are represented by a tricolpate form assigned to the genus *Rousea* Srivastava and a pollen tetrad with tricolpate pollen attributed to *Senectotetradites* Dettmann (Plate II, 8, 9).

### 3.2. The mesofossil flora

The mesofossil flora from Chicalhão includes a total of 245 specimens grouped in 25 different taxa. Angiosperms predominate both in species diversity and number of specimens with 196 specimens assigned to 21 taxa. Conifers are more rare with 34 specimens in three taxa and and lycophytes are represented by 15 specimens assigned to a single taxon (Table 2).

The lycophyte component of the mesofossil flora consists of megaspores with distinct selaginellaceous features. The material includes 15 megaspores, which is about 6% of the all the mesofossils. The megaspores are compressed from a more or less spherical shape, about 0.7 mm in diameter, and have a distinctly reticulate perispore. The arms of the trilete mark are about 0.25 mm.

Conifer cone scales are common in the mesofossil flora and include 32 specimens representing 13% of the mesofossils. Conifers also include two fragments of cheirolepidiaceae leafy axes and a few other fragments of axes of unknown affinity.

Remains of angiosperms constitute the major part of the mesofossil flora. Most of the specimens are seeds and fruits, but there are also four different kinds of

angiosperm flowers. We here summarise the angiosperm components in terms of general organisational and morphological diversity. Formal taxonomic descriptions will be provided in separate studies. These studies will include material from other contemporaneous floras of Portugal where more specimens and sometimes better preservation are available for more in depth taxonomic and phylogenetic analyses.

Flower 1 (P0085; Plate III, 1). This type is represented by a single specimen. The flower is about 1.25 mm long and 0.8 mm wide, borne on a long stalk. There are no traces of supporting bracts or bracteoles. The flower is preserved in a pre-anthetic stage. The perianth is apparently undifferentiated and consists of many overlapping parts. The inner organs are completely covered by the perianth parts and it is unknown whether the flower was unisexual or bisexual and there is no information on androecium or gynoecium.

A similar pre-anthetic flower borne on a long stalk and with perianth parts completely covering inner floral parts has been observed in a mesofossil assemblage from Vale de Água, but comparison between the flowers is impeded by lack of information on androecium and gynoecium.

Flower 2 (P0097; Plate III, 2). This type is represented by a single specimen. The flower is about 0.9 mm long and 0.75 mm wide. There are no traces of supporting bracts or bracteoles and there is no stalk. The flower is preserved in the anthetic stage. There are four undifferentiated, broadly ovate to elliptical tepals and scars from two other tepals. Three stamens are preserved, each placed in front of tepals. The arrangement of the preserved floral parts indicates that the flower had a trimerous or hexamerous perianth and androecium. The anthers are almost sessile, tetrasporangiate and with a distinct apical extension of the connective. No pollen was observed. The

ovary is inferior to semi-inferior. The number of carpels is not clear. The stylar region is solid. The hypanthium is ribbed.

Similar flowers are known from other Early Cretaceous floras of Portugal including the floras from Catefica, Vale de Água and Famalicão (e.g., Figure 1 in Friis et al. 1999 and Figure 9.15 in Friis et al. 2011). Pollen grains found *in situ* in some of these flowers are finely striate with a finger-print-like pattern and are very similar to pollen found in flower 3 described below.

Flower 3 (P0084; Plate III, 3-4). This taxon is represented by a single specimen. The flower is about 2.9 mm long and 1.4 mm broad. There are no traces of supporting bracts or bracteoles and there is no stalk. The flower is probably preserved in the anthetic stage, but most of the floral parts are broken off, leaving only scars of perianth parts and a single stamen. Pollen is monoaperturate, strongly flattened with an almost circular outline in polar view, about 11  $\mu\text{m}$  in diameter; outer surface of tectum is characterised by a finely fingerprint-like striate sculpture. The ovary is inferior to semi-inferior. The number of carpels is not clear and there is no information on ovules or placentation. The stylar region is massive. The hypanthium is faintly ribbed.

Similar flowers are known from other Early Cretaceous floras of Portugal including the flora of Catefica, Vale de Água and Famalicão. Pollen grains found *in situ* in these flowers are similar to those in the Chicalhão flower with a surface ornamentation of distinct fingerprint-like striation (e.g., Figure 2 in Friis et al., 1994; Figures 30-38 in Friis et al., 1999). The monoaperturate pollen indicates non-eudicot affinity of the flower.

Flower 4 (P0093; Plate III, 5-6). This taxon includes a single specimen. The flower is about 0.85 mm long and 0.9 mm broad. It is supported by a narrow, elongate bract. The floral parts are densely packed and the flower is probably preserved in the

pre-anthetic stage. The perianth is abraded and poorly preserved, but the remaining fragments indicate that perianth parts were free. There are four, almost intact stamens and scars from two other stamens and the androecium appears to be trimerous with the outer whorl of stamens in front of the carpels and the inner whorl between the carpels. The filament is broad and dorsiventrally flattened. Anthers are tetrasporangiate with theca projecting from the dorsal side of the stamen. Pollen observed *in situ* is monocolpate, tectate, compressed and more or less spherical in polar view with a diameter of about 15  $\mu\text{m}$ . The surface ornamentation shows a faint pattern of densely spaced, low and polygonal verrucae. The colpus is long and extends for almost the full length of the grains. The gynoecium is trimerous and superior with three free carpels that are densely adhering along the ventral faces. The carpels are of almost the same dimension for their full length. Stigmatic surfaces at top are undifferentiated. SXRTM shows that there are many, apparently slightly campylotropous ovules in each carpel, arranged in two longitudinal rows along ventral placentae (Plate IV).

Currently no other comparable flowers have been observed in other Early Cretaceous floras of Portugal and similar pollen grains are also unknown from the dispersed palynological assemblages. The monoaperturate pollen indicates non-eudicot affinity of the flower, but a more detailed description of the fossil including SXRTM analyses and a systematic assessment is in preparation.

*Canrightia resinifera* Friis & Pedersen (P0298 and P0299; Plate V, 1-3). This species is relatively well represented in the Chicalhão flora with 14 specimens (about 6% of all mesofossils). The fruits are well-preserved, about 1.2 mm long and 0.85 mm broad. Scars of stamens and remains of a hypanthium indicate that the fruit is derived from a bisexual and perigynous flower. One specimen with seeds exposed shows two seeds. Seeds have distinct crystalliferous seed wall. Pollen grains adhering to the fruit



are of the *Retimonocolpites*-type, about 11.3  $\mu\text{m}$  in diameter. In all features including size and shape, fruit epidermis, extension of hypanthium, position of staminate scars, seed organisation and structure, and adhering pollen grains the Chicalhão fossils correspond closely to *Canrightia resinifera* described from other Early Cretaceous mesofossil floras of Portugal (Friis and Pedersen, 2010). They are particularly similar to *Canrightia resinifera* fossils from the Famalicão locality that has predominantly two-seeded fruits.

*Canrightia*-like fruit and seeds (Plate V, 4-6). This type includes one fruit with fruit wall preserved and 15 abraded seeds. The fossils are closely similar to *Canrightia* in external morphology of the fruit, but differ in several critical characters. The *Canrightia*-like fruit is about 1.1 mm long and 0.9 mm broad. There are at least three distinct stamen scars on the lower half of the fruit surface at approximately one third the length of the fruit from the base indicating that the fruit was derived from bisexual flowers with a semi-inferior gynoecium. The upper delimitation of the hypanthium is marked only by the stamen scars and by the presence of slightly smaller epidermis cells below the insertion of the stamens. Pollen, adhering to the stigma of fruit is of the *Retimonocolpites*-type with semi-tectate, reticulate-columellate pollen wall. The gynoecium was apparently monomerous and stigma sessile. SXRTM shows a single pendant orthotropous to semi-orthotropous endotestal seed with palisade-shaped crystal cells of endotesta. The SXRTM also reveals fine grooves in the endotesta that are arranged in longitudinal furrows and allows a link to abraded, isolated grooved seeds that are also present in the flora (P0095; Plate VI, 1). Like in *Canrightia* the seeds have a distinct crystalliferous seed wall.

In fruit, seed and pollen features the fossils are very similar to those of *Canrightia resinifera*, but they are distinguished in several aspects, particularly in

having a single seed, an indistinct hypanthium without a continuous rim and no traces of perianth parts. Also seeds have a much thicker endotesta with distinct grooves in contrast to the smooth endotesta of *Canrightia*. Similar fruits and seeds are common in the Famalicão mesofossil flora (taxon 34, Figures 1A and 1B in Eriksson et al., 2000) and also known from several other mesofossil floras in Portugal. This taxon is relatively well represented in the Chicalhão flora with 16 specimens (about 7% of all mesofossils). Similar seeds from the Famalicão flora were originally interpreted as drupes with a ribbed-foveolate endocarp, but SXRTM analyses has documented that the fruits are instead one-seeded berries. A detailed description, formal naming and systematic assessment of the fossils from Chicalhão, Famalicão and other Early Cretaceous localities in Portugal is in preparation including the SXRTM analyses.

Rugulate fruits/seeds (P0205; Plate VI, 2). Small fossils with a rugulate surface are represented by five specimens (about 2% of all mesofossils). The outer wall is partly abraded and collapsed exposing the shape of the coarsely rugulate inner wall of coarse irregular, transversely oriented and slightly undulating ridges. The fossil is about 1.6 mm long and 0.9 mm broad, narrow ovoid in shape with a slightly pointed apex and rounded base. The number of carpels is unknown, but probably the fossils originate from a monocarpellate fruit with a single seed.

This species is common in the Famalicão mesofossil flora (taxon 37, Figure 1C in Eriksson et al., 2000) and was described as a drupe with a rugulate endocarp. The possibility that the fossil instead represents a one-seeded berry with a thick rugulate endotesta similar to the organisation of the *Canrightia*-like fossils cannot be ruled out.

Fruits with glandular cells (P0306; Plate VI, 3). This taxon includes three specimens (about 1% of all mesofossils). The fruit is about 1.2 mm long and 1.1 mm broad, broadly ellipsoidal to spherical in shape with an almost smooth outer surface.

The fruit was probably indehiscent either drupe or one-seeded berry. The outer epidermis is characterised by numerous circular cells, probably glandular that in some areas are seen as small holes.

Fruit with pits and furrows (P0308; Plate VI, 4). A single specimen (about 0.4% of all mesofossils). The fruit is about 1.1 mm long and 1.0 mm broad, spherical in shape with a slightly uneven surface with irregularly oriented pits and grooves. The fruit was indehiscent either drupe or one-seeded berry.

Wedge-shaped fruits (P0294 and P0303; Plate VI, 5-6). This fruit type includes 15 specimens (about 6% of all mesofossils). The fruits are wedge shaped indicating that they are fruitlets from an apocarpous fruit with densely packed fruitlets. There are very few details preserved, but comparison with similar fruits from other Early Cretaceous mesofossil floras indicates that the fruitlets were one-seeded.

Fruits with co-adhering seeds in row type 1 (P0212, P0310 and P0293; Plate VII, 1-3). These fossils are relatively common in the Chicalhão flora including 17 specimens (about 7% of all mesofossils). The fruits are indehiscent, interpreted as a berry with several seeds. The fruits are about 1.5 mm long and 1.2 mm broad. The fruit wall is composed of thin-walled cells that are often abraded leaving the seeds exposed. The cells of the outer epidermis are small with equiaxial and polygonal facets. The ventral suture is distinct extending from the basal attachment scar to the sessile stigmatic area. Seeds are about 1.2 mm long and 0.54 mm broad and closely adhering. Seeds in the middle have more or less flattened lateral faces while seeds at the end have one flat and one convex face. The seeds are anatropous, bitegmic and exotestal with micropyle formed from the inner integument.

This species is very distinct and widespread in the Early Cretaceous floras of Portugal, but is particularly common in the Famalicão (e.g., Figures 5-7 in Friis et al., 1999) and Catefica mesofossil floras.

Fruit with co-adhering seeds in row type 2 (P0092; Plate VII, 4). This type is very common in the Chicalhão mesoflora with 55 specimens (about 23% of all mesofossils). The fruits are indehiscent, interpreted as a berry with several seeds, about 1.9 mm long and 1.3 mm broad. The fruit wall is abraded in all specimens leaving the seeds exposed. Only the tissue around the ventral suture is preserved in the specimen figured here. The seeds are about 1.3 mm long and 0.2 mm broad, closely adhering laterally. As in type 1 the seeds in the middle part of the fruit have flattened lateral faces while in the seeds at the end of the fruits have one straight and one convex face.

This species is very similar to “Fruit with co-adhering seeds in row type 1” in general organisation with seeds strongly adhering/fused seeds and they may belong to the same complex of plants. Also this type is very common in the Catefica and Famalicão mesofossil floras. SXRTM of the Famalicão fossils (both type 1 and type 2) shows that the two types are distinguished in seed wall structure and other internal features.

Fruit with exotestal seed with smooth surface (P0088; Plate VIII, 1). This taxon includes a single fruit that is partly abraded exposing a single seed. The fruit is about 1.3 mm long and 1.1 mm broad. The fruit wall is thin and the seeds fill out the locule almost completely. The seed is exotestal and the outer testa thick composed of high palisade cells. The micropylar area is slit-like.

Similar seeds are also known from the Famalicão mesofossil flora, typically found isolated (Figure 16.16 in Friis et al., 2011).

Exotestal seeds with smooth surface (P0207; Plate VIII, 2). This taxon includes two seeds (about 0.8% of all mesofossils). The seeds are ellipsoidal, about 1.4 mm long and 0.9 mm broad, exotestal with a thick outer testa and smooth outer surface. The raphal region is raised extending from the almost circular micropyle to the rounded base. The faces next to the raphal ridge are slightly flattened which may indicate that the seeds were borne in a fruit with more seeds, or in one-seeded fruits that were closely packed. Similar seeds are also known from the Famalicão and other mesofossil flora of Portugal.

Exotestal seeds with verrucate surface (P0082 and P0083; Plate VIII, 3-4). This type is common in the Chicalhão mesofossil flora with 28 specimens (about 11% of all mesofossils). The seeds are broadly ovate in lateral view and slightly flattened dorsiventrally, about 1.1 mm long and 1.0 mm broad. They are exotestal and anatropous with a distinct raphal ridge. The hilum and micropyle are closely spaced on a raised structure. The exotesta cells are palisade-shaped, each with a central protrusion resulting in the distinctly verrucate seed surface.

This seed type is also common in the Early Cretaceous mesofossil floras of Portugal, particularly in the Famalicão flora (e.g., Figures 18-20 in Friis et al., 1999).

Exotestal seed with finely reticulate surface, type 1 (P0208; Plate IX, 1). This taxon includes a single specimen (about 0.4% of all mesofossils). The seed is narrow, ellipsoidal to ovoid in shape, about 1.8 mm long and 0.9 mm broad, exotestal with a distinct raphal ridge. The micropyle is seen as a circular opening. The exotestal cells are small and arranged in longitudinal rows; the facets are polygonal and isodiametric.

This seed type is common in other Early Cretaceous mesofossil floras of Portugal, particularly in the Famalicão and Catefica floras.

Exotestal seed type 2 (P0216; Plate IX, 2). This type includes 3 specimens (about 1.2% of all mesofossils). The seeds are ellipsoidal in shape, about 1.4 mm long and 1.1 mm broad. They are exotestal with a distinct raphal ridge. The micropylar area is slightly raised. The exotestal cells are small and arranged in irregular longitudinal rows; the facets are polygonal and isodiametric and the anticlinal cell walls raised.

This seed type is also known from other Early Cretaceous mesofossil floras of Portugal.

Exotestal seeds with rugulate-foveolate surface (P0104 and P0105; Plate IX, 3, 4). This seed type is common in the mesofossil flora with 32 specimens (about 13% of all mesofossils). The seeds are elliptical to circular in lateral view and slightly flattened dorsi-ventrally, about 0.9 mm long and 0.6 mm broad. They are exotestal and antropous with distinct raphal ridge. The hilum and micropylar region is seen as an elliptical opening. The exotestal cells have strongly undulate anticlinal walls and the seed surface is rugulate-foveolate.

Seeds of this type are very common in other Early Cretaceous mesofossil floras of Portugal and are particularly abundant in the Catefica and Famalicão mesofossil floras.

#### **4. Discussion**

##### *4.1. Taxonomic composition of the Chicalhão flora*

The total taxonomic diversity of the Chicalhão palynological and mesofossil assemblages is relatively high. There is, however, a marked discrepancy in taxonomic composition between the two assemblages and except for remains of Cheirolepidiaceae

and a single angiosperm taxon that are recorded in both assemblages there is almost no overlap of taxa in the palynoflora and mesofossil flora even at higher taxonomic levels.

Ferns and conifers are qualitative and quantitatively dominant in the palynoflora constituting about 85% of all spores and pollen and 28 of the 39 taxa recorded. No fern remains were recorded in the mesofossil flora and only three of the 25 taxa recorded in the mesofossil flora are attributed to conifers. Instead the mesofossil flora is quantitatively and qualitatively dominated by remains of angiosperms that constitute more than 80% of all the specimens in the mesofossil flora and 21 out of 25 taxa based on mesofossils are angiosperms. This is in contrast to the palynological assemblage where only two species of angiosperms, both assigned to the extinct genus *Clavatipollenites*, were encountered in the LM counts and further three species were observed in the SEM-preparations.

A prominent component of the Chicalhão fern assemblage is trilete spores with cicatricose to canaliculate sculpture assigned to species of *Cicatricosisporites*, *Costatoperforosporites* and *Plicatella*. This kind of spores are characteristic for members of the extant schizaeaceous fern *Anemia* Swartz (e.g., Giacosa et al., 2012) and has also been found *in situ* in sporangia of the extinct ferns *Ruffordia* Seward and *Pelletixia* Watson & Hill, both closely related to and perhaps part of the *Anemia* crown group (e.g., Skog, 1992; Dettman and Clifford, 1992; Wikström et al., 2002). Spores referable to *Plicatella* are also known from fronds attributed to *Schizaea* (Smith) Reed and *Schizaeopteris* Stopes & Fuji (Leopold and Pakiser, 1964; Davies, 1985).

Another prominent component in the fern assemblage is trilete, laevigate spores assigned to three different species of *Deltoidospora*. The *Deltoidospora*-type spores are known from sporangia of the extinct dicksoniaceous fern *Onychiopsis psilotoides* (Stokes & Webb) Ward (Friis and Pedersen, 1990). Remains of *Onychiopsis* have been

found in other contemporaneous floras from Portugal and it is possible that at least some of the *Deltoidospora* spores from the Chicalhão palynoflora were produced by *Onychiopsis* plants.

Non-angiospermous seed plants are represented in the Chicalhão flora mainly by conifers. The extinct Cheirolepidiaceae are particularly well-represented with numerous pollen grains of *Classopollis* placed in at least four different species. Other conifer pollen may represent the Araucariaceae and the Pinaceae. The only conifer remains in the mesofossil assemblage are a few fragments of cheirolepidiaceous twigs as well as a few other unidentified twigs and cone scales. Other non-angiospermous seed plants are represented in the palynological assemblage by species of *Monosulcites* (Cookson) Couper, typically ascribed to cycadophytes or ginkgos, and by pollen of *Eucommiidites* Erdtman assignable to the extinct Erdtmanithecales. None of these groups are present in the mesofossil flora.

Angiosperms are diverse in the Chicalhão flora and predominate the mesofossil flora with about 25 species of flowers, fruits and seeds. Two flowers have pollens grains *in situ* in stamens and one fruit has clusters of pollen grains on the stigmatic surface. Only one of these pollen types was observed also in the palynological assemblage.

Angiosperms related to basal lineages predominate. Based on a phylogenetic analysis *Canrightia resinifera* was resolved as a member of the lineages including extant Chloranthaceae (Friis and Pedersen, 2011) and the *Canrightia*-like fruits and seeds clearly belong to the same complex of plants. Pollen of *Clavatipollenites* has also been compared to pollen of extant Chloranthaceae (e.g., Couper, 1960; Walker and Walker, 1985). Other basal lineages are represented by different kinds of exotestal seeds closely similar to seeds of extant Nymphaeales and two other kinds of monoaperturate pollen probably also representing basal lineages. Eudicots were also established in the



Chicalhão flora represented by two different kinds of tricolpate pollen attributed to the genera *Rousea* Srivastava and *Senectotetradites* Dettmann.

#### 4.2. Vegetational structure and palaeoenvironment

The discrepancy in taxonomic composition between the fern-conifer dominated palynological assemblage and the angiosperm dominated mesofossil assemblage may be explained by differences in spore and pollen production, mode of dispersal, resistance of the various plant organs to transport and fossilization in the three groups of plants, and distance of the plants to the depositional basin. Ferns typically produce many spores that are abiotically dispersed. Ferns are also mostly of low stature and spores captured in the sediments probably represent mainly the local flora. The lack of fern remains in the mesofossil assemblage may, however, indicate that they were not in the immediate vicinity of the depositional site.

Conifers typically produce copious amounts of pollen grains that are dispersed by the wind over long distances and conifer pollen reaching the depositional site may represent both the local and the regional vegetation. Conifer seeds and twigs are relatively tough and resistant to transport and the lack of conifer remains in the mesofossil flora may indicate that conifers were not growing close to depositional site.

In contrast to ferns and conifers most Early Cretaceous angiosperms probably produced relatively little pollen and pollen was mostly biotically dispersed (Friis et al., 2011). Exceptions include the *Clavatipollenites* and *Asteropollis* plants that may have been pollinated both by insects and wind (e.g., Friis et al. 2011). Most Early Cretaceous angiosperms were probably also of low stature and angiosperm grains were most likely produced close to where they were deposited. The fact that angiosperm flowers, fruits

and seeds are common and well-preserved in the mesofossil flora while conifer remains are not further indicates that the angiosperms inhabited the zones near the depositional site and conifers may have been more remote.

Thus angiosperms may have grown on moister soil along ponds and river banks and some may have been fully aquatic.

The other plant remains in the Chicalhão flora indicate open and drier vegetation more remote from the water bodies. The schizaeaceous spores were produced by plants most similar to the extant *Anemia* and the extinct *Ruffordia* and *Pelletixia*. Today *Anemia* (including *Mohria* Swartz) inhabits mainly drier and warmer regions of the world and occurs often in open places (Kramer, 1990). Both *Ruffordia* and *Pelletixia* have tightly enclosed and protected sporangia indicating that they also inhabited drier environments (e.g, Watson and Alvin, 1996). The *Deltoidospora* producing fern *Onychiopsis* is another indicator of water stress with its strongly protected sporangia and reduced leathery vegetative parts (Friis and Pedersen 1990). Members of the extinct Cheirolepidiaceae are characterised by strongly reduced leaves, thick cuticle and deeply sunken stomata that further indicates water stress (Watson and Alvin, 1996; Friis et al., 2011).

The palaeoenvironmental conclusions drawn from the fossils are further supported by sedimentological inferences. The palaeolandscape was probably a wide, open distal plain crossed by a perennial, sandy meandering river. The relatively high proportion of coarse bed-load points to low geomorphic stability of the channel, levees and zones bordering the crevasse-splays. Accordingly, the plant cover of the active belt was probably occupied by plants with ruderal strategies associated with disturbed environments and the predominately small stature angiosperms might have been part of this vegetation. Elongated depressions like abandoned channels, swales between levee

ridges and ponds probably had groundwater connection with the channel through sandy levels. Such low-energy suboxic to anoxic environments were potential ideal for capturing and preservation of the plant remains.

In contrast, the distal floodplain should have been more stable, occupying large areas of the open plain, only reached by low-energy flood currents leaving suspension settling deposits, and developing relatively mature soils. Such landscape could have supported a mature mixed conifer forest dominated by cheirolepidiaceous conifers trees with an understorey dominated by representatives of the fern families Schizaeaceae and Dicksoniaceae.

The overall composition of the Chicalhão flora suggests a warm climate with seasonal dry conditions. Sedimentary proxies agree with such reconstruction, namely the kaolinite-dominated clay assemblage and hydromorphic ferrasols. The studied area was most likely located near the boundary between the Warm Humid and the Hot Arid mid-latitude belts during Barremian to Albian times (Chumakov et al., 1995), with a seasonal northward shift of the arid belt explaining the inferred dry season.

#### *4.3. Comparison with other Aptian-Albian floras*

Numerous mesofossil floras have been reported from strata of the late Early Cretaceous (Late Barremian-Early Albian) age in Portugal from Torres Vedras in the south to the region around Buarcos in north (e.g., Friis et al., 1999, 2000, 2010, 2011). Studies of these mesofossil floras have mainly focused on the systematic and organisational diversity of the mesofossils. In all cases the fossils are typically preserved as three-dimensional coalifications and occur in terrestrial sediments deposited in fluvial and lacustrine environments. Most of the floras are species rich and

dominated by angiosperms such as the Buarcos mesofossil flora that includes almost 100 species of angiosperms (e.g., Friis et al., 1999). For the Buarcos site there is also a published palynoflora (Pais and Reyre, 1981) and comparison between the two types of assemblage at the Buarcos site shows the same patterns as seen in the Chicalhão assemblages with the mesofossil flora dominated by angiosperms while only two angiosperm pollen types *Clavatipollenites cf. hugesii* and *Asteropollis vulgaris* (Groot & Groot) Singh were reported from the dispersed palynoflora. Interestingly these two pollen types may both have been produced by plants that were probably mostly wind pollinated but perhaps also insect pollinated (Friis et al., 2011).

The Chicalhão mesofossil flora shares several elements with other mesofossil floras of Portugal. There is a particular great correspondence to the Famalicão mesofossil flora and with a few exceptions all taxa encountered in the Chicalhão mesofossil flora are also known from the Famalicão flora. The Famalicão flora is, however, much more specious with more than 100 species of angiosperms (Eriksson et al., 2000; Friis et al., 1999). There are also many shared taxa between the Chicalhão and the Catefica floras, while many of the characteristic elements of the near-by Vale de Água assemblages are lacking.

## 5. Conclusions

The palaeolandscape of the Chicalhão site area is interpreted as a distal wide plain bordering an unconfined sandy, meandering river. The relatively coarse bed-load points to frequent changes in the channel position due to wandering and avulsion. Thus, the active belt including the channel, levees and crevasse-splays, had a low geomorphic

stability. This belt contrast with the much more stable distal floodplain, where fine deposits developed relatively mature soils.

The plant cover of the active belt was probably formed by taxa with ruderal strategies associated with disturbed environments and most likely included the diverse assemblages of angiosperms that are thought to have grown close to the depositional site. The vast distal floodplain would have supported a mature conifer forest dominated by trees of cheirolepidiaceus conifers. The forest understorey was probably dominated by schizaeaceous and dicksoniaceus ferns and scattered occurrence of lycophytes and plants related to the Erdtmanithecales and perhaps the Bennettitales.

The overall composition of the Chicalhão flora suggests a warm environment with seasonal dry conditions. Such as reconstruction is supported by the sedimentological proxies with a kaolinite-dominated clay assemblage and hydromorphic ferrasols.

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**Text to Figures**

**Figure 1.** (A) Geographical location of the Lusitanian Basin in western Portugal. (B) Map detail showing the approximate position of the opencast clay pit complex where the specimens were collected near the village of Juncal. 1 – Syncline, 2 – Anticline, 3 – Fault, 4 – Figueira da Foz Formation, 5 – Chicalhão site.

**Figure 2.** Picture of the Chicalhão clay pit and sample level (left, arrow), and schematic log of the Figueira da Foz Formation in the Juncal area, based on outcrops and two hydrogeological wells (right, after Dinis, 1999).

**Plate I.** SEM micrographs of some spore types recovered from the Early Cretaceous Chicalhão palynoflora. 1. *Deltoidospora australis* (Couper, 1953) Pocock, 1970. 2. *Patellasporites tavadensis* Groot & Groot, 1962. 3. *Cicatricosisporites venustus* Deák, 1963. 4. *Cicatricosisporites* sp. 5. *Costatoperforosporites* sp. 6. *Tessellatosporis escheri* Harding, 1988. Scale bars = 50 µm for all specimens.

**Plate II.** SEM micrographs of conifer and angiosperm pollen recovered from the Early Cretaceous of Chicalhão palynoflora. 1, 2. *Classopollis noeli* Reyre, 1970. 3. *Classopollis mirabilis* Reyre, 1970. 4. Bisacate pollen grain. 5. *Clavatipollenites*-type pollen. 6. Cluster of *Retimonocolpites* sp. 1. 7. Cluster of *Retimonocolpites* sp. 2. 8. *Rousea* sp. 9. *Senectotetradites* sp. Scale bars = 15 µm for all specimens.

**Plate III.** SEM micrographs of angiosperm flowers from the Early Cretaceous of Chicalhão mesofossil flora. 1. Lateral view of a pre-anthetic flower born on a long stalk

(P0085); scale bar = 500  $\mu\text{m}$ . 2. Lateral view of a flower preserved in the anthetic stage (P0097); scale bar = 500  $\mu\text{m}$ . 3. Lateral view of an epigynous flower probably preserved in the anthetic stage (P0084); scale bar = 1 mm. 4. Pollen grains from specimen P0084, showing colpus and fingerprint-like sculpture; scale bar = 10  $\mu\text{m}$ . 5. Apical view of a flower supported by an elongate bract and probably preserved in the pre-anthetic stage (P0093); scale bar = 500  $\mu\text{m}$ . 6. Monocolpate pollen grains from specimen P0093, showing a densely spaced and polygonal ornamentation; scale bar = 10  $\mu\text{m}$ .

**Plate IV.** Synchrotron radiation x-ray tomographic microscopy (SRXTM)

reconstructions of flower 4 (P0093) from the Early Cretaceous of Chicalhão mesofossil flora. 1. Longitudinal orthoslice sections of two carpels showing locule of one carpel and carpel wall of the other as well as two bulky stamens with dorsal pollen sacs (arrow head). 2. Longitudinal orthoslice through two carpels showing ovule attached to the ventral margin of both carpels. 3. Transverse orthoslice showing the three carpels with ovules borne on ventral placentae and sections through four stamens; note apparent campylotropous organisation of ovule (arrow head). All scale bars = 100  $\mu\text{m}$ .

**Plate V.** SEM micrographs of angiosperm fruits from the Early Cretaceous of

Chicalhão mesofossil flora. 1. Lateral view of *Canrightia resinifera* exposing two seeds (P0298); scale bar = 500  $\mu\text{m}$ . 2. Lateral view of *Canrightia resinifera* showing stamen scars (P0299); scale bar = 500  $\mu\text{m}$ . 3. Adherent pollen grains of the *Retimonocolpites*-type from specimen P0299; scale bar = 10  $\mu\text{m}$ . 4. Lateral view of *Canrightia*-like fruit with four distinct stamen scars spaced around the specimen (P0311); scale bar = 500  $\mu\text{m}$ . 5. Pollen grains of the *Retimonocolpites*-type adhering to raised area (stigma) from

specimen P0311; scale bar = 50  $\mu\text{m}$ . 6. Pollen grains of the *Retimonocolpites*-type from specimen P0311, showing coarse reticulum; scale bar = 20  $\mu\text{m}$ .

**Plate VI.** SEM micrographs of seeds and fruits from the Early Cretaceous Chicalhão mesofossil flora. 1. Lateral view of seed of *Canrightia*-like fossil showing endotesta with fine grooves arranged in longitudinal rows (P0095); scale bar = 1 mm. 2. Lateral view of seed exposing a rugulate surface and a slightly pointed apex (P0205); scale bar = 1 mm. 3. Lateral view of fruit with glandular cells exposing outer epidermis with numerous circular cells (P0306); scale bar = 500  $\mu\text{m}$ . 4. Lateral view of fruit with pits and furrows showing a surface with irregularly oriented pits and furrows (P0308); scale bar = 500  $\mu\text{m}$ . 5. Lateral view of wedged-shaped fruit showing a slightly pointed apex (P0294); scale bar = 1 mm. 6. Lateral view of wedged-shaped fruit probably from an apocarpous fruit with densely packed fruitlets (P0303); scale bar = 500  $\mu\text{m}$ .

**Plate VII.** SEM micrographs of fruits from the Early Cretaceous Chicalhão mesofossil flora. 1 and 3. Fruits with co-adhering seeds in row type 1 interpreted as a berry with several seeds (P0212 and P0293); scale bars = 1 mm. 2. Fruit with co-adhering seeds in row type 1 interpreted as a berry with several seeds exposing outer cuticle (P0310); scale bar = 500  $\mu\text{m}$ . 4. Fruit with co-adhering seeds in row type 2 inferred as a berry with some seeds exposing parenchyma cells (P0092); scale bar = 1 mm.

**Plate VIII.** SEM micrographs of fruits and seeds from the Early Cretaceous Chicalhão mesofossil flora. 1. Fruits partly abraded exposing a single exotestal seed with smooth surface (P0088); scale bar = 1 mm. 2. Dorsi-ventral view of exotestal seed showing a smooth outer surface and micropylar region (P0207); scale bar = 1 mm. 3 and 4. Dorsi-

ventral views of exotestal seeds exposing a verrucate outer surface and a distinct micropylar area (P0082 and P0083); scale bars = 500  $\mu\text{m}$ .

**Plate IX.** SEM micrographs of seeds from the Early Cretaceous Chicalhão mesofossil flora. 1. Dorsi-ventral exotestal seed type 1 exposing a finely reticulate surface, a distinct raphal ridge and micropylar area (P0208); scale bar = 1 mm. 2. Lateral view of exotestal seed type 2 showing small exotestal cells arranged in a irregular longitudinal rows (P0216); scale bar = 1 mm. 4 and 5. Lateral view of exotestal seeds exposing a distinctly regulate-foveolate outer surface and an elliptical opening in the micropylar region (P0104 and P0105); scale bars = 500  $\mu\text{m}$ .

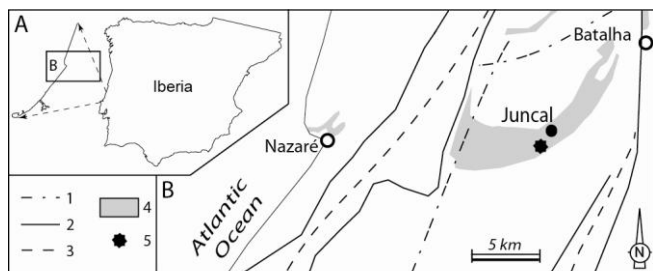


Fig. 1

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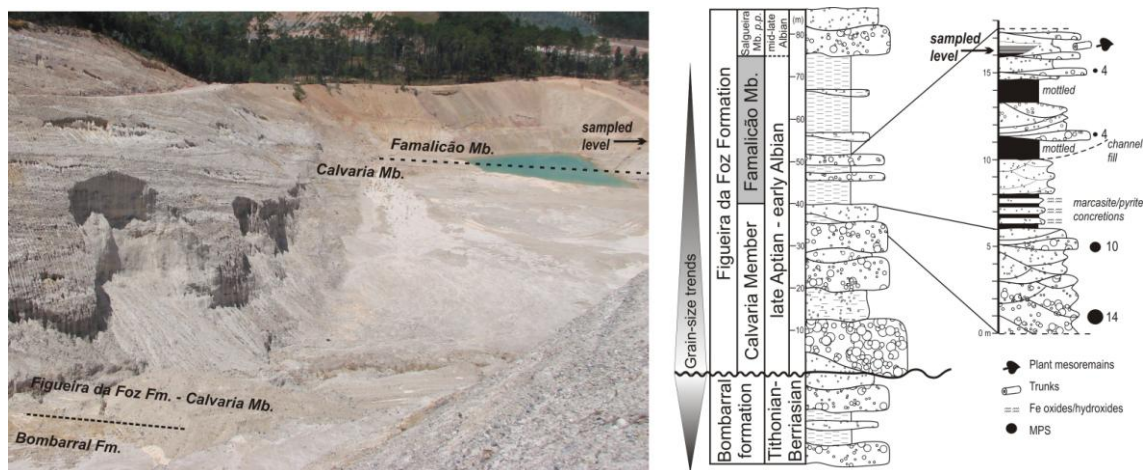


Fig. 2

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**Table 1.** Spore and pollen taxa identified in the Chicalhão palynoflora listed alphabetically within genera.

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**Bryophyta**

*Taurosporites segmentatus* Stover, 1962

**Lycophyta**

*Ceratosporites masculus* Norris, 1969

*Ceratosporites* sp.

*Patellaspores tavadensis* Groot & Groot, 1962

**Pteridophyta**

*Acritosporites oculatus* Deák, 1964

*Cicatricosisporites brevilaesuratus* Couper, 1958

*Cicatricosisporites sprumonti* Döring, 1965

*Cicatricosisporites venustus* Deák, 1963

*Cicatricosisporites* spp.

*Contignisporites* sp.

*Costatoperforosporites* sp.

*Deltoidospora australis* (Couper, 1953) Pocock, 1970

*Deltoidospora minor* Couper, 1953 (\*)

*Deltoidospora* spp.

*Ischyosporites* sp.

*Impardecispora* sp.

*Leiotriletes* sp.

*Leptolepidites major* Couper, 1958 (\*)

*Nodosisporites* sp.

*Plicatella pseudomacrorhyza* (Markova, 1961) Dörhöfer, 1977

*Plicatella* sp.

*Tessellatosporis escheri* Harding, 1988 (\*)

*Todisporites major* Couper, 1958

**Coniferophyta**

*Araucariacites australis* Cookson, 1947

*Araucariacites* sp.

Bisacate pollen (\*)

*Classopollis major* Groot & Groot, 1962

*Classopollis mirabilis* Reyre, 1970(\*)

*Classopollis noeli* Reyre, 1970

*Classopollis* spp.

*Inaperturopollenites* spp.

*Spheripollenites psilatus* Couper, 1958

#### **Cycadophyta/Ginkgophyta**

*Monosulcites* spp.

#### **BEG group**

*Eucommiidites* sp. (\*)

#### **Magnoliophyta**

*Clavatipollenites hughesi* (Couper, 1958) Kemp, 1968

*Clavatipollenites minutus* Brenner, 1963

*Retimonocolpites* spp. (\*)

*Rousea* sp. (\*)

*Senectotetradites* sp. (\*)

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(\*) Specimens recognised in the scanning electron microscopy.



**Table 2.** Mesofossil specimens identified in the Chicalhão mesoflora listed within five different groups.

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**Megaspores**

Sellaginellaceae megasopres

**Conifers**

Conifer cone scales

Cheirolepidiaceous remains

Conifers fragments

**Angiosperms flowers**

Flower 1

Flower 2

Flower 3

Flower 4

**Angiosperms seeds**

Seed showing fine grooves in the endotesta arranged in longitudinal furrows

Seed with a rugulate surface and a slightly pointed apex

Exotestal seed with a smooth outer surface

Exotestal seeds with a verrucate outer surface

Exotestal seed type 1 with finely reticulate surface

Exotestal seed type 2 with small exotestal cells arranged in irregular rows

Exotestal seeds with distinct regulate-foveolate outer surface

**Angiosperms fruits**

*Canrightia resinifera* Friis & Pedersen

*Canrightia*-like fruit

Fruit with glandular cells and outer epidermis with circular cells

Fruit with irregularly oriented pits and furrows

Wedge-shaped fruit probably from an apocarpous fruit

Fruits with co-adhering seeds in row type 1

Fruit with co-adhering seeds in row type 2

Fruits with a single exotestal seed

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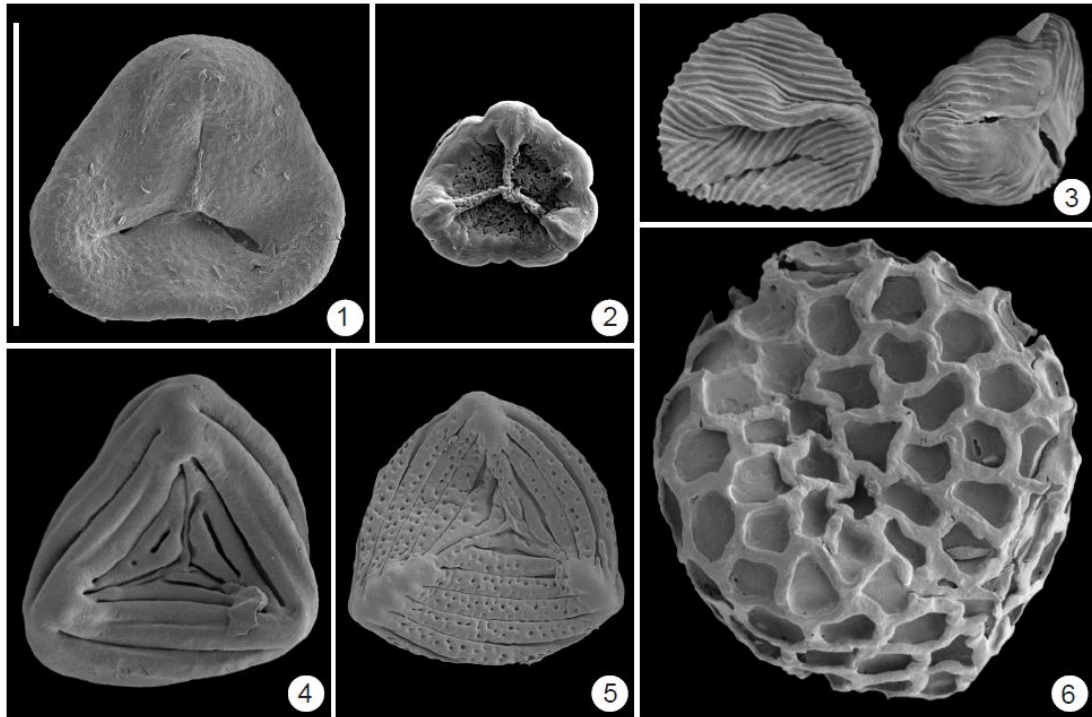


Plate 1

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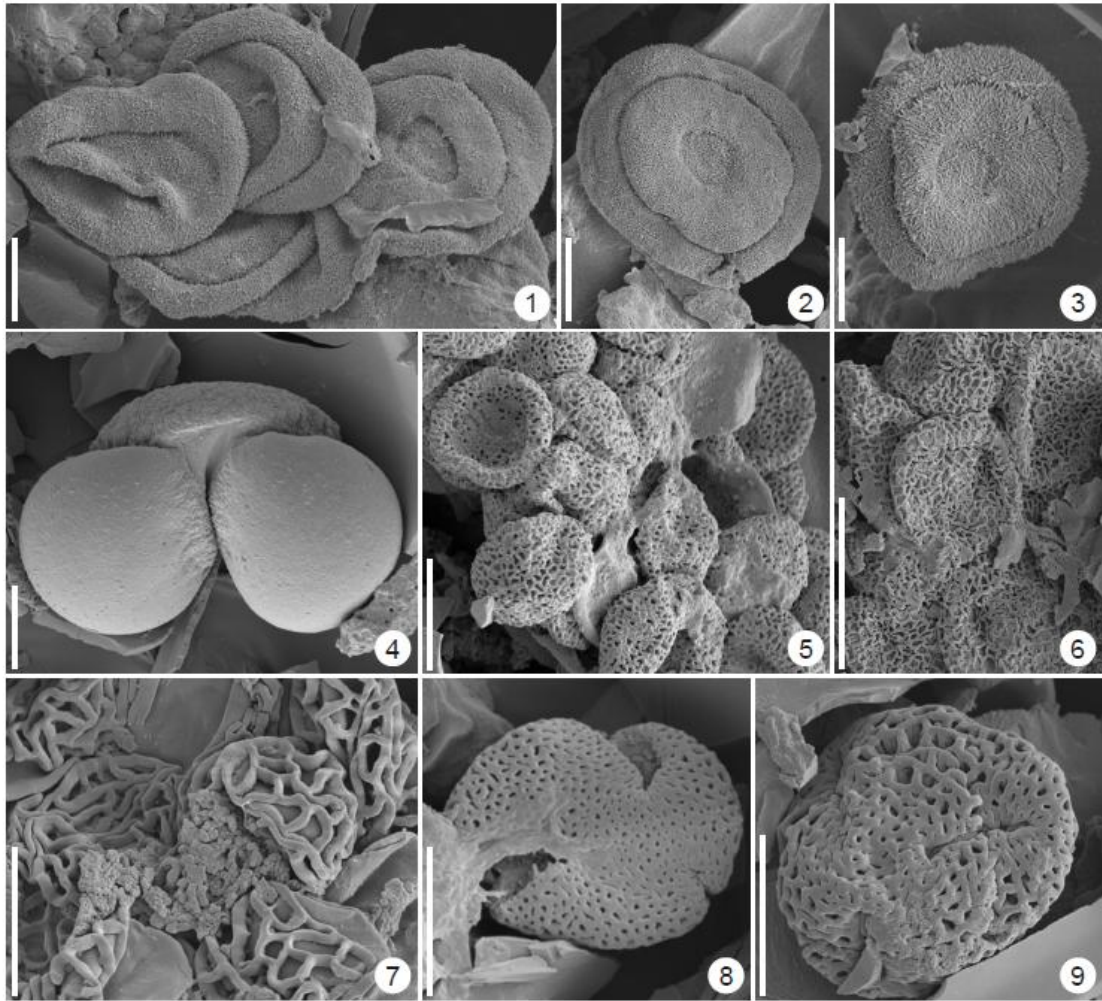


Plate 2

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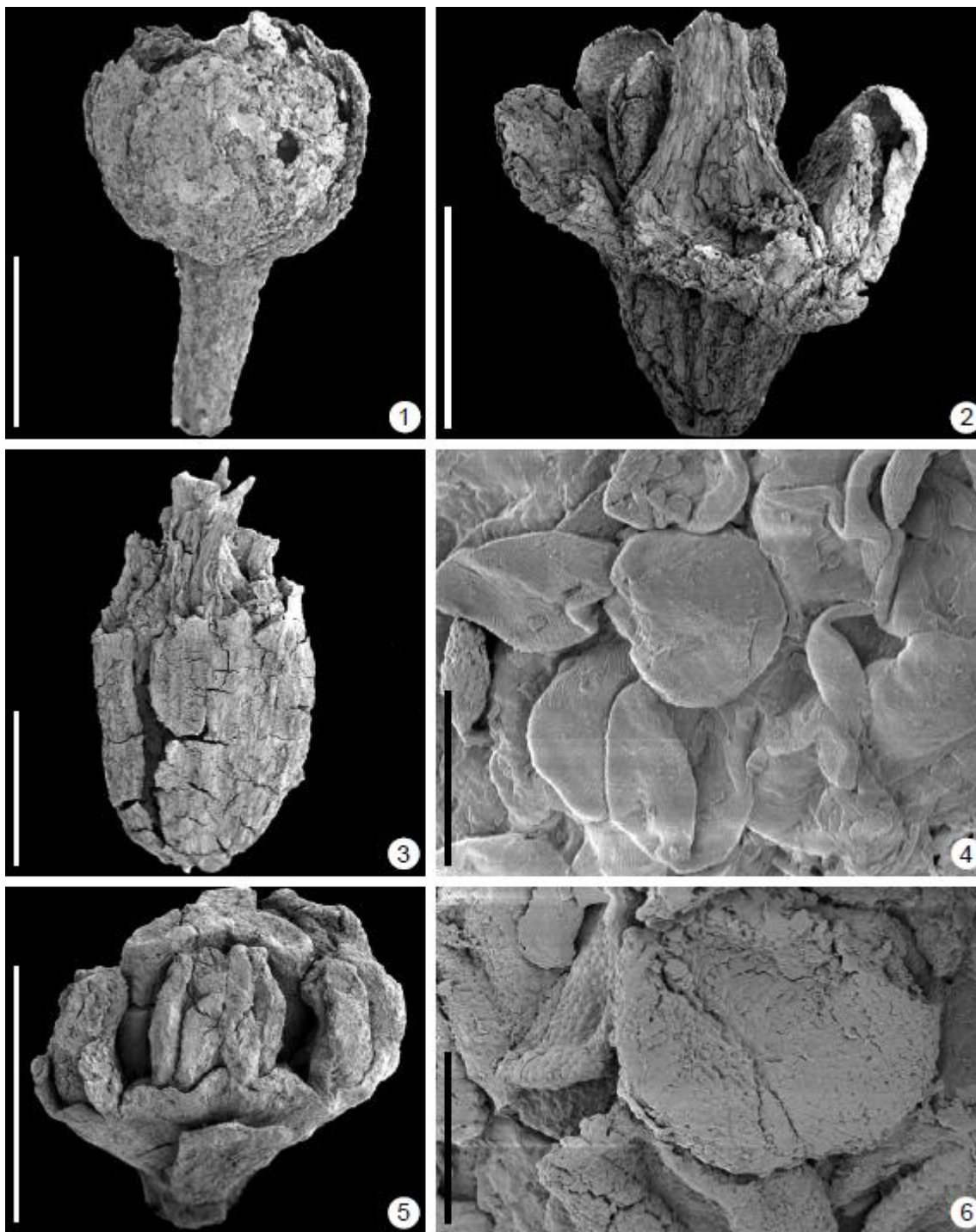


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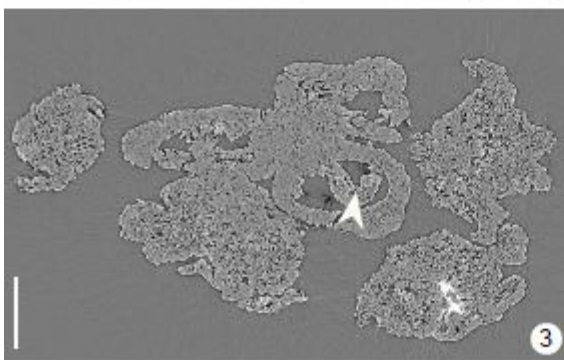
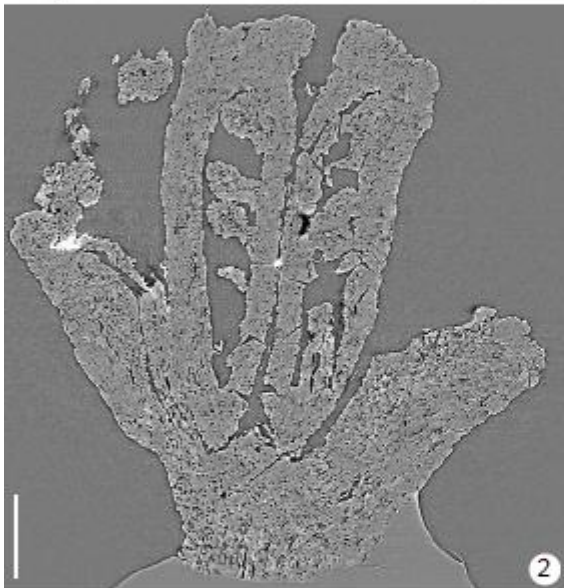
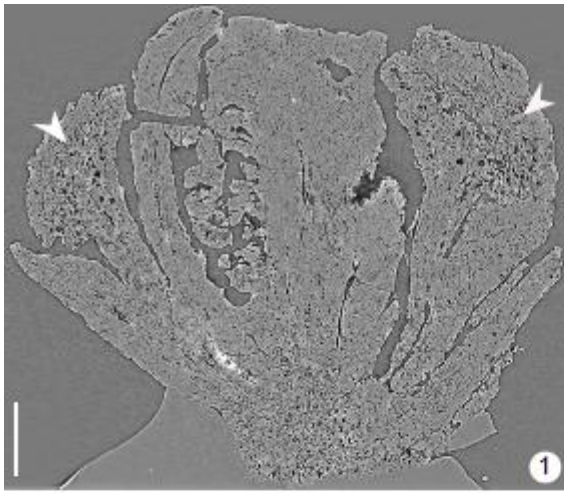


Plate 4

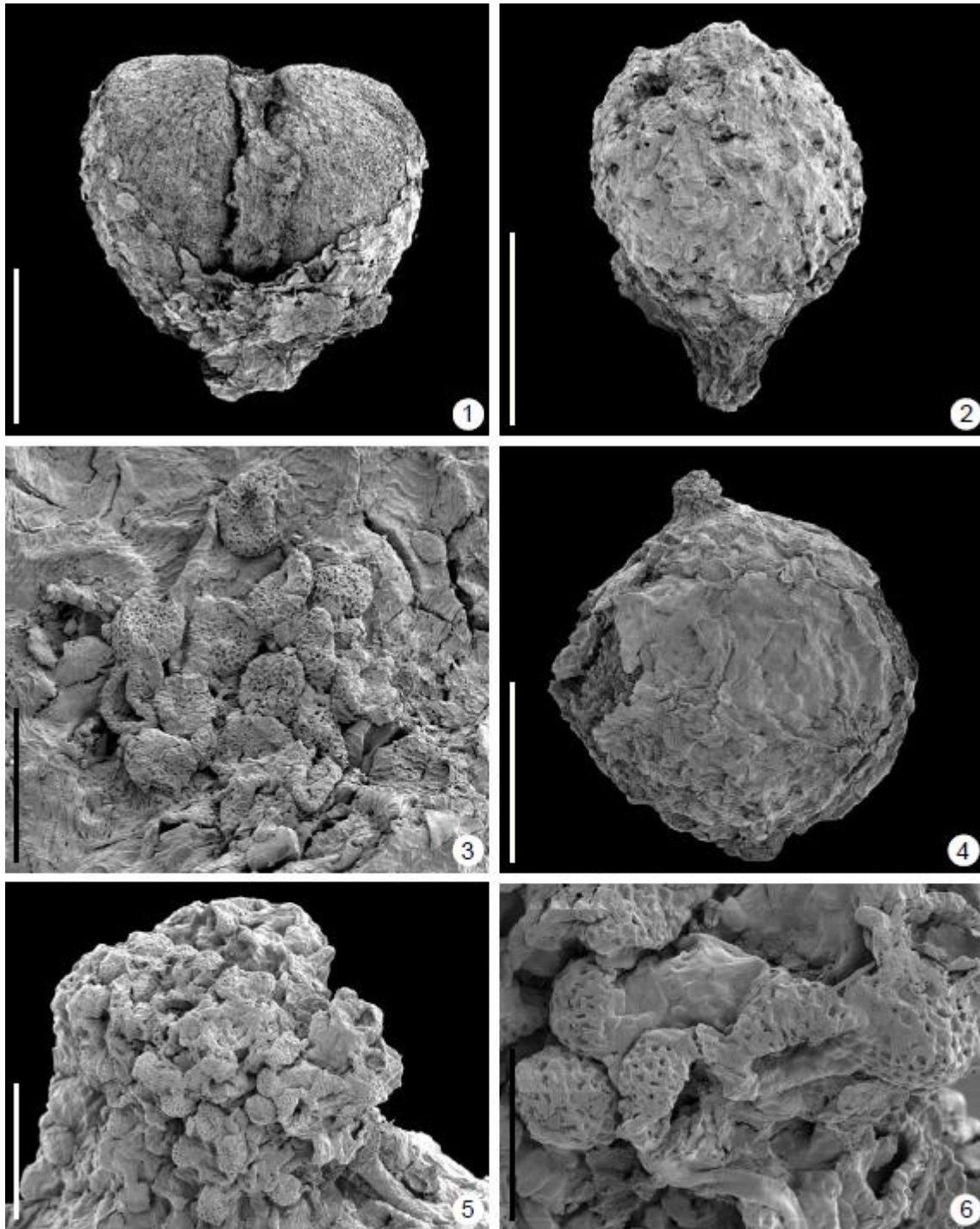


Plate 5

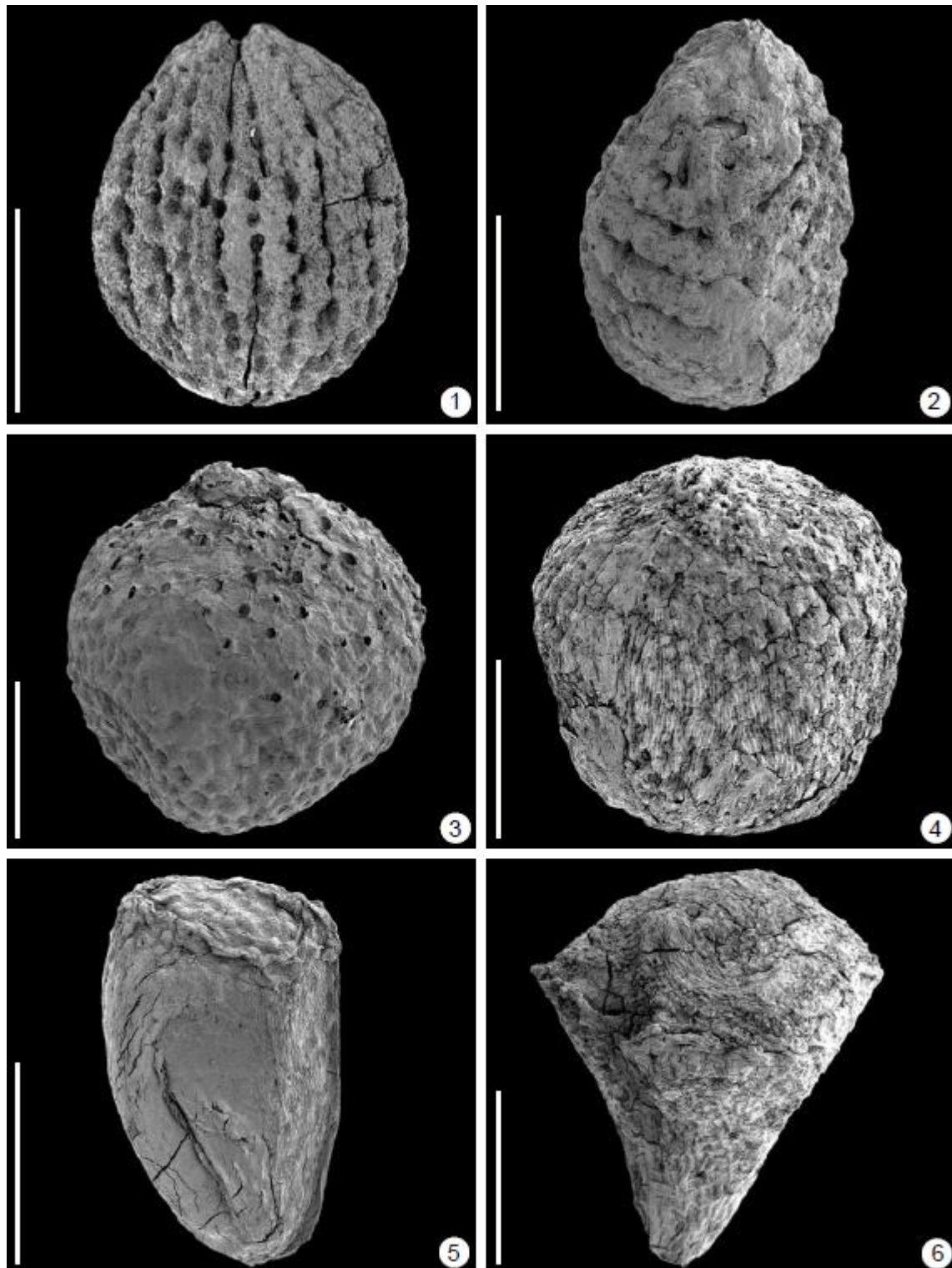


Fig. 6

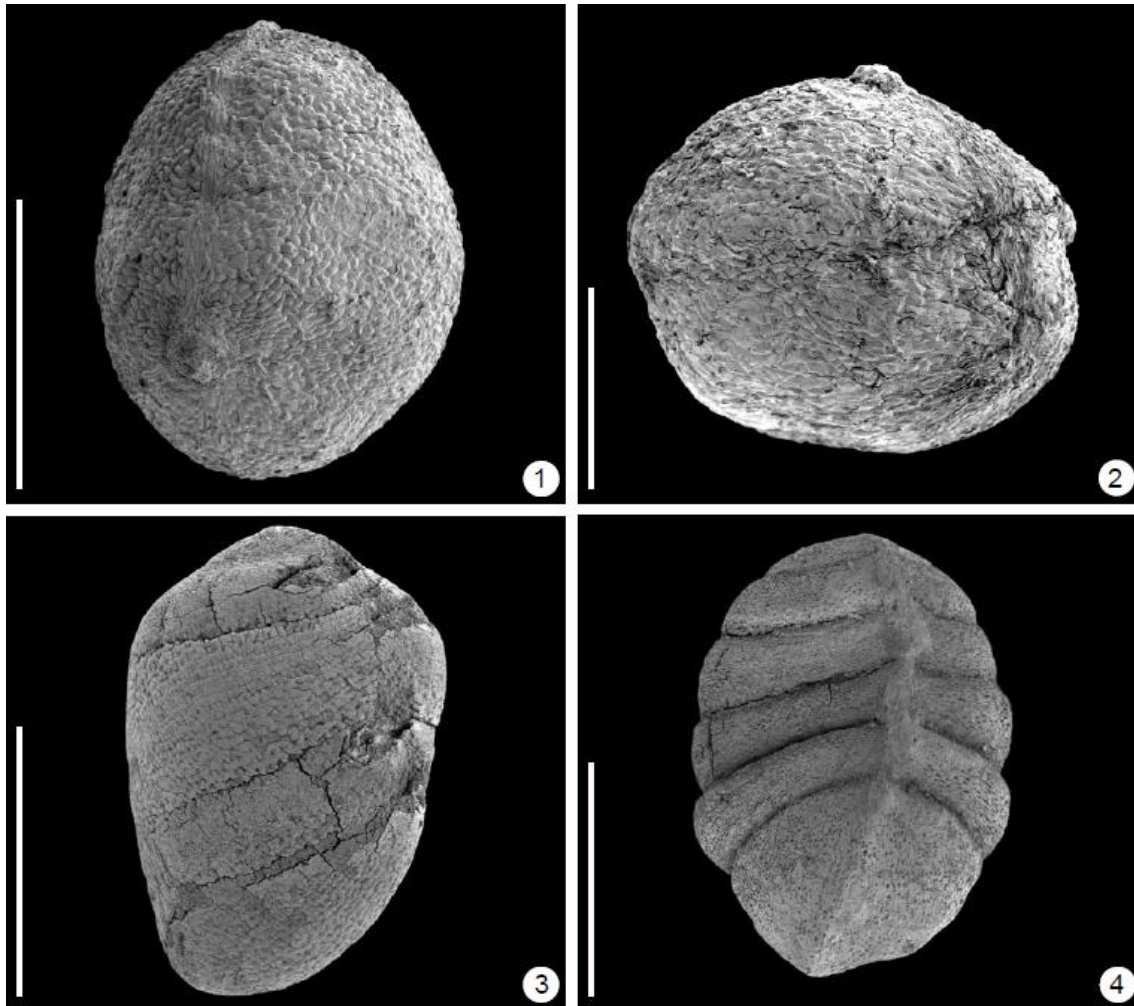


Fig. 7



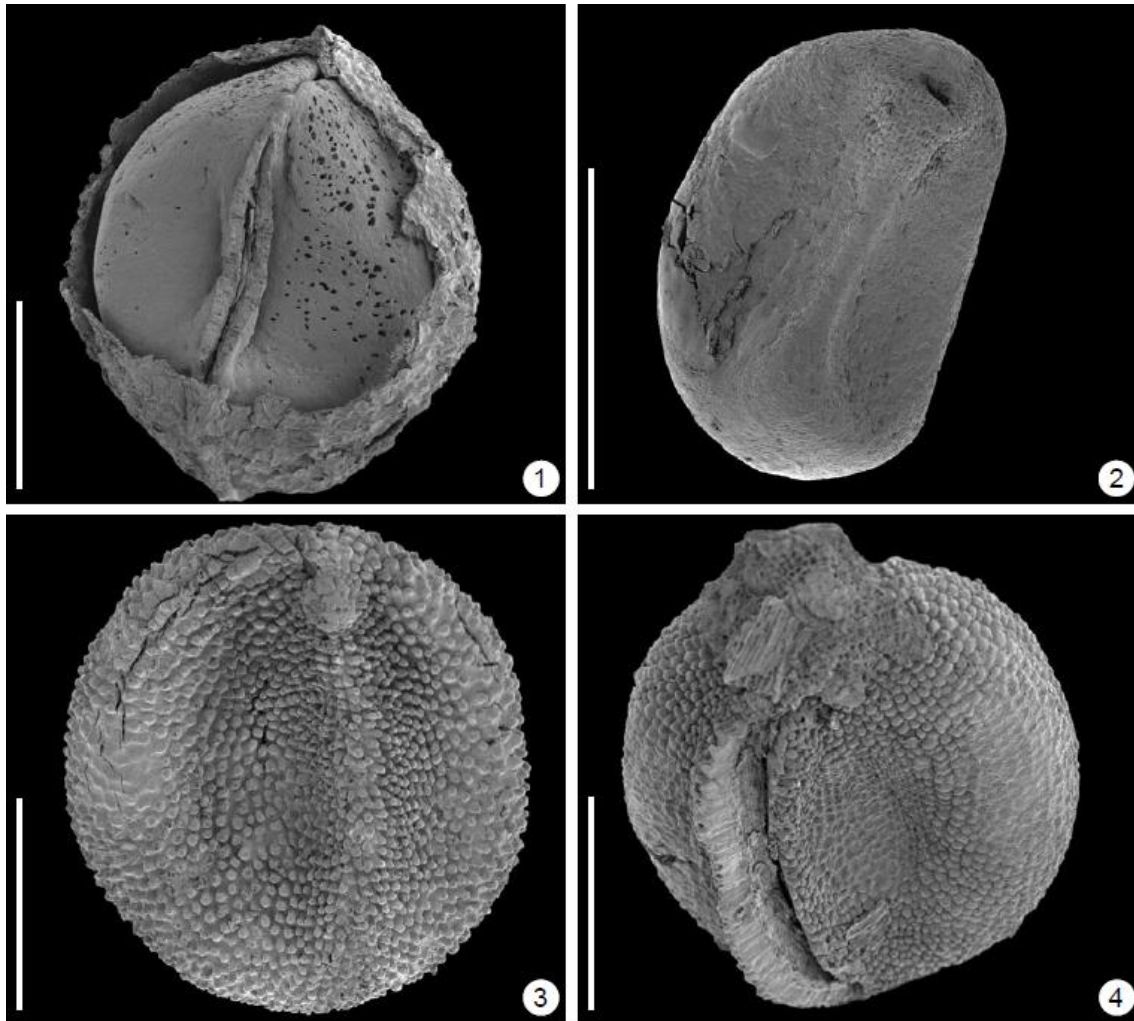


Fig. 8

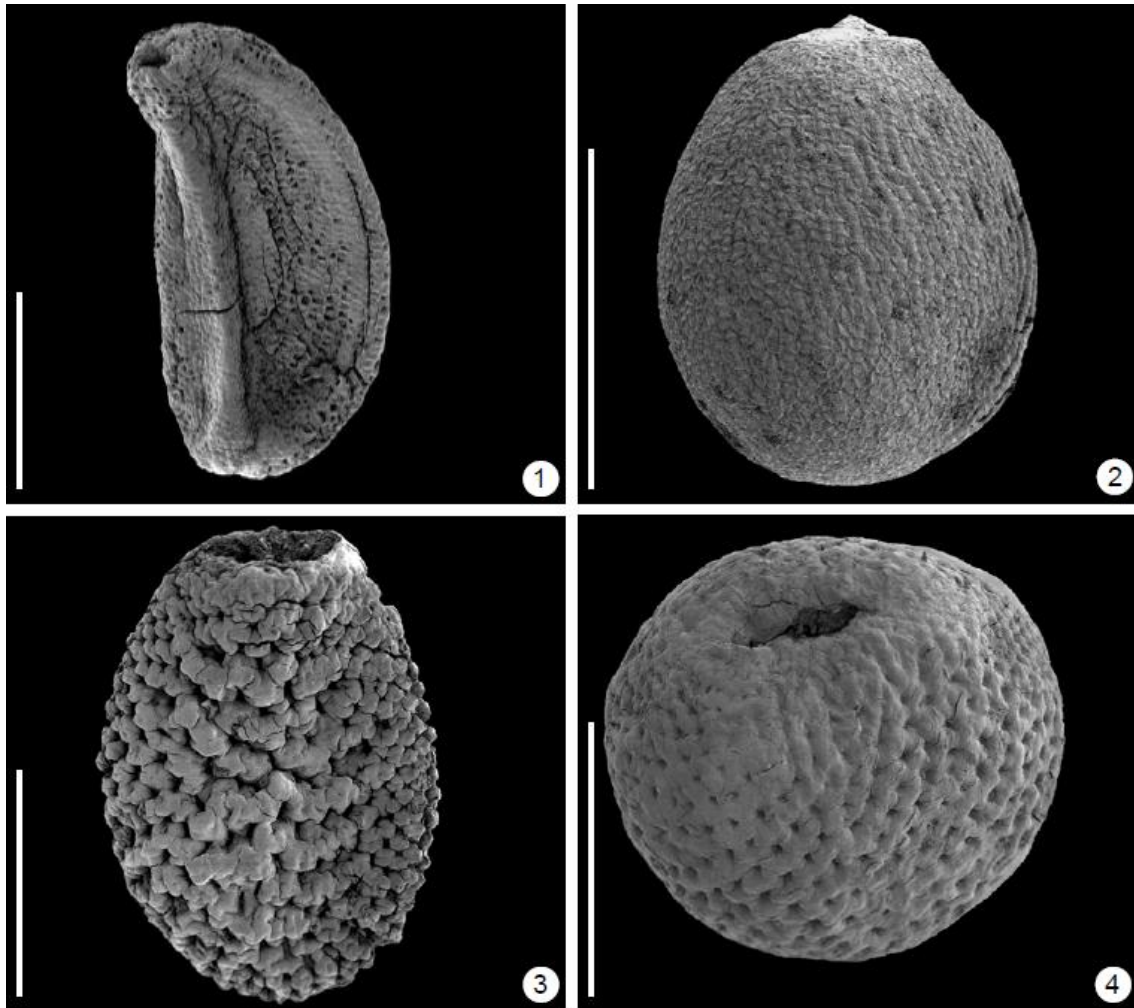


Fig. 9

### Highlights

- Describes a new Early Cretaceous flora based on palynomorphs and mesofossils.
- Insights into floristic composition of the Early Cretaceous angiosperm of Portugal.
- Supports the importance of integrated study of pollen-spores and mesofossil floras.
- Vegetation and sedimentology points to a warm climate with seasonal dry conditions.

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