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# The Nossa Senhora da Luz flora from the Early Cretaceous (early Aptian-late Albian) of Juncal in the western Portuguese Basin

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ABSTRACT. A new fossil flora is described from the Early Cretaceous of the western Portuguese Basin, based on a combined palynological-mesofossil study. The fossil specimens were extracted from samples collected in the Nossa Senhora da Luz opencast clay pit complex near the village of Juncal in the Estremadura region. The plant-bearing sediments belong to the Famalicão Member of the Figueira da Foz Formation, considered late Aptian-early Albian in age. The palynological assemblage is diverse, including 588 spores and pollen grains assigned to 30 genera and 48 species. The palynoflora is dominated by fern spores and conifer pollen. Angiosperm pollen is also present, but subordinate. The mesofossil flora is less diverse, including 175 specimens ascribed to 17 species, and is dominated by angiosperm fruits and seeds. The mesofossil flora also contains conifer seeds and twigs as well as fossils with selaginellaceous affinity. The fossil assemblage indicates a warm and seasonally dry climate for the Nossa Senhora da Luz flora.

KEYWORDS: Angiosperms, conifers, ferns, palynomorphs, mesofossils, Figueira da Foz Formation, Portugal

## INTRODUCTION

Early Cretaceous deposits exposed in western Portugal are rich in plant mesofossils crucial for understanding the large-scale changes that took place in the late Mesozoic plant communities following the initial radiation of angiosperms in the Early Cretaceous (e.g. Friis et al. 1994, 1997, 2000, 2006, 2010, 2011). Mesofossil floras from the Barremian-Albian typically are characterized by high diversity of angiosperms; in some of these Early Cretaceous floras, the number of angiosperm taxa is as high as recorded for some of the most diverse Late Cretaceous and Cainozoic floras (Eriksson et al. 2000a, b). The high diversity of angiosperms in Early Cretaceous mesofossil floras is, however, in contrast to the absence or low presence of angiosperm leaves and pollen in contemporaneous macrofossil floras and palynological assemblages. For instance, in the Early Cretaceous Chicalhão flora of Portugal, where palynological and mesofossil assemblages were prepared from the same samples, angiosperms constitute about 13% of all species identified in the palynoflora but 84% of the species identified in the mesofossil flora (Mendes et al. 2014). This discrepancy is undoubtedly linked to differences in fossilization potential and dispersal between different plant groups and plant organs, but it also contains an important ecological signal suggesting that angiosperms were diverse but ecologically subordinate in the Early Cretaceous vegetation (Friis et al. 2010, 2011).

To further investigate the systematic and ecological signals from combined palynological

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and mesofossil data, here we describe a new Early Cretaceous (late Aptian-early Albian) flora from the western Portuguese Basin. The new flora was collected in the Nossa Senhora da Luz opencast clay pit complex, near the village of Juncal and not far from the site where the Chicalhão flora was collected. Both floras belong to the Famalicão Member of the Figueira da Foz Formation, and they are similar in exhibiting a fern-conifer-dominated palynoflora and an angiosperm-dominated mesofossil flora.

## MATERIAL AND METHODS

The Early Cretaceous fossils described in this paper were isolated from six sediment samples (131, 132, 133, 134, 137, and 138) collected by M.M. Mendes and J.L. Dinis in 2008 from the Nossa Senhora da Luz opencast clay pit complex near the village of Juncal (39°55′24.5″N; 08°55′54.8″W) in the Lusitanian Basin, western Portugal (Fig. 1). The six sediment samples were collected from the same thin dark-grey and organic-rich mudstone horizon discovered in the basal part of the pit. The plant-bearing horizon was previously assigned to the Complexos Gresosos da Nazaré e Cós-Juncal (*Carta Geológica de Portugal*, Folha 26-B Alcobaça, Zbyszewski et al. 1961) and subsequently included in the Figueira da Foz Formation (Dinis 1999, 2001). The sediments from the Nossa Senhora da Luz clay pit belong to the Famalicão Member in the lower part of the Figueira da Foz Formation (Dinis 1999, 2001, Rey et al. 2006). A late Aptian to early Albian age was suggested by Dinis et al. (2002) for the Figueira da Foz lower boundary, based mainly on plant macrofossils, pollen and spores, as well as sedimentological and lithofacies correlations (Teixeira 1950, Dinis & Trincão 1991, Friis et al. 1999, Dinis et al. 2008); this was also supported by Rey et al. (2006), who suggested a late Aptian to early Albian age for the Famalicão Member of the Figueira da Foz Formation.

The bulk samples were dried in the laboratory and disaggregated in water, and mesofossils were separated with a 125 µm mesh sieve. The mesofossils were then cleaned in hydrofluoric acid (40% HF) and hydrochloric acid (10% HCl), thoroughly rinsed in water and then air-dried. The mesofossils are mostly lignified and three-dimensionally preserved, sometimes slightly compressed. The specimens were initially observed under a Nikon SMZ 800 stereomicroscope. The specimens selected for scanning electron microscopy were mounted on aluminium stubs with nail varnish, coated with gold for ca 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.

The palynomorphs were isolated by maceration from the same six samples used for extracting the mesofossils, following standard palynological processing methods (Traverse 2007). All samples were productive. They were first treated with hydrochloric acid (10% HCl) and hydrofluoric acid (40% HF), followed

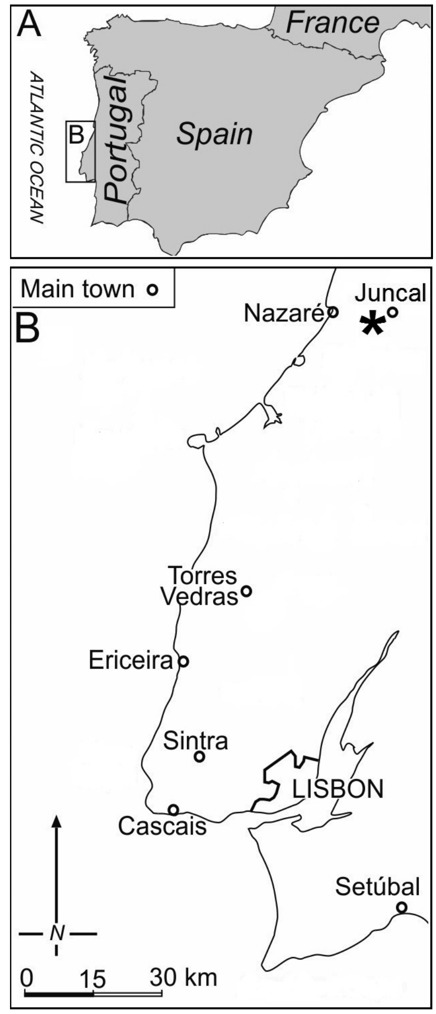


**Fig. 1**. (**A**) Location of the Lusitanian Basin in the western part of the Iberian Peninsula. (**B**) Map detail, showing the approximate position of the village of Juncal. The location of the Nossa Senhora da Luz opencast clay pit complex where the specimens were collected is indicated by an asterisk

by oxidation with nitric acid (65% $HNO_3$) with neutralization in distilled water between the acid treatments. The remaining residue was sieved through 125 µm mesh nylon sieves to remove small coal fragments. After sieving, all the material passing the nylon sieves was centrifuged and transferred to small glass vials for preservation in distilled water with a drop of HCl.

For light microscopy (LM) a droplet of residue from each sample was mounted on a slide with glycerine jelly and sealed with nail varnish. Five slides per sample were prepared. Palynomorphs were observed and counted using a Nikon Eclipse E600 microscope using 60× and 100× objectives. The position of the specimens on the slides was recorded using an England Finder.

Palynomorphs for scanning electron microscopy (SEM) were pipetted directly from the residue onto double-sided adhesive carbon tape attached to polished aluminium stubs. The suspension was then air-dried, sputter-coated with gold for 60 seconds, and examined under a Hitachi S-3700 N scanning electron microscope at 5 kV, at the Hércules Laboratory of the University of Évora, Portugal.

CS5 photoshop software was used to make an even black background for the SEM images of the mesofossils to enhance the morphology and to sharpen the outline of one pollen grain (Pl. 3, fig. d).

All the material is housed in the Geological Museum of Lisbon, Portugal (P).

## RESULTS

### THE NOSSA SENHORA DA LUZ PALYNOFLORA

The palynomorphs recovered from the Nossa Senhora da Luz opencast clay pit complex are generally well-preserved; only a few palynomorphs were too distorted for reliable identification. A total of 588 spores and pollen grains of terrestrial plants were identified and placed in 30 genera and 48 species (Tab. 1, Pl. 1–3; see also Table 1 for authorities of species reported here). Fern spores were dominant, constituting ca 62% of the total palynomorph recovery, while gymnosperm pollen accounted for 31% and angiosperm pollen for ca 7%. Spores of bryophytes and lycophytes were not recognised in the samples examined.

About a third of the fern spores were assignable to the Anemiaceae (Schizaeales), with at least eleven species belonging to five genera [*Appendicisporites* Weyland & Greifeld, *Cicatricosisporites* R.Potonié & J.Gelletich, *Costatoperforosporites* (Deák) emend. M.M.Mendes, Barrón, Batten & J.Pais, *Distaltriangulisporites* Singh, *Klukisporites* Couper]. Spores of *Cicatricosisporites* spp. and *Cicatricosisporites venustus* were particularly abundant, accounting for 21% of all palynomorphs (Pl. 1, fig. d), while other Anemiaceae spores such as *Klukisporites variegatus* (Pl. 1, fig. f) were subordinate. Spores representing Cyatheaceae/Dicksoniaceae accounted for ca 10% of all palynomorphs and included the verrucate spores of *Concavissimisporites verrucosus* (Pl. 1, fig. h) together with the psilate spores of *Cyathidites australis* (Pl. 1, fig. i) and *Cyathidites minor* (Pl. 1, fig. e). Spores of *Laevigatosporites ovatus* (Polypodiaceae), *Todisporites major* and *Todisporites minor* (Osmundaceae), together with the spores of *Patellasporites tavaredensis* (Pl. 1, fig. f) and *Leiotriletes* sp. (Pl. 1, fig. j), occurred sparsely in the samples.

Gymnosperms were represented mainly by conifer pollen, with *Classopollis* Pflug (Cheirolepidiaceae) (Pl. 2, figs a, b) and *Araucariacites australis* (Araucariaceae) (Pl. 2, fig. e) accounting for ca 17% of all palynomorphs. The remaining conifer pollen included a diversity of bisaccate grains (Pl. 2, figs c, d) referable to the genera *Alisporites* Daugherty (probably related to Pteridospermales), *Cedripites* Woodhouse (Pinaceae) and *Podocarpidites* Cookson (Podocarpaceae) (Tab. 1). Other gymnosperms were represented by pollen ascribed to the genus *Spheripollenites* (Couper) emend. Jansonius (Cupressaceae), *Cycadopites follicularis* (Cycadales or Ginkgoales) and *Eucommiidites* Erdtman (Erdtmanithecales) (Pl. 2, fig. g).

Pollen grains of angiosperms were subordinate in the assemblage, with the monoaperturate and crotonoid pollen of *Stellatopollis barghoornii* (Pl. 3, figs a, b) of uncertain botanical affinity accounting for almost half of all angiosperm pollen. The obligate tetrads of the tricolpate *Senectotetradites* Dettmann (Pl. 3, figs a, b) were represented by 8 grains, while the remaining angiosperm pollen types were represented by 1–3 grains. These rare elements include: *Afropollis zonatus* (Pl. 3, fig. d); a pollen type of uncertain systematic affinity; *Clavatipollenites* Couper (two different species) (Pl. 4, figs a, b); unassigned monocolpate grains perhaps related to the Chloranthaceae (Pl. 4, fig. c); and five different species of *Retimonocolpites* Pierce (Pl. 4, figs d–g). A single striate pollen grain ascribed to the *Saportanthus*-type was recognised under SEM (Pl. 4, fig. d). These finely striate grains were not observed under LM, probably due to their having a very thin, delicate wall.

### THE NOSSA SENHORA DA LUZ MESOFOSSIL FLORA

The mesofossil flora is small, comprising 175 specimens assigned to 17 species (Tab. 2; see also Tab. 2 for authorities of species reported here). Most specimens are fruits and seeds of angiosperms but the mesofossil flora also includes a few specimens of lycopsids and conifers.

The lycopsids are represented by a fragment of an axis (Pl. 5, figs a, b) and megaspores ascribed to the genus *Erlansonisporites* R.Potonié (Pl. 5, fig. c). The axis is ca 2.4 mm long, with microphylls arranged in an opposite and decussate phyllotaxis. Small stomata are scattered over the blade and oriented along the longitudinal axis of the blade. Phyllotaxis and the arrangement of stomata indicate a relationship with Selaginellaceae but the fragmentary nature of the axis and the lack of reproductive features preclude a more precise systematic assignment of the fossil.

**Table 1**. Spore and pollen taxa identified in the Nossa Senhora da Luz palynoflora listed in alphabetically within the genera

| Taxon | Botanical affinity |
|---|---|
| Spores | |
| *Appendicisporites erdtmanii* Pocock 1964 | Pteridophyta (Anemiaceae) |
| *Cicatricosisporites baconicus* Deák 1963 | Pteridophyta (Anemiaceae) |
| *Cicatricosisporites hallei* Delcourt & Sprumont 1955 | Pteridophyta (Anemiaceae) |
| *Cicatricosisporites myrtelli* Burger 1966 | Pteridophyta (Anemiaceae) |
| *Cicatricosisporites potomacensis* Brenner 1963 | Pteridophyta (Anemiaceae) |
| *Cicatricosisporites venustus* Deák 1963 | Pteridophyta (Anemiaceae) |
| *Cicatricosisporites* spp. | Pteridophyta (Anemiaceae) |
| *Concavissimisporites verrucosus* Delcourt & Sprumont 1955 | Pteridophyta (Cyatheaceae/Dicksoniaceae) |
| *Concavissimisporites* sp. | Pteridophyta (Cyatheaceae/Dicksoniaceae) |
| *Costatoperforosporites* spp. | Pteridophyta (Anemiaceae) |
| *Cyathidites australis* Couper 1953 | Pteridophyta (Cyatheaceae/Dicksoniaceae) |
| *Cyathidites minor* Couper 1953 | Pteridophyta (Cyatheaceae/Dicksoniaceae) |
| *Distaltriangulisporites* sp. | Pteridophyta (Anemiaceae) |
| *Impardecispora apiverrucata* (Couper) Venkatachala, Kar & Raza 1969 | Pteridophyta (Schizaeaceae) |
| *Kluklisporites variegatus* Couper 1958 | Pteridophyta (Anemiaceae) |
| *Klukisporites* sp. | Pteridophyta (Anemiaceae) |
| *Laevigatosporites ovatus* Wilson & Webster 1946 | Pteridophyta (Polypodiaceae) |
| *Leiotriletes* sp. | Pteridophyta |
| *Patellasporites tavaredensis* Groot & Groot 1962 | Pteridophyta (Incertae sedis) |
| *Pilosisporites trichopapillosus* (Thiergart 1949) Delcourt & Sprumont 1955 | Pteridophyta (Lygodiaceae) |
| *Plicatella potomacensis* (Brenner 1963) Davies 1985 | Pteridophyta (Schizaeaceae) |
| *Plicatella* spp. | Pteridophyta (Schizaeaceae) |
| *Todisporites minor* Couper 1953 | Pteridophyta (Osmundaceae) |
| *Todisporites major* Couper 1958 | Pteridophyta (Osmundaceae) |
| *Todisporites* sp. | Pteriodophyta (Osmundaceae) |
| Pollen grains (Gymnosperms) | |
| *Araucariacites australis* Cookson 1947 | Coniferophyta (Araucariaceae) |
| *Alisporites* sp. | Bisaccate pollen (?Pteridospermales) |
| *Callialasporites dampieri* (Balme 1957) Dev 1961 | Coniferophyta (Araucariaceae) |
| *Cycadopites follicularis* Wilson & Webster 1946 | ?Cycadopsida/Ginkgoopsida |
| *Cedripites* sp. | Coniferophyta (Pinaceae) |
| *Classopollis noeli* Reyre 1970 | Coniferophyta (Cheirolepidiaceae) |
| *Classopollis* spp. | Coniferophyta (Cheirolepidiaceae) |
| *Eucommiidites* sp. | BEG group (Erdtmanithecales) |
| *Inaperturopollenites* sp. | Coniferophyta (?Taxodiaceae) |
| *Spheripollenites psilatus* Couper 1958 | Coniferophyta (Cupressaceae) |
| *Spheripollenites* sp. | Coniferophyta (Cupressaceae) |
| *Podocarpidites* sp. | Coniferophyta (Podocarpaceae) |
| Undetermined bisaccate pollen grains | unknown Coniferophyta |
| Pollen grains (Angiosperms) | |
| *Afropollis zonatus* Doyle, Jardiné & Doerenkamp 1982 | Magnoliophyta (Winteraceae) |
| *Clavatipollenites*-type pollen sp. 2 | Magnoliophyta (Chloranthaceae) |
| *Clavatipollenites*-type pollen sp. 2 | Magnoliophyta (Chloranthaceae) |
| Monocolpate pollen | unknown Magnoliophyta |
| *Retimonocolpites*-type pollen sp. 1 | Magnoliophyta |
| *Retimonocolpites*-type pollen sp. 2 | Magnoliophyta |
| *Retimonocolpites*-type pollen sp. 3 | Magnoliophyta |
| *Retimonocolpites*-type pollen sp. 4 | Magnoliophyta |
| *Retimonocolpites*-type pollen sp. 5 | Magnoliophyta |
| *Stellatopollis barghoornii* Doyle 1975 | Magnoliophyta |
| *Senectotetradites* sp. (obligate tetrads) | Magnoliophyta |

*Erlansonisporites* sp. (Pl. 5, fig. c). The megaspores are trilete, ca 1.1 mm in diameter, circular equatorial in outline, typically strongly compressed proximally-distally. The perispore is abraded but shows the remains of coarsely reticulate ornamentation of raised muri formed from fibrous elements on both the proximal and distal surfaces. The laesurae of the trilete mark are short, ca 0.25 mm. This kind of megaspore is common in many of the Early Cretaceous mesofossil floras of Portugal. The genus *Erlansonisporites* is usually placed in the Selaginellaceae, based on the characteristic beaded ultrastructure of the spore wall (Taylor & Taylor 1988).

Conifers are represented by fragments of axes and seeds. The seeds (11 specimens) are all of the same type, obovate in outline, ca 2 mm long, with a pointed apex at the micropyle and a truncate base with a wide attachment scar (Pl. 5, fig. d). The axes include 19 shoot fragments referred to the cheirolepidiaceae genus *Frenelopsis* (Schenk) emend. J.Watson and 15 shoots assigned to the conifer genus *Brachyphyllum* Brongn. (Pl. 5, figs e, f). The *Brachyphyllum* specimens are mostly small apical shoots with helically arranged scale leaves with a fringed margin. Stomata are present on the abaxial surface of the scale, arranged in short longitudinal rows and each surrounded by a distinct raised ring on the outer surface (Pl. 5, fig. f).

Angiosperms constitute the major part of the Nossa Senhora da Luz mesofossil flora, with 12 species recognised based on flowers, fruits and seeds.

*Anacostia teixeiraea* (Pl. 5, figs g, h, i). This taxon is the most abundant of the angiosperm fossils in the mesofossil flora. It is based on one-seeded berries or isolated seeds. The fruit wall is thin, with a thick, usually strongly wrinkled outer cuticle (Pl. 5, figs h, i). The seeds are exotestal, with tiny crystals in the exotestal cells (Pl. 5, fig. g). *Anacostia* E.M. Friis, P.R.Crane & K.R.Pedersen is also common in other Early Cretaceous mesofossil floras of Portugal such as Catefica, Buarcos, Famalicão and Vale de Água, and in the Kenilworth and Puddledock mesofossil floras of Virginia and Maryland, USA (Friis et al. 1997). Characteristic trichotomocolpate pollen grains occur abundantly on the stigmatic area or fruit surfaces of *Anacostia* fruits described from other mesofossil floras (Friis et al. 1997), but no pollen was observed on the Nossa Senhora da Luz fruits and no trichotomocolpate pollen was reported from the dispersed palynological samples.

*Canrightia resinifera* (Pl. 5, fig. j). The species includes fruits with characteristic endotestal seeds with crystalliferous endotestal cells. It is a common element in almost all mesofossil floras recognised in the western Portuguese Basin (Friis & Pedersen 2011) and is also present in the Chicalhão flora (Mendes et al. 2014). The species was compared to the Chloranthaceae based on details of seed and pollen. No pollen grains were observed on the Nossa Senhora da Luz fruits, but pollen grains observed on the stigmatic surface of *Canrightia resinifera* from other localities (Friis & Pedersen 2011) are monocolpate, semitectate-reticulate, similar to dispersed grains of the *Retimonocolpites*-type also observed in the Nossa Senhora da Luz palynoflora.

*Canrightiopsis* sp. (Pl. 6, fig. a). The fruits are abraded, each exposing a single seed characterized by its foveolate crystalliferous endotesta. The genus *Canrightiopsis* E.M.Friis, G.W.Grimm, M.M.Mendes & K.R.Pedersen occurs commonly in almost all Early Cretaceous mesofossil floras of Portugal, including the Chicalhão flora (Friis et al. 2015). Several species were established based mainly on differences in the seed coat. Seed coat structure is not clearly exposed in the Nossa Senhora da Luz specimens and they are therefore not assigned to the genus at species level. No pollen was observed on the fruit surface from the Nossa Senhora da Luz flora, but pollen grains observed on *Canrightiopsis* fruits from other mesofossil floras are of the *Clavatipollenites*-type, with a rather coarse reticulum and beaded muri (Friis et al. 2015).

*Saportanthus dolichostemon* (Pl. 6, fig. c). The flowers are ca 3.3 mm long and 1.8 mm wide and have tepals and stamens preserved. Flowers of *Saportanthus* E.M.Friis, P.R.Crane & K.R.Pedersen are widespread in the Early Cretaceous mesofossil floras of Portugal and were assigned to core Laurales (Friis et al. 2017). *Saportanthus dolichostemon* is also present in the Chicalhão flora (Flower 3 in Mendes et al. 2014). Pollen grains found *in situ* in *Saportanthus* flowers from other mesofossil floras are trichotomocolpate or dicolpate, with a characteristic thin tectum and finely striate, fingerprint-like ornamentation. Pollen was not observed in the Nossa Senhora da Luz flowers, but a single dispersed

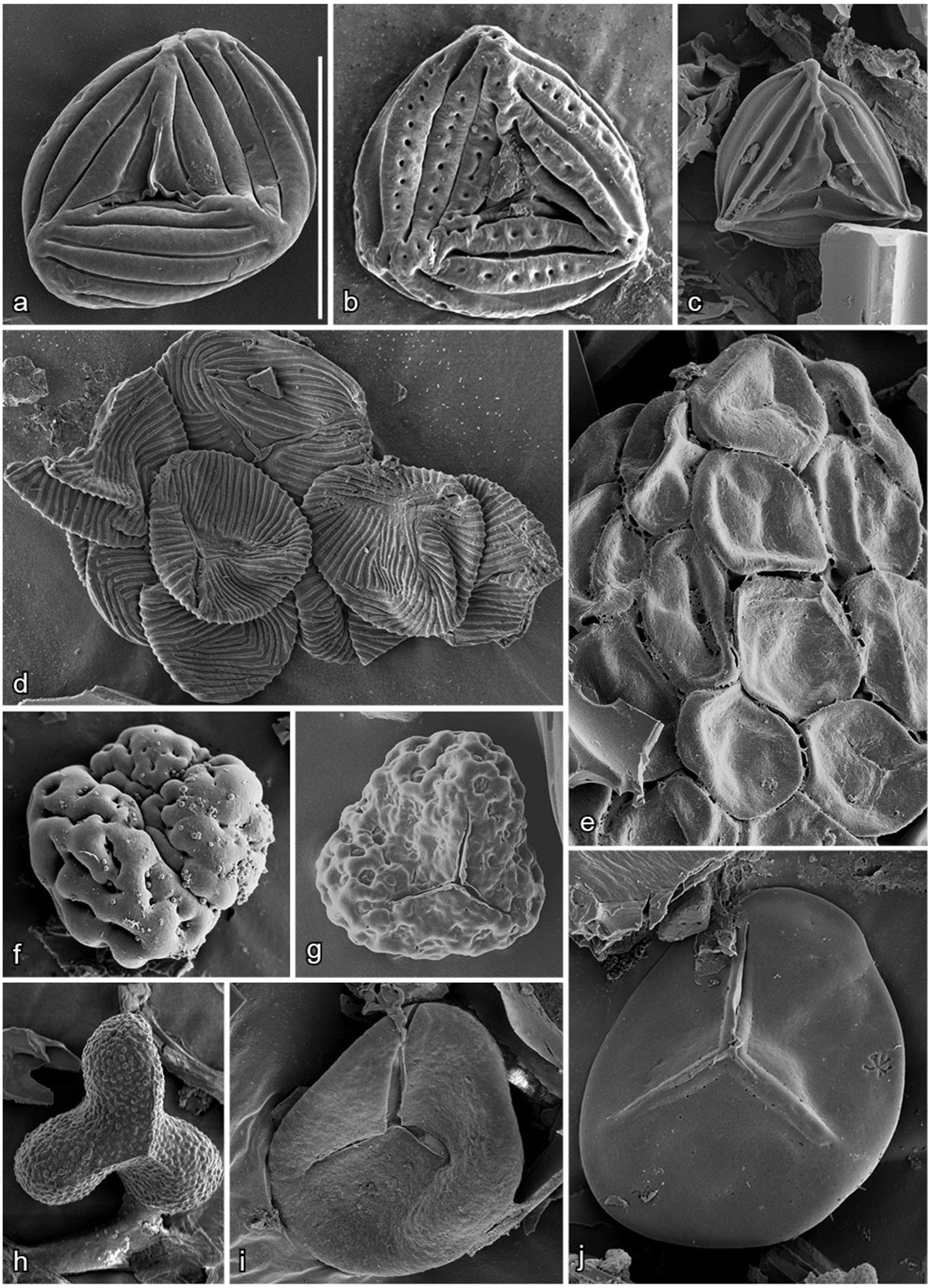


**Plate 1**. SEM micrographs of some spore types recovered from the Early Cretaceous palynoflora of the Nossa Senhora da Luz site; **a**. *Cicatricosisporites baconicus* Deák 1963 (sample Juncal 134); **b**. *Costatoperforosporites* sp. (sample Juncal 133) **c**. *Appendicisporites erdtmanii* Pocock 1964 (sample Juncal 131); **d**. Cluster of *Cicatricosisporites venustus* Deák 1963 (sample Juncal 133); **e**. Cluster of *Cyathidites minor* Couper 1953 (sample Juncal 134); **f**. Tetrade of *Patellasporites tavaredensis* Groot & Groot 1962 (sample Juncal 131); **g**. *Klukisporites variegatus* Couper 1958 (sample Juncal 134); **h**. *Concavissimisporites verrucosus* Delcourt & Sprumont, 1955 (sample Juncal 133); **i**. *Cyathidites australis* Couper 1953 (sample Juncal 132); **j**. *Leiotriletes* sp. (sample Juncal 134). Scale bars: 50 µm for all specimens

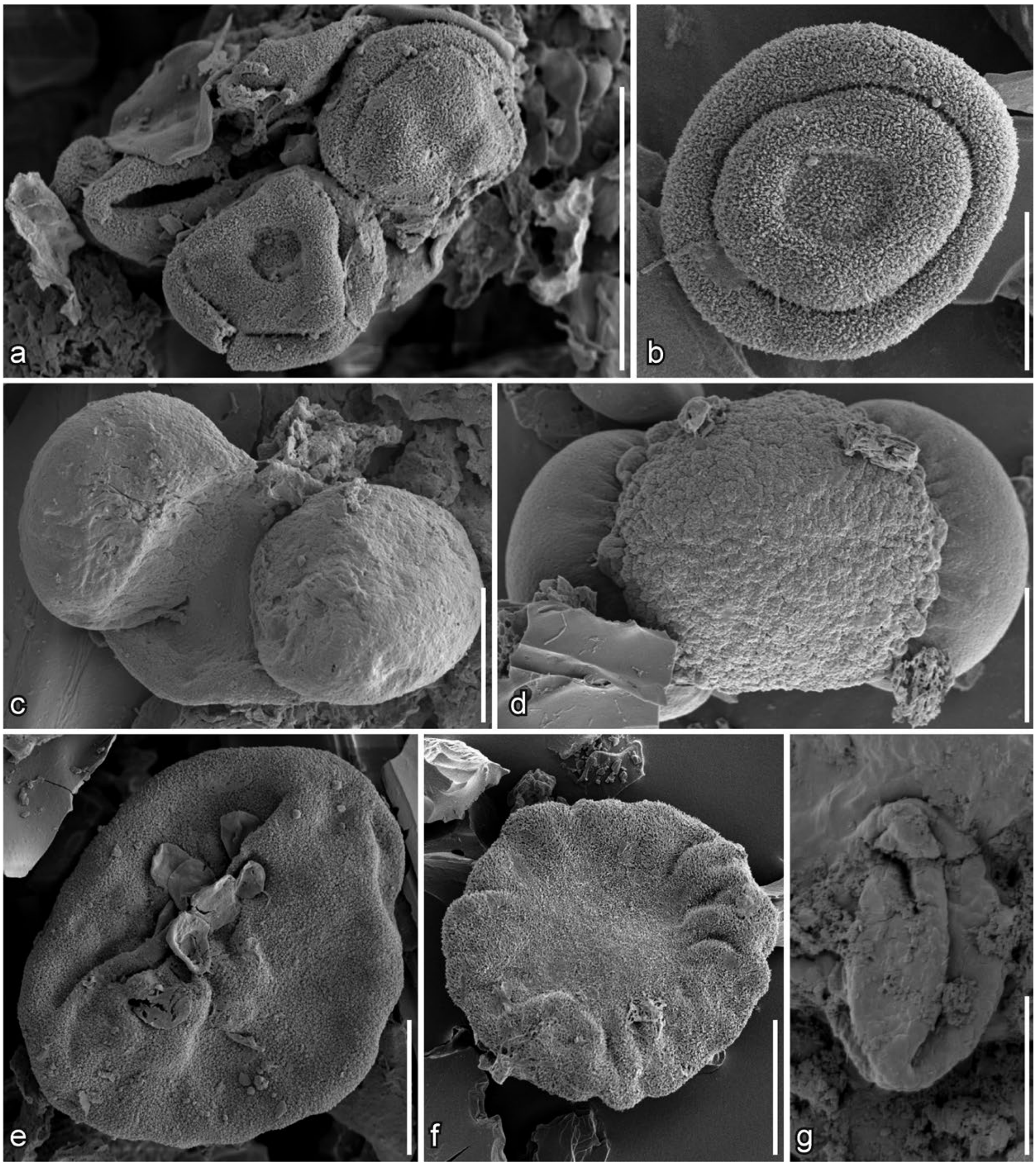


**Plate 2**. SEM micrographs of some gymnosperm pollen recovered from the Early Cretaceous palynoflora of Nossa Senhora da Luz site; **a**, **b**. *Classopollis noeli* Reyre, 1970 (sample Juncal 131); **c**, **d**. Bisaccate pollen grains (sample Juncal 138); **e**. *Araucariacites australis* Cookson 1947 (sample Juncal 131); **f**. *Callialasporites dampieri* (Balme 1957) Dev 1961 emend. Norris 1969 (sample Juncal 134); **g**. *Eucommiidites* sp. (sample Juncal 134). Scale bars: 10 µm (b, g), 20 µm (c, d, e, f), 30 µm (a)

*Saportanthus* pollen showing a finely striate tectum was observed in the SEM survey of dispersed palynomorphs, partly obscured by a larger grain (Pl. 4, fig. d).

*Gastonispermum portugallicum* (Pl. 6, fig. b). The species is based on anatropous and bitegmic exotestal seeds ca 1.5 mm long and 1 mm wide, with a smooth surface and Y-shaped micropyle opening. The seeds are elliptical in lateral view and laterally compressed with a raised rounded ridge over the raphe. The exotestal cells have thick undulate anticlinal walls that form a jigsaw-puzzle-like pattern on the outer surface. Seeds of *Gastonispermum portugallicum* are common in other mesofossil floras of Portugal (Friis et al. 2018a) but are not reported for the Chicalhão flora. Seed coat features indicate a relationship to some extant members of the Austrobaileyales-Nymphaeales (Friis et al. 2018a) and seeds of other

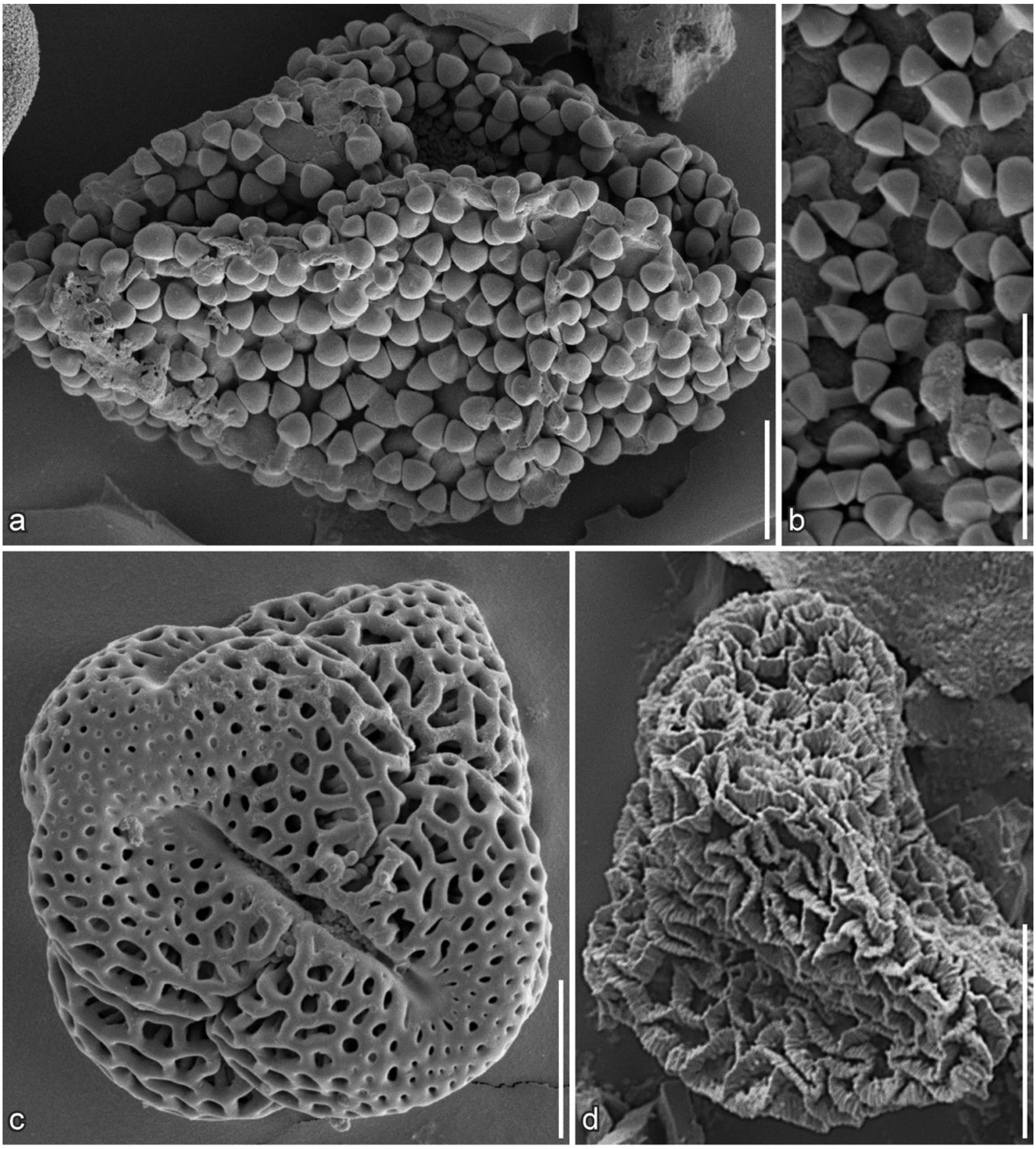


**Plate 3**. SEM micrographs of some angiosperm pollen recovered from the Early Cretaceous palynoflora of the Nossa Senhora da Luz site; **a**. *Stellatopollis barghoornii* Doyle, 1975 (sample Juncal 134); **b**. Detail of pollen grain illustrated in a, showing crotonoid sculpture pattern (sample Juncal 134); **c**. *Senectotetradites* sp. (obligate tetrad) (sample Juncal 134); **d**. *Afropollis zonatus* Doyle, Jardiné & Doerenkamp, 1982 (sample Juncal 133). Scale bars: 10 μm for all specimens

Early Cretaceous taxa such as *Nitaspermum* E.M.Friis, P.R.Crane & K.R.Pedersen from the Potomac Group of Virginia and Maryland, USA (Friis et al. 2018b).

Unnamed angiosperm 1 (Pl. 6, fig. d). This taxon includes fragments of one-seeded fruits. The fruits are thin-walled and partly abraded, including a single exotestal seed with a deep slit in the hilar area. The seed is smooth and shiny, circular to broadly elliptic in outline and ca 1.4 mm long. No details of seed wall or micropyle are exposed in the seeds from the Nossa Senhora da Luz flora, but similar fruits and seeds are known from other mesofossil floras in Portugal, including the Chicalhão flora (Plate VIII: 1 in Mendes et al. 2014) and are part of the highly diverse complex of seeds including *Gastonispermum* E.M.Friis, P.R.Crane & K.R.Pedersen and *Nitaspermum*.

Unnamed angiosperm 2 (Pl. 6, fig. e). The taxon includes anatropous and exotestal seeds, almost spherical to broadly ovate, ca 1.1 mm

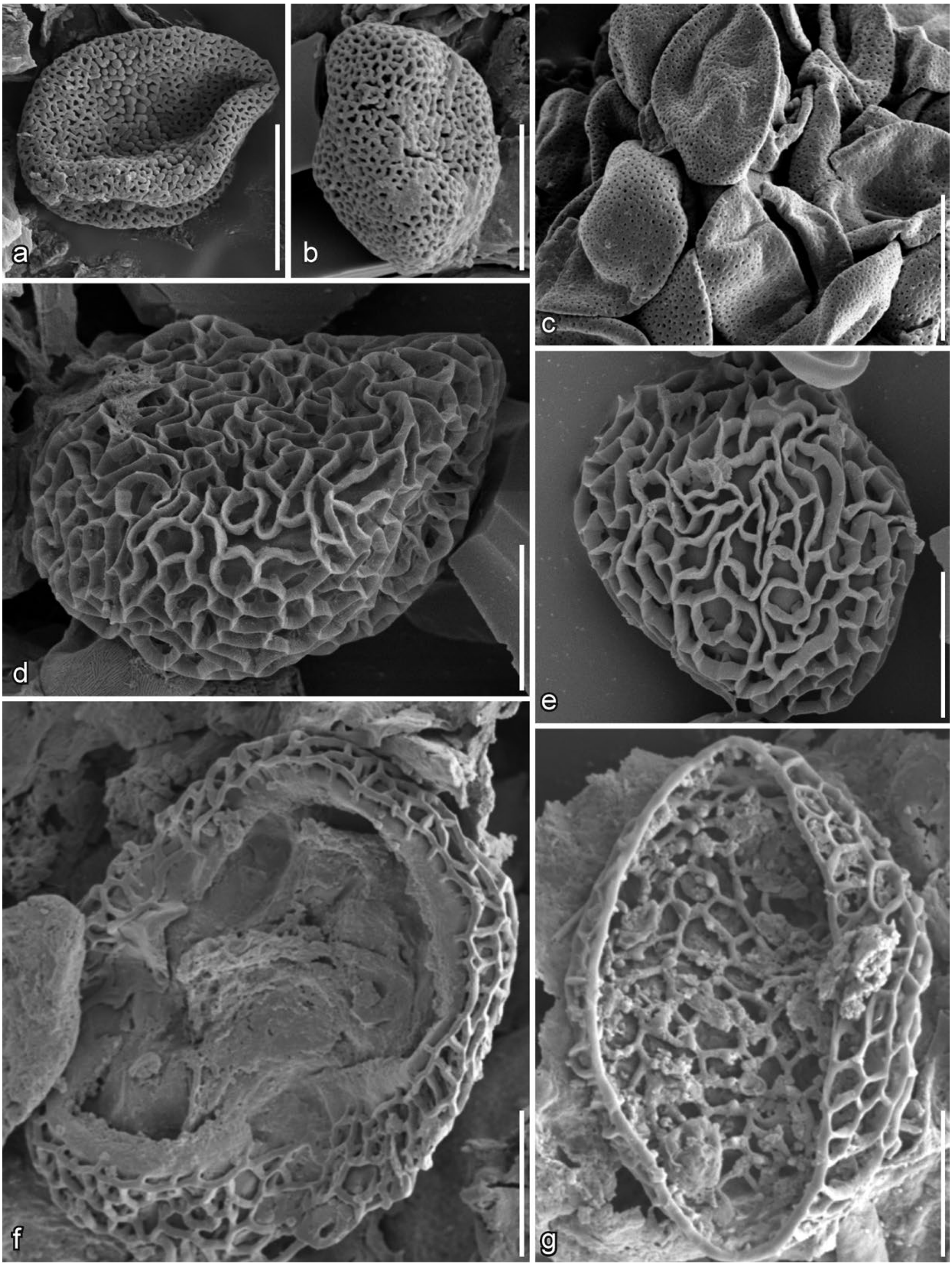


**Plate 4**. SEM micrographs of some angiosperm pollen recovered from the Early Cretaceous palynoflora of the Nossa Senhora da Luz site; **a**. *Clavatipollenites*-type pollen sp. 1. (sample Juncal 133); **b**. *Clavatipollenites*-type pollen sp. 2 (sample Juncal 138); **c**. Cluster of monocolpate pollen grains (sample Juncal 134); **d**. *Retimonocolpites*-type pollen sp. 1 (sample Juncal 132); **e**. *Retimonocolpites*-type pollen sp. 2 (sample Juncal 134); **f**. *Retimonocolpites*-type pollen sp. 3 (sample Juncal 133); **g**. *Retimonocolpites*-type pollen sp. 4 (sample Juncal 133). Scale bars: 10 μm for all specimens

long, with surface ornamentation of short blunt spines. In the Nossa Senhora da Luz specimens the spines are best developed around the hilar-micropylar region and over the raphe. Similar seeds are common in other Early Cretaceous mesofossil floras of Portugal, particularly

**Table 2**. List of mesofossil specimens recorded in the Nossa Senhora da Luz mesoflora listed within different groups

| | Botanical affinity |
|---|---|
| Lycophytes | |
| *Erlansonisporites* sp. | Lycopsid, Selaginellaceae |
| Lycopsid axis | Lycopsid, uncertain |
| Conifers | |
| Conifer seeds | Coniferales, uncertain |
| *Frenelopsis* sp. | Coniferales, Cheirolepidiaceae |
| *Brachyphyllum* sp. | Coniferales, uncertain |
| Angiosperms | |
| *Anacostia teixeiraea* E.M.Friis, P.R.Crane & K.R.Pedersen | Angiospermae, uncertain |
| *Canrightia resinifera* E.M.Friis & K.R.Pedersen | Angiospermae, Chloranthaceae |
| *Canrightiopsis* sp. | Angiospermae, Chloranthaceae |
| *Saportanthus dolichostemon* E.M.Friis, P.R.Crane & K.R.Pedersen | Angiospermae, Laurales |
| *Gastonispermum portugallicum* E.M.Friis, P.R.Crane & K.R.Pedersen | Angiospermae, Austrobaileyales-Nymphaeales |
| Unnamed angiosperm 1 | Angiospermae, Austrobaileyales-Nymphaeales |
| Unnamed angiosperm 2 | Angiospermae, Austrobaileyales-Nymphaeales |
| Unnamed angiosperm 3 | Angiospermae, Magnoliales |
| Unnamed angiosperm 4 | Angiospermae, uncertain |
| Unnamed angiosperm 5 | Angiospermae, uncertain |
| Unnamed angiosperm 6 | Angiospermae, uncertain |
| Unnamed angiosperm 7 | Angiospermae, uncertain |

in the Famalicão flora (figures 18–20 in Friis et al. 1999) and were also reported from the Chicalhão flora (Pl. VIII: 3, 4 in Mendes et al. 2014). These seeds are also thought to be closely related to *Gastonispermum* and *Nitaspermum*.

Unnamed angiosperm 3 (Pl. 6, fig. f). The taxon includes almost-spherical groups of seeds adhering in a row, ca 1.4 mm in diameter. The seeds belong to a larger complex of extinct magnolialean taxa that are extremely common in other Early Cretaceous mesofossil floras of Portugal, particularly in the Famalicão mesofossil flora where more than 2500 specimens were recorded (E.M. Friis, P.R. Crane & K.R. Pedersen, accepted).

Unnamed angiosperm 4 (Pl. 6, fig. g). Elongate, elliptical and anatropous seeds, ca 2 mm long and 1 mm wide, with a reticulate surface formed from the equiaxial facets of the outer epidermis, are represented by 5 specimens. This seed type is also known from other Early Cretaceous mesofossil floras of Portugal, but details of anatomy are poorly known and the systematic affinity is not yet established.

Unnamed angiosperm 5 (Pl. 6, fig. h). A single elongate fruit with several seeds. This taxon is represented by only a single specimen. The fruit is elliptical in lateral view and almost circular in transverse section, ca 2.4 mm long and 1.2 mm wide. The fruit wall is thin and encloses a number of seeds. As the fruit wall completely covers the seeds, the seed morphology was not observed by SEM.

Unnamed angiosperm 6 (Pl. 7, figs a, b). Exotestal seed with finely reticulate surface ornamentation and a distinct raphal ridge. This taxon includes 3 seeds. The seeds are poorly preserved, elliptical in outline, ca 1.6 mm long and 1.1 mm wide, with palisade-shaped exotestal cells arranged in longitudinal rows. Similar seeds are known from other Early Cretaceous mesofossil floras of Portugal (e.g. Pl. IX: 2 in Mendes et al. 2014); further information is needed before these can be formally described and their systematic affinity established.

Unnamed angiosperm 7 (Pl. 7, fig. c). Fruit with strongly curved stylar region. This specimen is fragmentary, with only the apical part preserved. The stylar region is also fragmented but clearly shows a strongly recurved style. It is similar to one-seeded fruits from the Vale de Água and Famalicão mesofossil floras (figure 7c–e in Friis et al. 1994). Further information is needed before these can be formally described and their systematic affinity established.

## DISCUSSION

### COMPOSITION AND ENVIRONMENTAL SIGNAL OF THE NOSSA SENHORA DA LUZ FLORA

The Nossa Senhora da Luz palynoflora is qualitatively and quantitatively dominated by spores of ferns related to the Anemiaceae, Cyatheaceae/Dicksoniaceae and Osmundaceae,

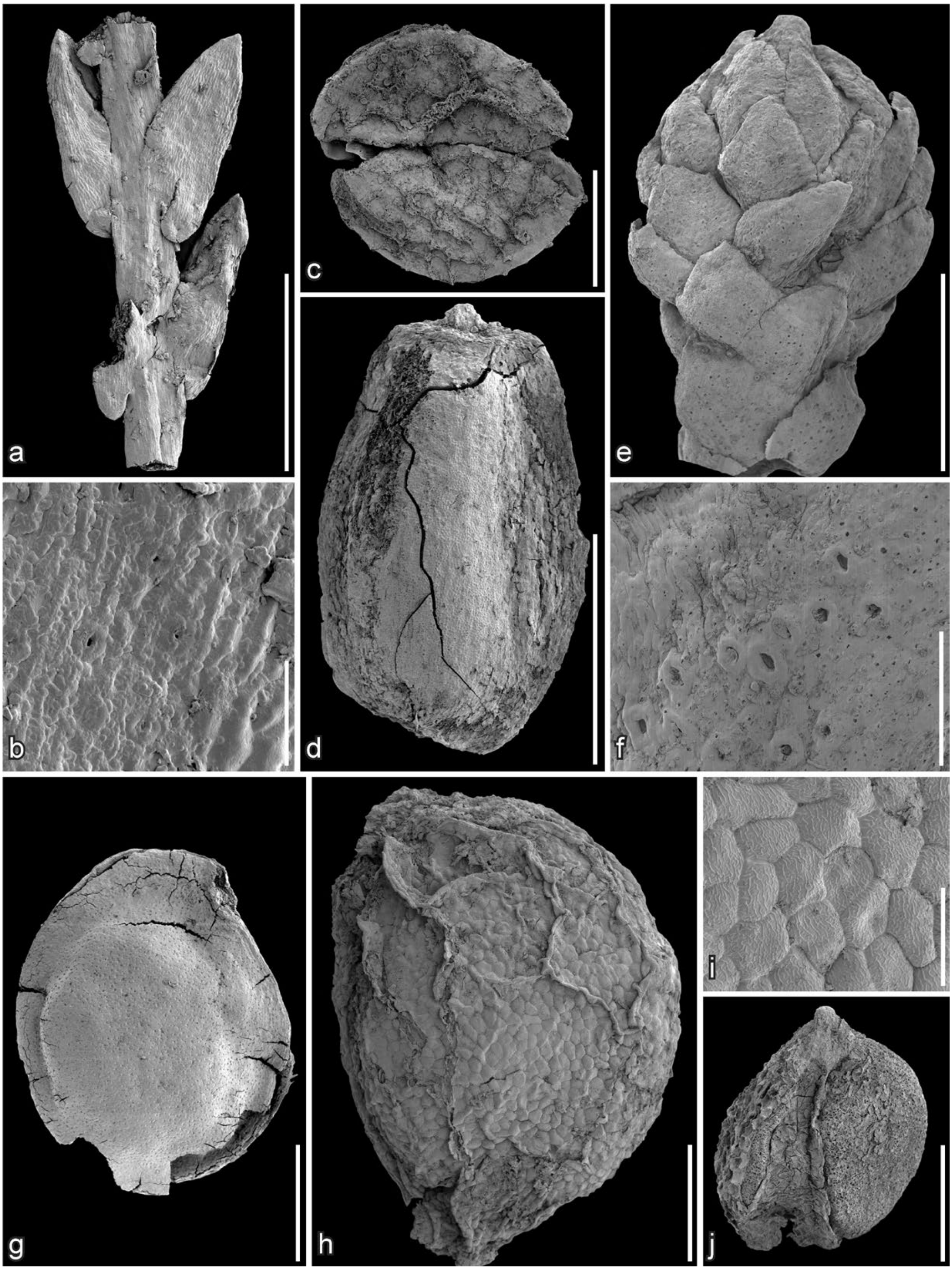


**Plate 5**. SEM micrographs of some mesofossils recovered from the Early Cretaceous mesoflora of the Nossa Senhora da Luz site; **a**. Lycopsid axis, showing microphyles arranged in opposite and decussate phyllotaxis (P0345, sample Juncal 138); **b**. Microphyll surface, showing epidermal cells and stomata distribution (P0345, sample Juncal 138); **c**. *Erlansonisporites* sp. megaspore, showing finely reticulate exine structure (P0182, sample Juncal 137); **d**. Conifer seed, showing pointed apex and wide attachment scar (P0173, sample Juncal 133); **e**. Shoot of *Brachyphyllum* sp., showing small helically arranged leaves (P0170, sample Juncal 137); **f**. Abaxial surface of *Brachyphyllum* sp., showing stomata irregularly arranged in longitudinal rows (P0170, sample Juncal 137); **g**. Seed of *Anacostia teixeiraea* E.M.Friis, P.R.Crane & K.R.Pedersen, showing tiny crystals in exotestal cells (P0175, sample Juncal 131); **h**. Fruit of *Anacostia teixeiraea* E.M.Friis, P.R.Crane & K.R.Pedersen, showing typically wrinkled cuticle (P0352, sample Juncal 138); **i**. Detail of *Anacostia* fruit surface, showing wrinkled outer cuticle (P0352, sample Juncal 138); **j**. *Canrightia resinifera* E.M.Friis & K.R.Pedersen, exposing two seeds in lateral view (P0178, sample sample Juncal 137). Scale bars: 1 mm (a, d); 50 µm (b); 500 µm (c, g, h, i); 2 mm (e); 200 µm (f); 100 µm (j)

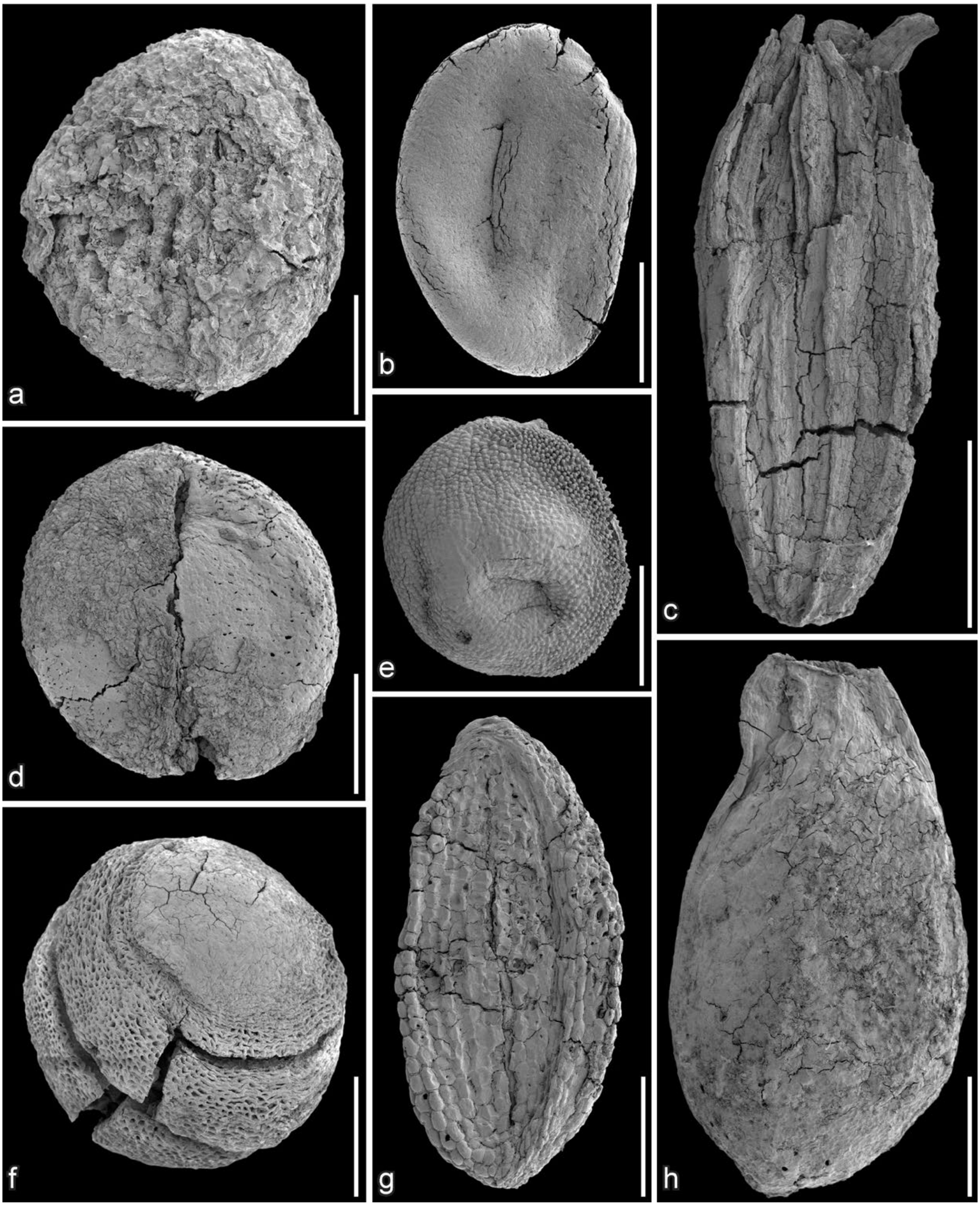


**Plate 6**. SEM micrographs of some mesofossils recovered from the Early Cretaceous mesoflora of the Nossa Senhora da Luz site; **a**. Fruit of *Canrightiopsis* sp., showing foveolate crystalliferous endotesta (P0176, sample Juncal 138); **b**. Exotestal seed, showing smooth surface and Y-shaped micropyle opening (P0171, sample Juncal 137); **c**. Flower of *Saportanthus dolichostemo*n E.M.Friis, P.R.Crane & K.R.Pedersen, probably preserved in anthetic stage (P0351, sample Juncal 138); **d**. Fruit with exotestal seed with smooth surface and deep hilar slit (P0177, sample Juncal 138); **e**. Exotestal seed, exposing verrucate outer surface (P0347, sample Juncal 134); **f**. Seeds in row, exposing parenchyma cells (P0179, sample Juncal 138); **g**. Anatropous seed, showing reticulate surface (P0348, sample Juncal 134); **h**. Elongate fruit, probably with several seeds inside (P0349, sample Juncal 134). Scale bars: 500 µm (a, b); 100 µm (c); 500 µm (d, e, f, g, h)

represented by more than 25 species constituting about 62% of all palynomorphps. Pollen of non-angiospermous seed plants is also common, with more than 13 species forming about 31% of all palynomorphs, while angiosperm pollen accounting for about 7% of the palynomorphs in 11 species. In number of specimens and number of taxa the mesofossil flora is much less

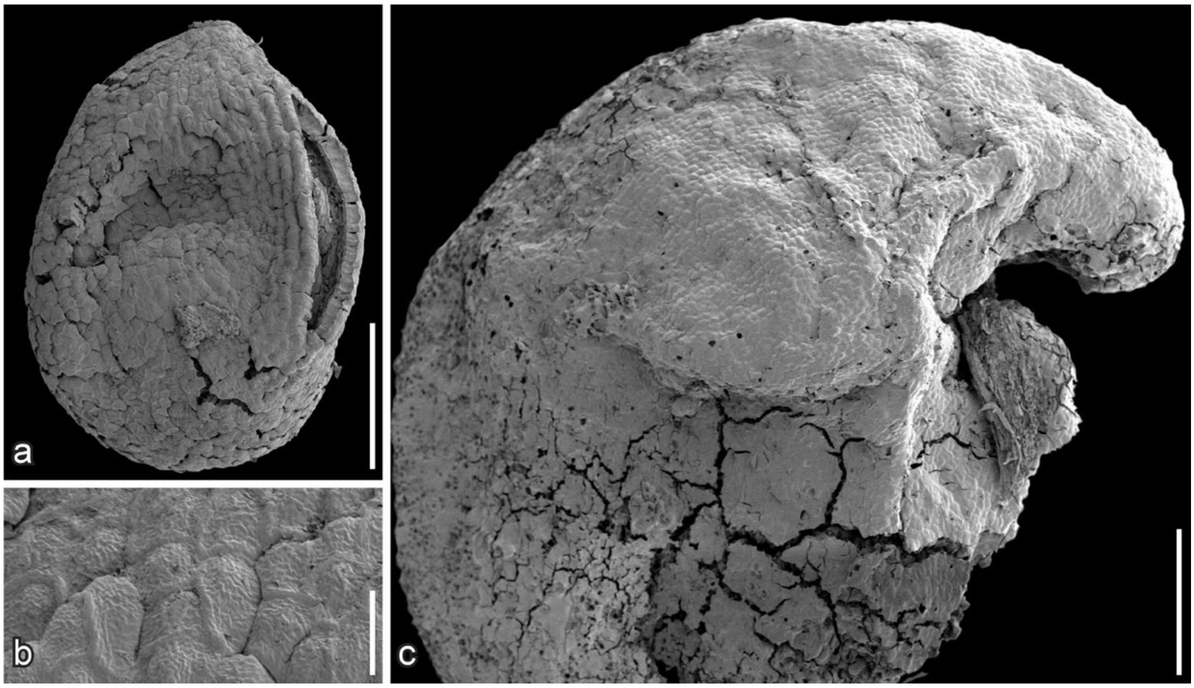


**Plate 7**. SEM micrographs of some mesofossils recovered from the Early Cretaceous mesoflora of the Nossa Senhora da Luz site; **a**. Exotestal seed, showing finely reticulate surface ornamentation and distinct raphal ridge (P0346, sample Juncal 134); **b**. Detail of exotestal seed surface, showing palisade-shaped exotestal cells (P0346, sample Juncal 134); **c**. Fruit, showing sturdy curved stylar region (P0350, sample Juncal 134). Scale bars: 500 μm (a, c); 50 μm (b)

diverse than the palynoflora, and it also differs from the palynoflora in taxonomic composition. The Nossa Senhora a Luz mesoflora is clearly dominated by angiosperms, represented by 12 species which comprise about 64% of the diversity of all mesofossils. Fern spores are often used as indicators of humid habitats. However, many Early Cretaceous ferns known from macrofossil remains, such as *Pelletixia* J.Watson & C.R.Hill and *Ruffordia* Seward (Anemiaceae), *Onychiopsis* Yokoyama (Dicksoniaceae) and *Weichselia* Stiehler (Matoniaceae), have small coriaceous leaves and spores protected in capsule-like structures, suggesting xeric rather than humid conditions (Friis & Pedersen 1990, Watson & Alvin 1996). Although no macrofossil or mesofossil remains of ferns have been detected in the Nossa Senhora da Luz deposits, xeromorphic conditions are also indicated by the abundant *Classopollis* pollen, which constitutes 10.9% of all palynomorphs. *Classopollis* pollen is produced by the extinct conifer family Cheirolepidiaceae, which in vegetative morphology shows strongly xeromorphic traits (Batten & Uwins 1985). In the mesofossil flora the Cheirolepidiaceae family constitutes 10.9% of all mesofossils (the same as in the palynoflora) and is represented by 19 shoot fragments of *Frenelopsis*. *Brachyphyllum*, the only other conifer represented in the mesofossil flora by shoot fragments, also shows xeromorphic traits and constitutes 8.6% of all mesofossils. Conifer diversity is higher in the palynoflora than in the mesofossil flora. Pollen of *Araucariacites australis*, thought to represent the Araucariaceae (Schrank & Mahmoud 1998), constitutes 7.7% of the palynomorphs and is also thought to signal xeromorphic conditions (Batten & Uwins 1985). Other conifers are subordinate in the flora. The majority of conifers in the Nossa Senhora da Luz flora probably were wind-pollinated and the pollen may have been transported to the deposition basin from a drier hinterland. The relatively high number of conifer shoots in the mesofossil flora indicates, however, that conifers may also have been closer to the basin.

Most angiosperm pollen grains are monocolpate non-eudicots. The only exception is the eudicot genus *Senectotetradites*, which has tricolpate pollen. No eudicot angiosperm was identified among the mesofossils. In cases where the systematic affinity could be established with relative high confidence, the mesofossils represent early-diverging lineages at the level of Nymphaeales-Austrobaileyales, Chloranthaceae, Magnoliales and Laurales. The ecological signal from the angiosperm remains is not strong, but their dominance in the mesofossil flora and the preservation of floral structures indicate that they probably were not transported over long distances and may have grown close to the depositional basin, perhaps under moister conditions than those of the ferns, conifers and other non-angiospermous seed plants.

The diversity of the mesofossil assemblage is low as compared to Early Cretaceous mesofossil floras recorded from localities such as Buarcos, Catefica, Famalicão and Vale de Água (Eriksson et al. 2000b, Friis et al. 2010, 2011), but comparable to the diversity of Chicalhão mesofossil flora collected close to the Nossa Senhora da Luz site. In general terms, however, the two species-poor mesofossil floras are comparable to the more species-rich mesofossil floras in their predominance of angiosperms.

Combined palynological-mesofossil studies were carried out for two other Early Cretaceous floras from Portugal: the Vale Painho flora (Mendes et al. 2008a, b, 2011) and Chicalhão flora (Mendes et al. 2014), both collected in the Juncal area close to where the Nossa Senhora da Luz flora was collected.

The Vale Painho flora is from the informal Bombarral formation of the earliest Cretaceous (probably of Berriasian age) and is distinct from the two other floras in many respects. It lacks angiosperms and is otherwise characterized by conifers and ferns and by two distinct members of the BEG-group – *Erdtmanispermum* K.R.Pedersen, P.R.Crane & E.M.Friis and *Raunsgaardispermum* M.M.Mendes, J.Pais & E.M.Friis – which are not recorded from the younger Early Cretaceous floras of Portugal. The Nossa Senhora da Luz and Chicalhão floras are both recovered from the Famalicão Member of the Figueira da Foz Formation (late Aptian-early Albian) and are in general composition very similar. In both the Chicalhão flora and the Nossa Senhora da Luz flora, fern spores and conifer pollen grains dominate the palynological assemblages quantitatively as well as qualitatively, while angiosperm pollen grains are subordinate. However, the results presented here also show that angiosperm pollen grains are more diverse in the Nossa Senhora da Luz flora, including grains of *Afropollis zonatus* and *Stellatopollis barghoornii* not recognised in the Chicalhão palynoflora. Furthermore, in both the Chicalhão and Nossa Senhora da Luz floras there is a marked discrepancy in taxonomic composition between the mesofossil and palynological assemblages. In both floras the mesofossil components are dominated by angiosperms. The Nossa Senhora da Luz mesofossil flora shares some taxa with that from Chicalhão, supporting their close stratigraphic position in the lower part of the Figueira da Foz Formation.

## CONCLUSIONS

The dominance of angiosperms in the Nossa Senhora da Luz mesofossil flora is in marked contrast to the taxonomic composition of the Nossa Senhora da Luz palynological assemblage, which is dominated by ferns. This corroborates earlier observations that different organs may represent different parts of the total diversity of the local and regional area at the time of deposition (Friis et al. 2011, Mendes et al. 2011, 2014). The discrepancy between the palynological and mesofossil signals may very well be related to differences in pollen and spore production, dispersion mode, distance of the parent plants to the depositional basin, and mainly the degree of resistance of plant remains during transport and fossilization. The overall composition of the Nossa Senhora da Luz flora suggests that the vegetation grew in a warm and generally dry climate, probably with seasonal wet periods and humid conditions.

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