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A new Hauterivian palynoflora from the Vale Cortiço site (central Portugal), and its palaeoecological implications for western Iberia

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ABSTRACT. Palynofloral assemblages are an invaluable source of information about the interactions between fossil plants and their environments. Here we describe a new Early Cretaceous palynoflora from the Lusitanian Basin in the Estremadura region of central western Portugal. A palynological assemblage of 28 genera and 40 species was extracted from 14 samples collected in the Vale Cortiço clay pit complex near the small village of Ameal (Torres Vedras Municipality). The source is a dark grey mudstone layer belonging to the lower part of the Santa Susana Formation, which is considered to be of early Hauterivian age. The palynoflora is dominated by fern spores and gymnosperm pollen. Bryophyte and lycophyte palynomorphs are also present but subordinate. Angiosperm pollen and algal or dinoflagellate cysts were not recognised in the studied samples. The palynological assemblage represents mixed conifer forest with the ground cover and understorey vegetation dominated by ferns, with patchy occurrences of bryophytes and lycophytes. A riverine environment with surrounding vegetation of open woodland and ground cover primarily of ferns is strongly indicated for the region.

KEYWORDS: Palynomorphs, conifers, ferns, Santa Susana Formation, lower Hauterivian, Portugal

INTRODUCTION

One of the most dramatic changes during the later part of Earth's history was the rise of the angiosperms to ecological dominance during the Cretaceous, from about 130 to 66 million years ago. The first unequivocal record of angiosperms is from Lower Cretaceous strata, and data from the fossil record convincingly document the first major radiation of angiosperms during the Barremian–Albian (Friis et al. 2010, 2011). As a result of it, several other plant groups that characterized earlier Cretaceous vegetation

decreased in abundance, and some went extinct later as modern ecosystems evolved.

The western Portuguese Margin has an extensive sequence of Lower to Upper Cretaceous rocks containing abundant and well-preserved plant fossils, and is well suited for sequential studies of environmental changes during the Cretaceous. The terrestrial sediments are rich in angiosperm fossils as well as remains of other plant groups, first described by Saporta (1894). Later works concerning Portuguese Cretaceous plants include studies of fossil leaves (e.g. Teixeira 1946, 1947, 1948, 1950), plant microfossils (e.g. Groot & Groot

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1962, Hasenboehler 1981, Pais & Reyre 1981, Berthou & Leereveld 1990, Trincão 1990, Heimhofer et al. 2005, 2007, Horikx et al. 2016, 2017) and plant mesofossils (e.g. Friis et al. 1999, 2006, 2010, 2011, 2015, 2018, 2019).

While dispersed palynomorphs are an invaluable source of information on the diversification, distribution and extinction of different plant groups through time, palynological investigations have to a large extent been devoted to some stratigraphic features, and only for scattered intervals. Palynofloral assemblages can provide important data to complement interpretations from macroflora and mesoflora studies related to vegetational changes (e.g. Schrank 2010, Mendes et al. 2011, 2014, 2017, 2018, Mendes & Friis 2018, Tanrikulu et al. 2018).

To shed more light on pre-Barremian environmental and climatic conditions during the Early Cretaceous deposition of the Santa Susana Formation, here we describe a new palynoflora from Vale Cortiço near the Ameal locality, Torres Vedras Municipality (Lusitanian Basin, western Portugal), considered to be of early Hauterivian age.

GEOLOGICAL SETTING

On the 1:50 000 geological map of the Portuguese Geological Survey (Carta Geológica de Portugal, Folha 30-B, Bombarral; Zbyszewski et al. 1966), the Lower Cretaceous of the Torres Vedras area (central western mainland Portugal, westernmost Iberia) was previously referred to as the *Grés com vegetais fósseis de Torres Vedras e Cercal* (“Sandstones with fossil plants of Torres Vedras and Cercal”) lithostratigraphic unit. This geological map has been revised, and the updated version follows the lithostratigraphic units defined by Rey (1993). From the outcrops in the area, we selected an opencast clay pit (located at 39°07'26"N; 09°14'17"W) near the small village of Ameal (Torres Vedras Municipality) for study in detail. The nearest topographic site on the 1:25 000 map (Carta Militar de Portugal, Folha 362-Ramalhal, 1971 edition) is Vale Cortiço (Fig. 1).

In the study area, allostratigraphic unit UBS3 of the Lusitanian Basin, recording the upper Berriasian to middle Aptian (Wilson

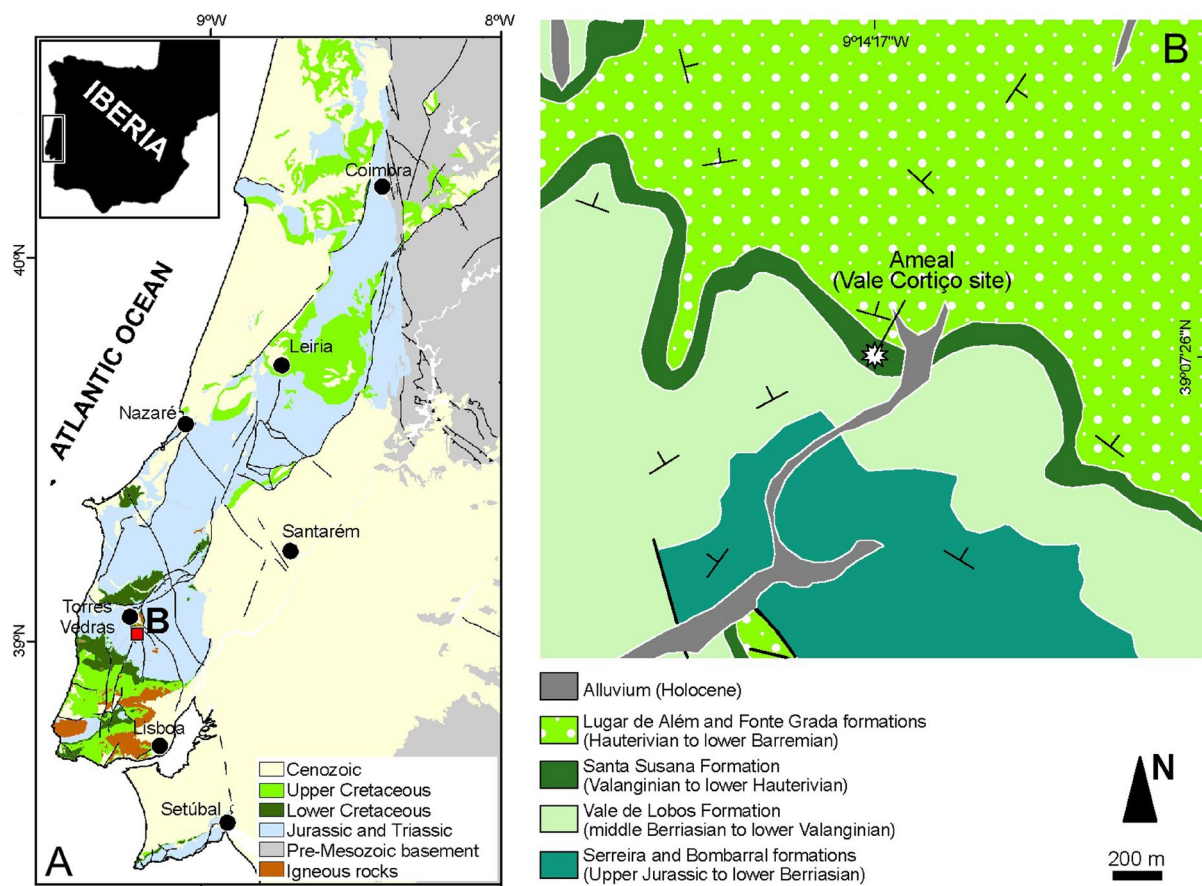


Fig. 1. Geological setting of the investigated site. **A.** Sketch map of the Lusitanian Basin in central west Iberia. **B.** Detailed geological map showing the approximate position of the Vale Cortiço opencast clay pit complex, where the specimens were collected. Asterisk indicates the location of the examined section

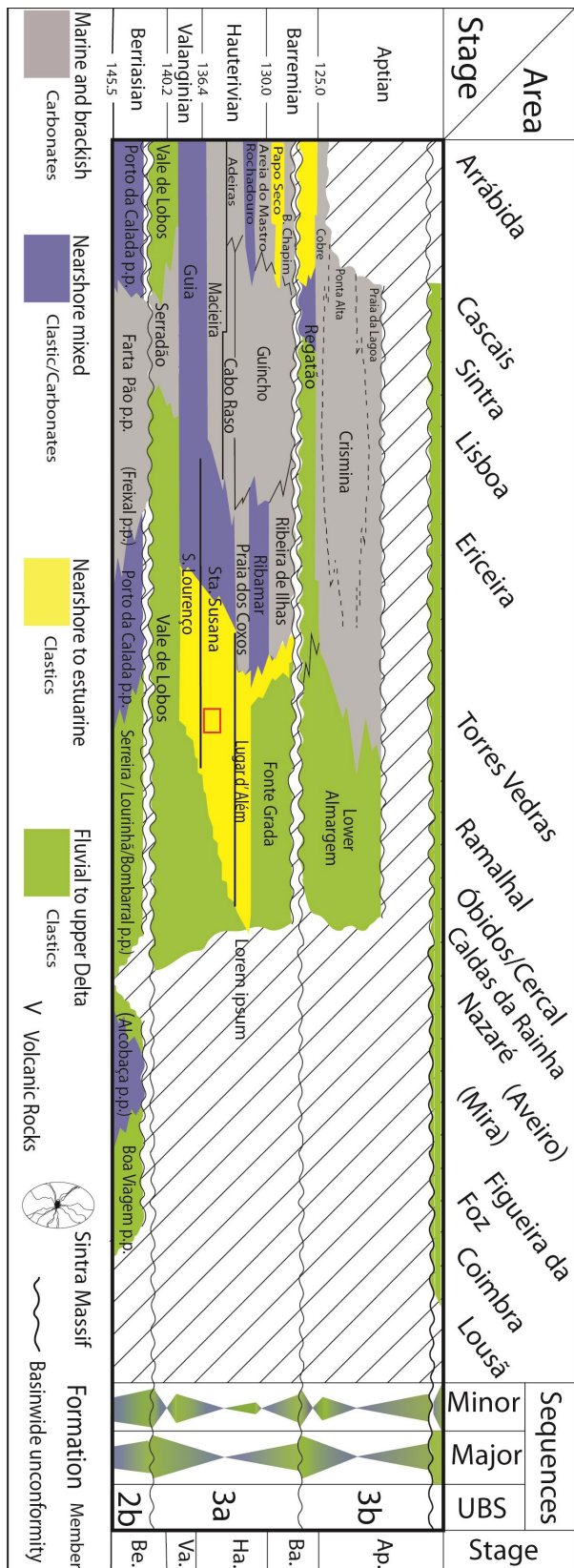


Fig. 2. Synthetic stratigraphic chart of the Lower Cretaceous of the Lusitanian Basin (adapted from Dinis et al. 2008). Informal lithostratigraphic units are within parentheses. Triangles: blue – transgressive phase; green – regressive phase. UBS: unconformity-bounded sequences after Cunha and Pena dos Reis (1995). Red square indicates the sedimentary record studied in this work, corresponding to the succession exposed at the Vale Cortiço site

et al. 1989, Cunha 1992, Dinis et al. 2008) (Fig. 2), is dominated by coarse sandstone and comprises the following sedimentary environments and lithostratigraphic units (Rey 1993): (i) fluvial to upper delta siliciclastics – Vale de Lobos Formation; (ii) upper delta, estuarine to nearshore siliciclastics – São Lourenço, Santa Susana and Lugar d'Além formations; and (iii) upper delta to fluvial siliciclastics – Fonte Grada and lower Almargem formations.

The lutitic and marly beds of the Santa Susana Formation include moulds of arenaceous foraminifera and bivalves (Ferreira 1958, Rey 1972). Based on stratigraphic studies of foraminifera assemblages (Rey 1972, 1993), the deposition of the formation is considered to have occurred between the latest Valanginian and early Hauterivian. The overall sedimentological and palaeontological data point to a tidal flat to estuarine environment (Rey 1993, 2006). Further information on the geological context is given in Mendes et al. (2010).

The Vale Cortiço site exposes four of the above-mentioned Lower Cretaceous formations: Vale de Lobos, São Lourenço, Santa Susana and Lugar d'Além. The grey mudstone layer sampled in the present study is located between the lower and middle parts of the Santa Susana Formation, so this stratigraphic level is more likely to be of early Hauterivian rather than late Valanginian age.

MATERIAL AND METHODS

The Vale Cortiço opencast clay pit complex exposes the Vale de Lobos, São Lourenço, Santa Susana and Lugar d'Além formations. Only one layer in the lower part of the Santa Susana Formation, considered to be of early Hauterivian age, yielded productive palynological samples (Fig. 3A). At the Vale Cortiço site, the Santa Susana Formation is ~6 m thick and consists mainly of cross-stratified yellowish sandstone, showing locally intense iron oxide-hydroxide cementation, and massive or laminated bluish siltstone and mudstone, with characteristic reticulated limonitic laminations (Fig. 3C, 3D). Fossil tree trunks occur, most of them covered with a Fe-oxidized coat or pyrite.

Fourteen rock samples were recovered from the lower part of the Santa Susana Formation in the Vale Cortiço opencast clay pit complex; they were processed following standard methods (Traverse 2007) but only six yielded palynomorphs (142, 143, 144, 145, 146 and 147). All the palynologically productive samples were collected from the same stratigraphic layer.

Processing involved initial treatment of ~50 g sediment per sample with hydrochloric acid (10% HCl) and hydrofluoric acid (40% HF) for 48 h to remove

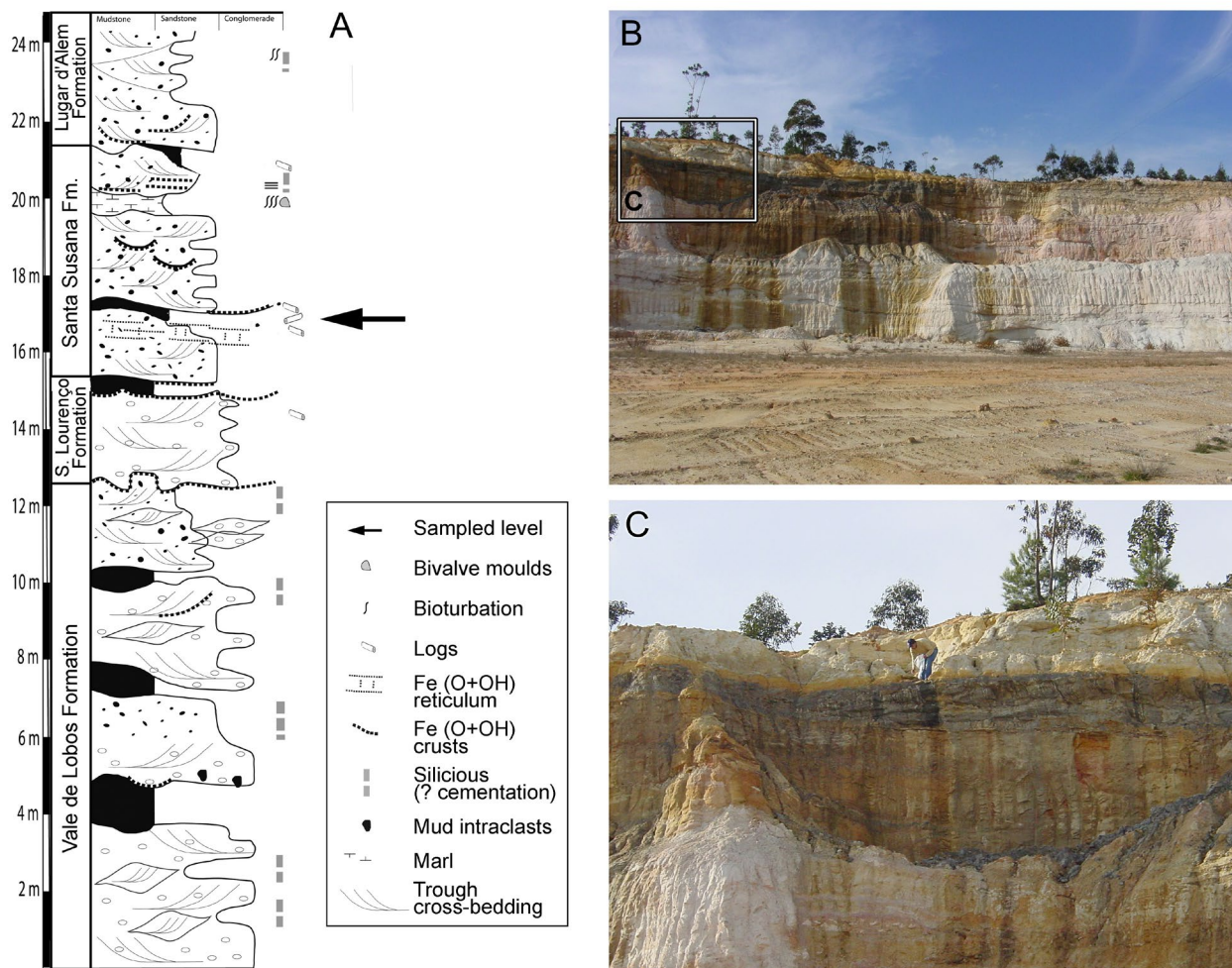


Fig. 3. Torres Vedras Group at the studied site. **A.** Stratigraphic sequence. **B.** General view of the Vale do Cortiço opencast clay pit complex. **C.** Sampled bed in the Vale do Cortiço opencast clay pit complex

carbonates and to digest silicates, respectively. The organic residue was then oxidized with nitric acid (65% HNO_3), with neutralization in distilled water between the acid treatments. The remaining residue was washed repeatedly using nylon sieves (125 μm mesh) in order to remove small coal fragments. All the material passing through the nylon sieves was concentrated by centrifuging and then transferred to small glass vials for preservation in distilled water with a drop of HCl.

For light microscopy (LM), five glycerine jelly slides containing the recovered organic matter were prepared for each sample and sealed with nail varnish. Palynomorphs were observed, counted and photographed under a Nikon Eclipse E600 microscope with 60 \times and 100 \times objectives, fitted with a Nikon Coolpix 5400 digital camera. The position of the specimens on the slides was recorded using an England Finder.

All the material used for this study is housed in the Geological Museum of Lisbon.

RESULTS

The palynomorphs recovered from the Vale Cortiço palynoflora are generally well-preserved. Only a few specimens were too

distorted for reliable identification. A total of 1302 spores and pollen grains were identified and placed in 28 genera and 40 species (Tab. 1, Pl. 1–3; see Tab. 1 for authorities of species documented here). The Vale Cortiço palynoflora includes spores of bryophytes, lycophytes and pteridophytes, and gymnosperm pollen grains (Tab. 1; Fig. 4). The palynoflora is quantitatively dominated by gymnosperm pollen, comprising ~54.6% of the total recovered from the productive samples. Pteridophytes spores accounted for 42.5%, bryophyte spores 2.4%, and lycophyte spores only ~0.5% of the whole assemblage.

However, the pteridophyte and bryophyte spores showed high diversity (Pl. 1, 2) similar to that of the gymnosperm pollen grains (Fig. 4). Among the pteridophyte spores, representatives of the families Cyatheaceae/Dicksoniaceae (11%) and Anemiaceae (11%) predominate in the Vale Cortiço palynoflora. Cyatheaceae/Dicksoniaceae are represented by verrucate spores ascribed to the genus *Concavissimisporites*

Table 1. Spore and pollen taxa identified in the Vale Cortiço palynoflora, listed in alphabetically within the genera

Taxon	Botanical affinity
Spores	
<i>Aequitriradites spinulosus</i> (Cookson & Dettmann 1958) Cookson & Dettmann 1961	Bryophyta (Hepaticae)
<i>Appendicisporites tricornitatus</i> Weyland & Greifeld 1953	Pteridophyta (Anemiaceae)
<i>Ceratosporites masculus</i> Norris 1968	Lycophyta (Selaginellaceae)
<i>Cicatricosisporites australiensis</i> Potonié 1956	Pteridophyta (Anemiaceae)
<i>Cicatricosisporites hallei</i> Delcourt & Sprumont 1955	Pteridophyta (Anemiaceae)
<i>Cicatricosisporites sprumontii</i> Döring 1965	Pteridophyta (Anemiaceae)
<i>Cicatricosisporites</i> spp.	Pteridophyta (Anemiaceae)
<i>Concavissimisporites apiverrucatus</i> Döring 1965	Pteridophyta (Cyatheaceae/Dicksoniaceae)
<i>Concavissimisporites verrucosus</i> Delcourt & Sprumont 1955	Pteridophyta (Cyatheaceae/Dicksoniaceae)
<i>Concavissimisporites punctatus</i> (Delcourt & Sprumont 1955) Brenner 1963	Pteridophyta (Cyatheaceae/Dicksoniaceae)
<i>Cooksonites</i> sp.	Bryophyta (Hepaticae)
<i>Crybelosporites striatus</i> (Cookson & Dettmann 1958) Dettmann 1963	Pteridophyta (Marsileaceae)
<i>Crybelosporites</i> sp.	Pteridophyta (Marsileaceae)
<i>Cyathidites australis</i> Couper 1953	Pteridophyta (Cyatheaceae/Dicksoniaceae)
<i>Dictyophyllidites harrisii</i> Couper 1958	Pteridophyta (Matoniaceae)
<i>Gleicheniidites circinidites</i> Dettmann 1963	Pteridophyta (Gleicheniaceae)
<i>Impardecispora texensis</i> Srivastava 1975	Pteridophyta (Schizaeaceae)
<i>Matonisorites</i> sp.	Pteridophyta (Matoniaceae)
<i>Osmundacidites wellmanii</i> Couper 1953	Pteridophyta (Osmundaceae)
<i>Patellasporites tavaredensis</i> Groot & Groot 1962	Pteridophyta
<i>Pilosisorites trichopapillosus</i> (Thiergart 1949) Delcourt & Sprumont 1955	Pteridophyta (incertae sedis)
<i>Pilosisorites</i> sp.	Pteridophyta (incertae sedis)
<i>Stereisorites</i> sp.	Bryophyta (Hepaticae)
<i>Verrucosisporites rarus</i> Burger 1966	Pteridophyta
Pollen grains (Gymnosperms)	
<i>Alisporites</i> sp.	Bisaccate pollen (?Pteridospermales)
<i>Araucariacites australis</i> Cookson 1947	Coniferophyta (Araucariaceae)
<i>Balmeiopsis limbata</i> (Balme 1957) Archangelsky 1979	Coniferophyta (Araucariaceae)
<i>Callialasporites dampieri</i> (Balme 1957) Dev 1961 emend. Norris 1969	Coniferophyta (Araucariaceae)
<i>Callialasporites trilobatus</i> (Balme 1957) Dev 1961	Coniferophyta (Araucariaceae)
<i>Callialasporites</i> sp.	Coniferophyta (Araucariaceae)
<i>Cedripites canadensis</i> Pocock 1962	Coniferophyta (Pinaceae)
<i>Cedripites</i> sp.	Coniferophyta (Pinaceae)
<i>Cerebropollenites mesozoicus</i> (Couper 1958) Nilsson 1958	Coniferophyta (?Taxodiaceae/Pinaceae)
<i>Classopollis noeli</i> Reyre 1970	Coniferophyta (Cheirolepidiaceae)
<i>Classopollis torosus</i> Burger 1965	Coniferophyta (Cheirolepidiaceae)
<i>Classopollis</i> spp.	Coniferophyta (Cheirolepidiaceae)
<i>Inaperturopollenites dubius</i> (Potonie & Venitz 1934) Thomson & Pflug 1953	Coniferophyta (Taxodiaceae/Cupressaceae)
<i>Parvisaccites radiatus</i> Couper 1958	unknown Coniferophyta
<i>Podocarpidites</i> sp.	Coniferophyta (Podocarpaceae)
<i>Spheripollenites psilatus</i> Couper 1958	Coniferophyta (Cupressaceae)
Undetermined bisaccate pollen grains	unknown Coniferophyta

(Pl. 1, figs J, K, L), together with psilate spores of *Cyathidites australis* (Pl. 2, fig. A), and the family Anemiaceae is represented by trilete spores with coarse, compact ridges assigned to the genera *Cicatricosisporites* (Pl. 1, figs E, G, H) and *Appendicisporites* (Pl. 1, fig. F). The fern spores *Cicatricosisporites hallei*, *Cicatricosisporites australiensis*, *Concavissimisporites apiverrucatus* and especially *Cyathidites australis* are the most abundant species from the Vale Cortiço palynoflora (Tab. 1). Among the other

pteridophytic spores of high relative abundance are numerous smooth-walled forms belonging to the Matoniaceae, such as *Matonisorites* (Pl. 2, fig. B) and *Dictyophyllidites* (Pl. 2, fig. D). Osmundaceae specimens ascribed to the species *Osmundacidites wellmanii* are also common (Pl. 2, fig. H). On the other hand, only a few specimens of the smooth-walled gleicheniaceous form *Gleicheniidites circinidites* (Pl. 2, fig. C) were recorded here, representing 3% of the spore assemblage and 2% of the whole

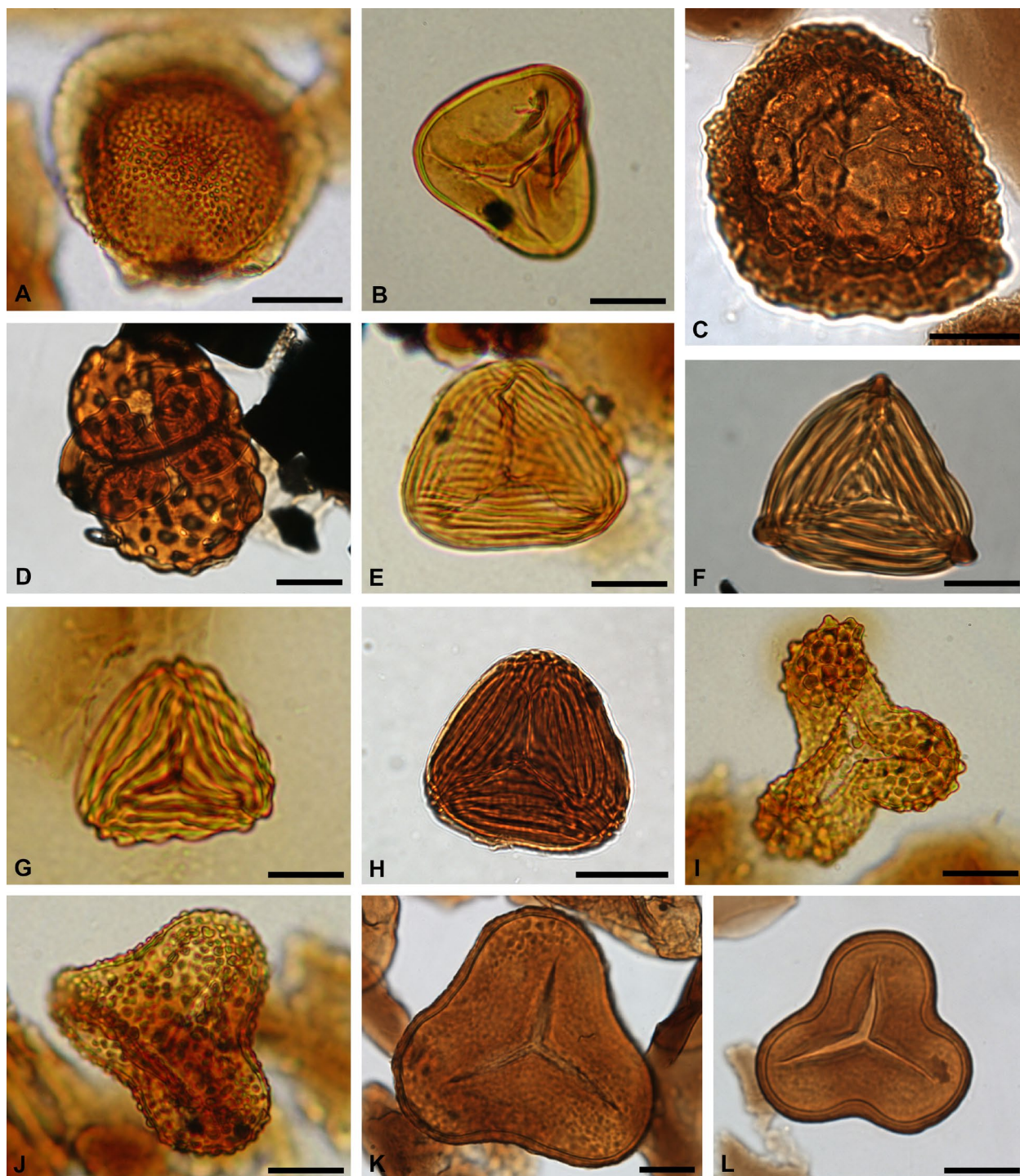


Plate 1. Transmitted light photomicrographs of some spore types recovered from the Vale Cortiço section. Letters and numbers after each entry are slide references. **A.** *Aequitriradites spinulosus* (Cookson & Dettmann 1958) Cookson & Dettmann 1961 (MS.4 VAL-C 147; sample Vale Cortiço 147). **B.** *Stereisporites* sp. (MS.1 VAL-C 142; sample Vale Cortiço 142). **C.** *Cooksonites* sp. (MS.1 VAL-C 142; sample Vale Cortiço 142). **D.** Tetrad of *Patellasporites tavadensis* Groot & Groot 1962 (MS.3 VAL-C 145; sample Vale Cortiço 145). **E.** *Cicatricosisporites hallei* Delcourt & Sprumont 1955 (MS.1 VAL-C 144; sample Vale Cortiço 144). **F.** *Appendicisporites tricornitatus* Weyland & Greifeld 1953 (MS.2 VAL-C 145; sample Vale Cortiço 145). **G.** *Cicatricosisporites sprumonti* Döring 1965 (MS.2 VAL-C 146; sample Vale Cortiço 146). **H.** *Cicatricosisporites australiensis* Potonié 1956 (MS.4 VAL-C 144; sample Vale Cortiço 144). **I.** *Impardecispora texensis* Srivastava 1975 (MS.2 VAL-C 147; sample Vale Cortiço 147). **J.** *Concavissimisporites verrucosus* Delcourt & Sprumont 1955 (MS.1 VAL-C 143; sample Vale Cortiço 143). **K.** *Concavissimisporites apiverrucatus* Döring 1965 (MS.5 VAL-C 143; sample Vale Cortiço 143). **L.** *Concavissimisporites punctatus* (Delcourt & Sprumont 1955) Brenner 1963 (MS.1 VAL-C 142; sample Vale Cortiço 142). Scale bars: 20 µm for all specimens

palynofloral assemblage (Tab. 1; Fig. 4). Relatively abundant and diverse ornamented spores include marsileaceous *Crybelosporites striatus*

(Pl. 2, fig. E) and specimens of uncertain botanical affinity identified as *Pilosisporites* (Pl. 2, fig. F) and *Patellasporites* (Pl. 1, fig. D).

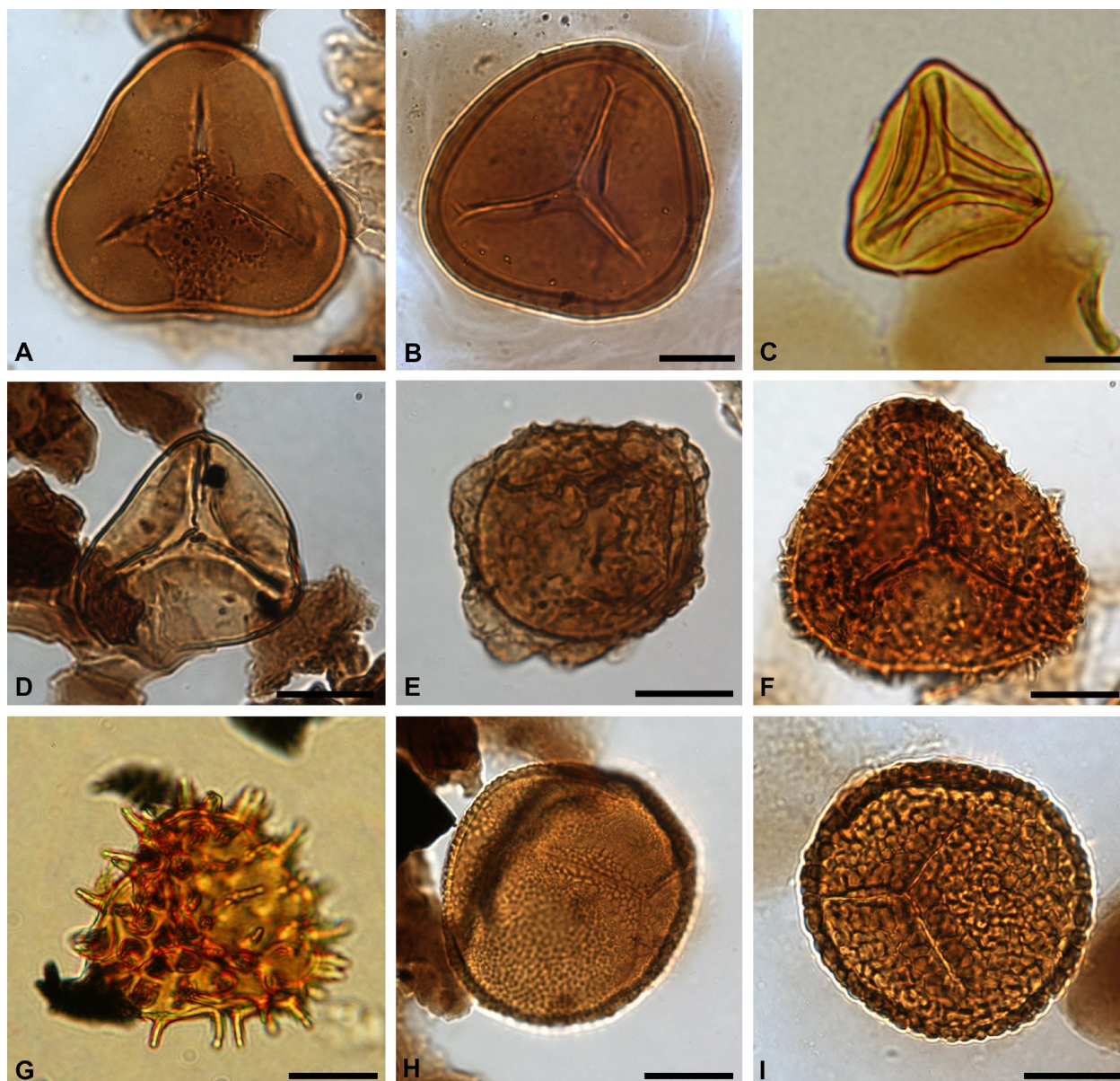


Plate 2. Transmitted light photomicrographs of some spore types recovered from the Vale Cortiço section. Letters and numbers after each entry are slide references. **A.** *Cyathidites australis* Couper 1953 (MS.2 VAL-C 143; sample Vale Cortiço 143). **B.** *Matonisporites* sp. (MS.5 VAL-C 143; sample Vale Cortiço 143). **C.** *Gleicheniidites circinidites* Dettmann 1963 (MS.4 VAL-C 144; sample Vale Cortiço 144). **D.** *Dictyophyllidites harrisii* Couper 1958 (MS.3 VAL-C 142; sample Vale Cortiço 142). **E.** *Crybelosporites striatus* (Cookson & Dettmann 1958) Dettmann 1963 (MS.4 VAL-C 144; sample Vale Cortiço 144). **F.** *Pilosisporites trichopapillosus* (Thiergart 1949) Delcourt & Sprumont 1955 (MS.1 VAL-C 146; sample Vale Cortiço 146). **G.** *Ceratosporites masculus* Norris 1968 (MS.2 VAL-C 146; sample Vale Cortiço 146). **H.** *Osmundacidites wellmanii* Couper 1953 (MS.3 VAL-C 145; sample Vale Cortiço 145). **I.** *Verrucosporites rarus* Burger 1966 (MS.1 VAL-C 147; sample Vale Cortiço 147). Scale bars: 20 μ m for all specimens

Lycophyte spores are neither abundant nor diverse. Specimens belonging to the genus *Ceratosporites* (Pl. 2, fig. G) represent only 1% of the spore assemblage (Fig. 4). Bryophyte spores of the genera *Aequitriradites* (Pl. 1, fig. A), *Stereisporites* (Pl. 1, fig. B) and *Cooksonites* (Pl. 1, fig. C) are fairly abundant.

Gymnosperms are very well represented in the Vale Cortiço palynoflora. Their abundance is balanced between grains belonging to the circumsulcate *Classopollis* (Cheirolepidiaceae)

(Pl. 3, figs A, B), *Araucariacites australis* (Araucariaceae) (Pl. 3, fig. D), *Callialasporites* (Araucariaceae) (Pl. 3, figs E, F) and *Balmeiopsis* (Araucariaceae) (Pl. 3, fig. H), accounting for ~32% of all palynomorphs. Bisaccate pollen grains are also prominent and morphologically diverse in the Vale Cortiço palynoflora, represented by species of *Alisporites* (probably related to Pteridospermales) (Pl. 3, fig. I), *Parvisaccites* (Taxodiaceae/Cupressaceae) (Pl. 3, fig. J), *Cedripites* (Pinaceae) (Pl. 3, fig. K) and

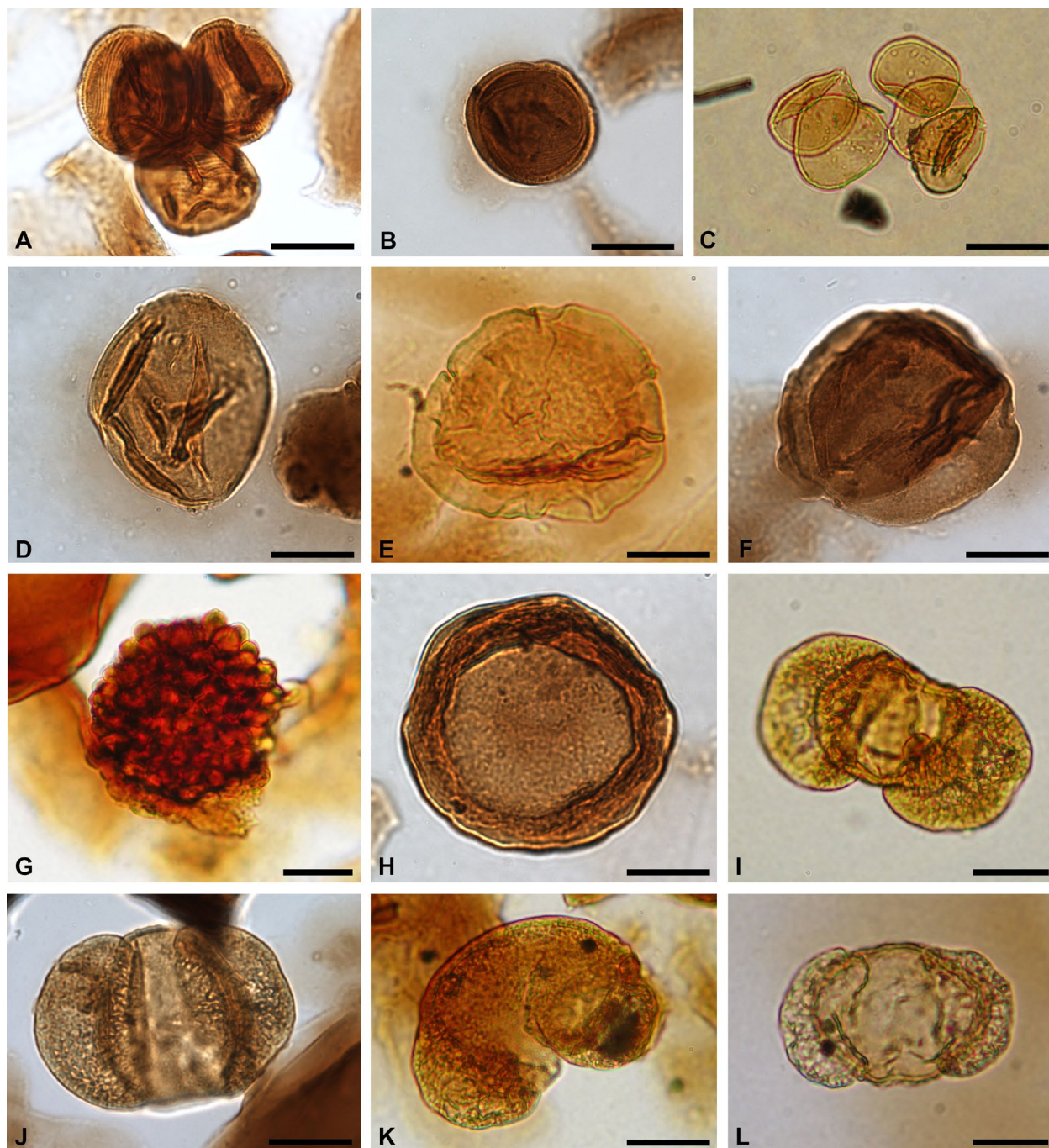


Plate 3. Transmitted light photomicrographs of some pollen types recovered from the Vale Cortiço section. Letters and numbers after each entry are slide references. **A.** Tetrad of *Classopollis torosus* Burger 1965 (MS.4 VAL-C 147; sample Vale Cortiço 147). **B.** *Classopollis* sp. (MS.2 VAL-C 142; sample Vale Cortiço 142). **C.** *Spheripollenites psilatus* Couper 1958 (MS.5 VAL-C 145; sample Vale Cortiço 145). **D.** *Araucariacites australis* Cookson 1947 (MS.3 VAL-C 146; sample Vale Cortiço 146). **E.** *Callialasporites dampieri* (Balme 1957) Dev 1961 emend. Norris 1969 (MS.3 VAL-C 143; sample Vale Cortiço 143). **F.** *Callialasporites trilobatus* (Balme 1957) Dev 1961 (MS.1 VAL-C 142; sample Vale Cortiço 142). **G.** *Cerebropollenites mesozoicus* (Couper 1958) Nilsson 1958 (MS.3 VAL-C 147; sample Vale Cortiço 147). **H.** *Balmeiopsis limbata* (Balme 1957) Archangelsky 1979 (MS.4 VAL-C 143; sample Vale Cortiço 143). **I.** *Alisporites* sp. (MS.1 VAL-C 142; sample Vale Cortiço 142). **J.** *Parvisaccites radiatus* Couper 1958 (MS.4 VAL-C 144; sample Vale Cortiço 144). **K.** *Cedripites canadensis* Pocock 1962 (MS.1 VAL-C 143; sample Vale Cortiço 143). **L.** *Podocarpidites* sp. (MS.4 VAL-C 145; sample Vale Cortiço 145). Scale bars: 20 μ m for all specimens

Podocarpidites (Podocarpaceae) (Pl. 3, fig. L), reaching relative abundance of ~16% of the palynomorphs (including undetermined bisaccate pollen grains).

Other less abundant gymnosperm pollen grains are ascribed to the species *Ina-*

perturopollenites dubius (Taxodiaceae/Cupressaceae), *Cerebropollenites mesozoicus* (probably related to Taxodiaceae or Pinaceae) (Pl. 3, fig. G) and *Spheripollenites psilatus* (Cupressaceae) (Pl. 3, fig. C), accounting for ~2% of the palynofloral assemblage.

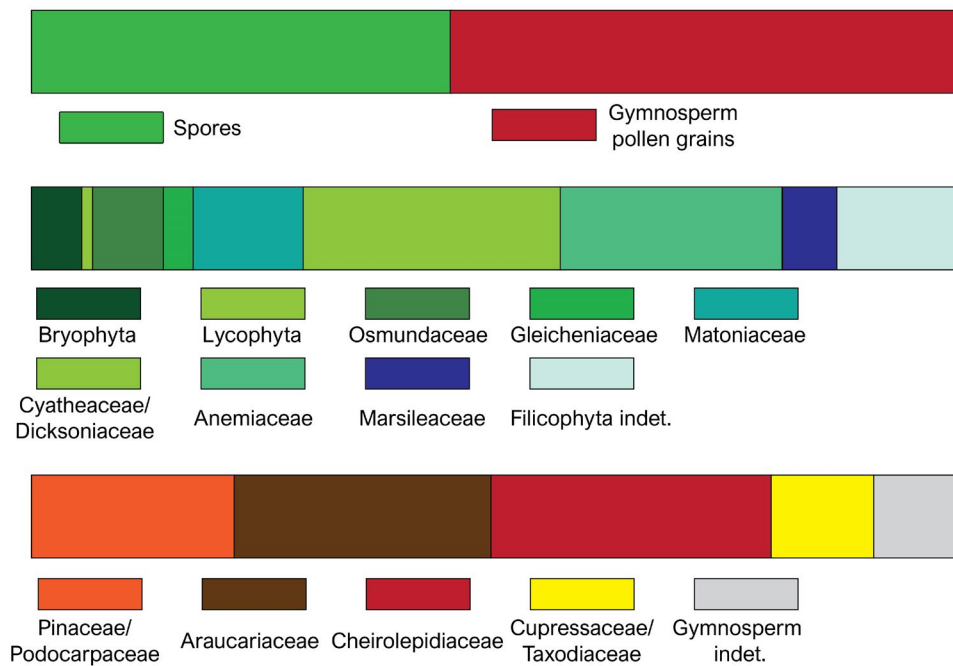


Fig. 4. Plots of relative abundance of the Vale Cortiço palynological assemblage, based on the botanical affinities of the various spore and pollen morphotypes

No dinoflagellate or algae spores or angiosperm pollen grains were recognised in the studied samples.

DISCUSSION

AGE DETERMINATION OF THE VALE CORTIÇO PALYNOFLORA

The age of the strata we analysed has been established as late Valanginian to early Hauterivian, based on sedimentological evidence and foraminifera biostratigraphy (Rey 1972, 1993). However, no palynological evidence has so far supported this age determination. The Vale Cortiço palynoflora lacks typical strong stratigraphic markers such as dinoflagellates. Dating Lower Cretaceous deposits using continental palynomorphs can be challenging, the encountered forms often being long-ranging. In the Vale Cortiço palynoflora, no species typically indicative of late Valanginian or early Hauterivian age has been identified. Indeed, species such as *Aequitriradites spinulosus*, *Cyathidites australis*, *Pilosporites trichopapillosus*, *Gleicheniidites circinidites*, *Dictyophyllidites harrisii* and all the species of gymnosperm pollen grains we recovered are very common forms whose temporal distribution extended through the Early Cretaceous in Western Europe. While

they can often be fairly precise stratigraphic markers, all the species of *Cicatricosisporites*, *Concavissimisporites* and *Appendicisporites* we identified are also long-ranging. However, regardless of the species names, the comparative species diversity of some genera assigned to Anemiaceae (*Cicatricosisporites*, *Appendicisporites*) and Cyatheaceae/Dicksoniaceae (*Concavissimisporites*, *Trilobosporites*) can be useful in making stratigraphic determinations. It has been observed that cyatheaceous/dicksoniaceae spores are more diverse during the earliest part of the Cretaceous (Berriasian–mid-Hauterivian), while anemiaceous spores, mainly *Appendicisporites*, become more diverse than cyatheaceous/dicksoniaceae spores from the mid-Hauterivian onward (Burden & Hills 1989). *Cicatricosisporites* species are quite diversified throughout the Early Cretaceous. In the Vale Cortiço palynoflora only one *Appendicisporites* species was recorded, and three species assigned to both *Cicatricosisporites* and *Concavissimisporites* were identified. Diversity is therefore quite balanced between anemiaceous and cyatheaceous/dicksoniaceae species, as is typical of Hauterivian assemblages, the latter often comprising comparatively more species assigned to Cyatheaceae/Dicksoniaceae. Furthermore, the absence of earliest-Cretaceous forms, such as *Trilobosporites canadensis* or *Concavissimisporites montuosus*, coupled

with the presence of large, concave, finely verrucate forms identified as *Concavissimisporites verrucosus*, also corroborate a Hauterivian age of deposition. *Concavissimisporites verrucosus* has been found commonly in lower Valanginian to Barremian strata in Western Europe (Delcourt & Sprumont 1955, Delcourt et al. 1963, Herngreen 1971, Dörhöfer & Norris 1977, Dejoux et al. 2007a) but is more likely to be associated with *Trilobosporites canadensis* and *Concavissimisporites montuosus* in Valanginian assemblages.

Finally, the specimen identified as *Appendicisporites tricornitatus* (Pl. 1, fig. F) shows great similarity to specimens illustrated and described by Couper (1958) as *Appendicisporites tricornitatus*, and by Pocock (1964) as *Appendicisporites erdtmanii*. Possibly a portion of the morphological space characteristic of *Appendicisporites tricornitatus* overlaps with a part of the *Appendicisporites erdtmanii* form. *Appendicisporites tricornitatus* has been widely encountered throughout the Early Cretaceous and therefore cannot be used for detailed dating.

Appendicisporites erdtmanii has been recorded mostly within Barremian to lower Cenomanian deposits of North America (Pocock 1964, Singh 1971, Wingate 1974, Allen 1977) and Europe (Van Amerom 1965, Habib 1979, Berthou et al. 1981, Juhász 1983). Burden & Hills (1989) indicated a stratigraphic distribution ranging from early Hauterivian to Albian–Cenomanian. The presence of such a similar form in the Vale Cortiço palynological assemblage suggests that the palynoflora should not be older than early Hauterivian. Thus, the general composition of the Vale Cortiço palynological assemblage suggests an age of deposition corresponding to early Hauterivian rather than late Valanginian age.

VEGETATION COMPOSITION AND PALAEOENVIRONMENTAL IMPLICATIONS

Dispersed palynomorphs can provide invaluable information about the taxonomic composition of past vegetation, useful for palaeoecological and palaeoclimatic interpretations. The palynoflora of the Vale Cortiço samples is dominated by fern spores. Based on the spore data, the Anemiaceae and Cyatheaceae/Dicksoniaceae were prominent elements of the ground cover under humid conditions and were

represented by several species. Fern spores ascribed to extant Anemiaceae, Osmundaceae and Cyatheaceae/Dicksoniaceae can be found in a wide range of environments, including watersides. However, the sporangia of many Early Cretaceous taxa attributed to Dicksoniaceae (*Onychiopsis* Yokoyama) and Matoniaceae (*Weichselia* Stiehler) are protected in capsule-like structures, and their coriaceous fronds may indicate adaptation to stressful environments and xeromorphic conditions (Friis & Pedersen 1990, Watson & Alvin 1996, van Konijnenburg-van Cittert 2002). The relative abundance of Anemiaceae, Cyatheaceae/Dicksoniaceae, Osmundaceae and Marsileaceae in the Vale Cortiço palynoflora points to the occurrence of a diverse and at least partly riparian community of ferns. Ferns attributed to Matoniaceae preferred drier and warm conditions (Abbink 1998). The presence of bryophytic forms may indicate that enriched soil permitted the establishment of a diversified plant community.

The Vale Cortiço palynoflora is quantitatively dominated by xerophilous taxa assigned to the gymnosperms. Almost 20% of that assemblage is composed of forms attributed to the genus *Classopollis* (Tab. 1), produced by the extinct conifer family Cheirolepidiaceae. Furthermore, the mesofossil flora recovered from the same stratigraphic layer as the new palynoflora described here is dominated by cheirolepidiaceous conifer shoot/leaf remains assigned to *Frenelopsis teixeirae* (Alvin & Pais) emend. Mendes, Dinis, Gomez & Pais; and the frenelopsid fragments show strongly xeromorphic traits (Mendes et al. 2010). The cheirolepidiaceous conifers were xerophytic plants, and are believed to have grown in dry or saline environments under arid conditions (Jardiné et al. 1974, Alvin 1982). In other palynological assemblages the association of *Classopollis* and marine dinoflagellate cysts has been linked to coastal deposition (Srivastava 1976) in a warm and arid climate (Vakhrameev 1981). However, the absence of dinoflagellate cysts in the Vale Cortiço palynoflora suggests that deposition occurred in a terrestrial situation not exposed to marine inputs, and the presence of Cheirolepidiaceae representatives could then be linked to dry rather than saline conditions.

Pollen grains assigned to the genera *Araucariacites* and *Calliasporites*, thought to represent Araucariaceae (Schrank & Mahmoud

1998), are well represented in the Vale Cortiço palynoflora. They are indicative of xeromorphic conditions (Batten & Uwins 1985) or warm-temperate and relatively humid environments in a seasonal climate (Oliveira et al. 2015). Among the less abundant gymnosperm pollen grains are forms assigned to Pinaceae, Taxodiaceae/Cupressaceae and Podocarpaceae, which are interpreted to be derived from woodland plants growing on well-drained soil under mesic conditions (Batten & Uwins 1985). However, some extant species of modern cupressaceous conifers, such as the bald cypress as well as members of the Podocarpaceae, have a high water requirement and grow in swamp environments and on saturated soil and wetlands subject to periodic flooding. The abundant shoot/leaf remains of *Frenelopsis teixeirae* in the Vale Cortiço mesofossil flora suggest that cheirolepidiaceous conifers grew close to the depositional basin.

Overall, the composition of the Vale Cortiço palynoflora suggests that the depositional environment was not subject to marine inputs and that the vegetation grew in a dry and generally warm climate, probably with seasonal wet periods and humid conditions. The depositional environment was then likely to have been a riverine situation, with surrounding vegetation of open woodland and ground cover primarily of ferns.

COMPARISON WITH HAUTERIVIAN PALYNOLOGICAL ASSEMBLAGES FROM NEIGHBOURING AREAS

There are few palynological studies of the Hauterivian strata of Western Europe, owing to the paucity of Lower Cretaceous outcropping continental deposits and to the relatively short duration of the Hauterivian period as compared to other Early Cretaceous stages. Solé de Porta & Salas (1994) described an Early Cretaceous palynoflora of Hauterivian age from the Maestrazgo successions in northeastern Spain. The Maestrazgo and Vale Cortiço palynofloras are very similar in general composition. In both the Maestrazgo and Vale Cortiço palynofloras, fern spores and conifer pollen grains dominate the palynological assemblages. However, dinoflagellates were not recognised in the Vale Cortiço palynoflora. In France, Médus (1970) briefly introduced the palynological content of the Hauterivian portion of the marine succession from Angles (southeastern France) but recorded

only six species, all very common within Lower Cretaceous deposits and not age-diagnostic. Néraudeau et al. (2012) described a rich continental palynoflora from the Angeac–Charente bone beds dated initially as Hauterivian–Barremian, but this age has been questioned and is now considered to be Berriasian–Valanginian (Polette et al. 2018). The Vale Cortiço palynoflora is relatively similar to the assemblage recovered from Wealden-type facies deposits in northern France (Delcourt & Sprumont 1955, 1959), in that they both yielded numerous very large concave spores identified as *Concavissimisorites verrucosus*, and several species assigned to the genus *Cicatricosisporites*. However, the Vale Cortiço palynoflora differs in the absence of specimens ascribed to the genus *Trilobosporites*. In Belgium only younger continental palynofloras have been described within the Mons Basin (Dejax et al. 2007a, b). They differ quite substantially owing to the presence of pollen grains with angiospermous affinities, and numerous *Trilobosporites* spores. Surprisingly, few studies of Hauterivian continental palynofloras of southern England have been carried out. This may be explained by the fact that continental Hauterivian and Barremian successions have been grouped within the “Wealden Clay” Formation (Allen & Wimbledon 1991). Nevertheless, Hughes et al. (1991) documented angiosperm-like pollen grains within strata of supposedly Hauterivian age. These pollen grains were associated with a palynological assemblage composed of 98% fern spores, mainly assigned to the genera *Pilosisorites* and *Concavissimisorites*, and to the smooth-walled spores, but quite different from the ones recognised in the Vale Cortiço palynoflora.

CONCLUSIONS

Here we reported, for the first time, a palynoflora recovered from Lower Cretaceous rocks of the Santa Susana Formation in the Vale Cortiço clay pit complex near the small village of Ameal in the western Portuguese Basin. The pollen-spore assemblage described herein yielded information about the systematic composition of the plant community, useful for inferring palaeoecological and palaeoclimatic conditions. The Vale Cortiço palynoflora is dominated by fern spores assigned to the families Anemiaceae, Cyatheaceae, Dicksoniaceae

and Osmundaceae, suggesting derivation from a local pteridophyte wetland vegetation. The presence of bryophyte and lycophyte spores indicates moist, humid conditions. The gymnosperm pollen grains are quantitatively dominated by Araucariaceae and Cheirolepidiaceae pollen produced by xerophytic plants; this is consistent with the macrofloral record from the same site. Their presence is indicative of a warm climate and clearly reflects a conifer-dominated vegetation. A riverine situation is clearly indicated, with surrounding vegetation of open woodland and ground cover primarily of ferns, growing in a generally warm and dry climate, probably with seasonal wet periods creating humid conditions.

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