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Contributions to the palaeoenvironmental knowledge of the Escucha Formation in the Lower Cretaceous Oliete Sub-basin, Teruel, Spain

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Abstract

The Oliete Sub-basin is located in the link zone between the Iberian and the Catalonian Coastal Ranges (Teruel Province, Spain). The palynological samples have been collected in the Upper Aptian–lower Albian rocks of the Escucha Formation, which present an organic-rich sedimentary succession deposited in a variety of continental and coastal environments. Four detailed sections have been studied in order to establish the stratigraphical framework to perform the palynological study. The rocks of these sections contained abundant and well-diversified palynomorph assemblages. Their study allowed the identification of 78 taxa or taxonomic groups (dinoflagellate cysts, acritarchs, phycomes of prasinophytes, algae, bryophytes, lycophytes, pteridophytes, gymnosperms, and primitive angiosperms). The quantitative percentual and the multivariate analysis performed upon the supplied palynological data supports the hypothesis of subtropical palaeoenvironments controlled by non-uniform conditions. The assemblages are comprised of parautochthonous and allochthonous elements, which reflect the existence of coniferous forests and wetlands. ***To cite this article: D. Peyrot et al., C. R. Palevol 6 (2007).***

Résumé

Contributions à la reconstruction paléoenvironnementale de la formation Escucha du Crétacé inférieur du sous-bassin d'Oliete, Teruel, Espagne. Le sous-bassin d'Oliete est situé dans une zone de transition située entre les cordillères Ibérique et prélittorale Catalane (province de Teruel, Espagne). Les échantillons polliniques ont été prélevés sur du matériel daté de l'Aptien supérieur–Albien inférieur de la formation Escucha, qui présente une succession riche en matière organique, déposée en divers environnements paraliques et continentaux. Quatre sections détaillées ont été étudiées de façon à établir le cadre

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stratigraphique nécessaire à l'élaboration de l'étude palynologique. Le matériel de ces sections a révélé des associations palynologiques riches et diversifiées. Soixante-dix-huit taxa ou groupes taxonomiques ont pu être déterminés (kystes de dinoflagellés, acritarches, phycomes de prasynophytes, algae, bryophytes, lycophytes, pteridophytes, gymnospermes et angiospermes primitives). Les résultats apportés par les analyses quantitatives classiques et multivariées réalisées confortent l'hypothèse d'un paléoenvironnement subtropical non uniforme. Les associations sont constituées par des éléments parautochtones et allochtones, qui reflètent l'existence de forêts dominées par les conifères et d'environnements plus humides. ***Pour citer cet article : D. Peyrot et al., C. R. Palevol 6 (2007).***

Keywords: Palynology; Palaeoecology; Upper Aptian–lower Albian; Oliete Sub-basin; Spain

Mots clés : Palynologie ; Paléoécologie ; Aptien supérieur–Albien inférieur ; Sous-bassin d'Oliete ; Espagne

1. Introduction

The Early Cretaceous, and especially the Aptian–Albian interval (125–100 Ma), are considered as key periods in the evolution of modern ecosystems [15,16,32]. Exceptional palaeoenvironmental conditions characterized by globally warm temperatures [12,20,59], high atmospheric CO_2 levels [10,48], active tectonic [37] or large-scale sea level changes [23,25] have been proposed as possible controls of the observed changes in palaeovegetation. Besides biological factors [19], a possible low equator-to-pole temperature gradient, inferred by geochemical data [30], climate simulations [6] and supported by palaeontological evidences [27,51,54] may also account for the poleward expansion of tropical vegetation including

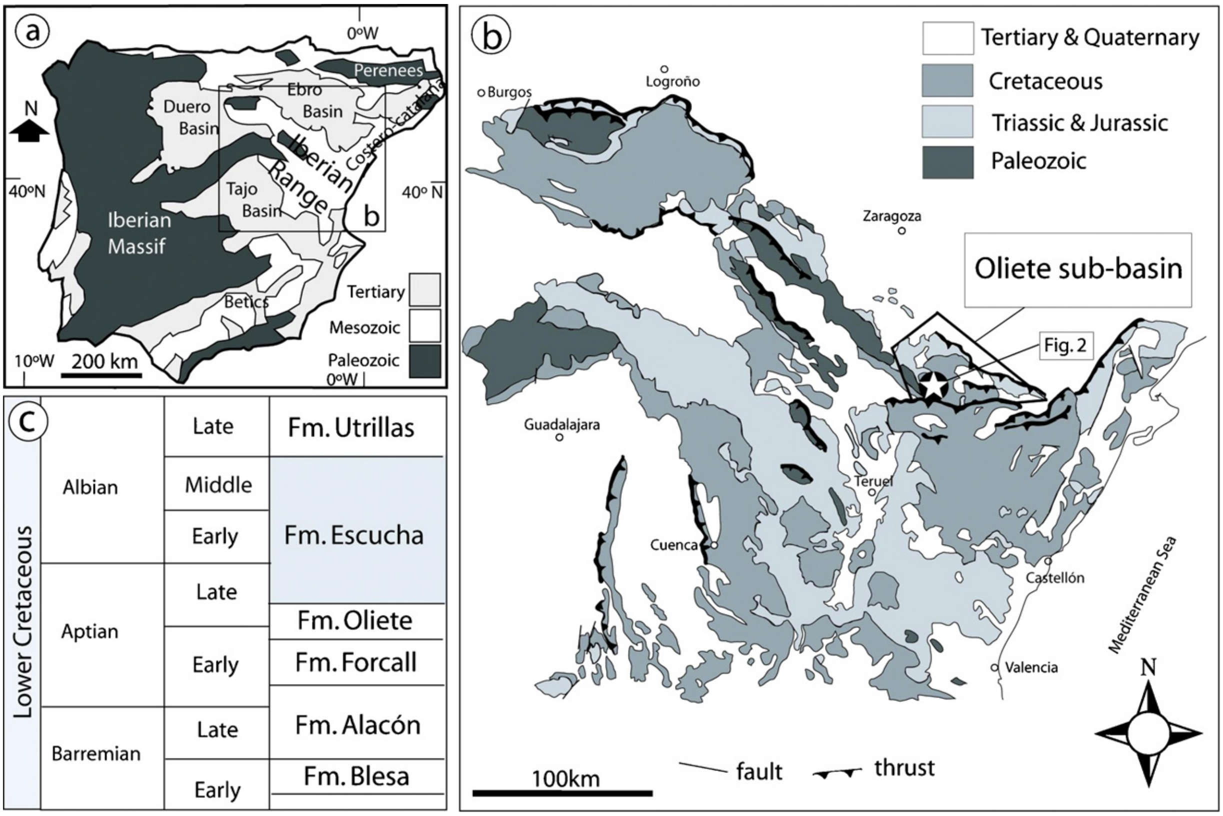

Fig. 1. (**a**) Geological map of the Iberian Peninsula. (**b**) Geological map of the Iberian Range, showing the location of the Oliete Sub-basin. (**c**) Chronostratigraphic chart of the Lower Cretaceous of the Oliete Sub-basin.

Fig. 1. (**a**) Carte géologique de la péninsule Ibérique. (**b**) Carte géologique de la cordillère Ibérique, avec le sous-bassin d'Oliete. (**c**) Tableau chronostratigraphique du Crétacé inférieur du sous-bassin d'Oliete.

sensitive organisms such as primitive angiosperms. In this context, palaeogeography turns out to be as a major factor controlling the migration of organisms.

Situated between Eurasia and Gondwana, the Iberian Peninsula may prove to be ideally located to perform palaeobotanical studies. Among other appropriate sedimentary basins, the Oliete Sub-basin (Escucha Formation) is particularly interesting to carry out a palaeoecological analysis, since the area has been the object of a previous promising palynological studies establishing the precise taxonomical and temporal landmarks [40,41,49]. We propose here a detailed quantitative palynological study of materials from the Escucha Formation, which includes a multivariate statistical analysis in order to infer the palaeoenvironmental conditions of the region.

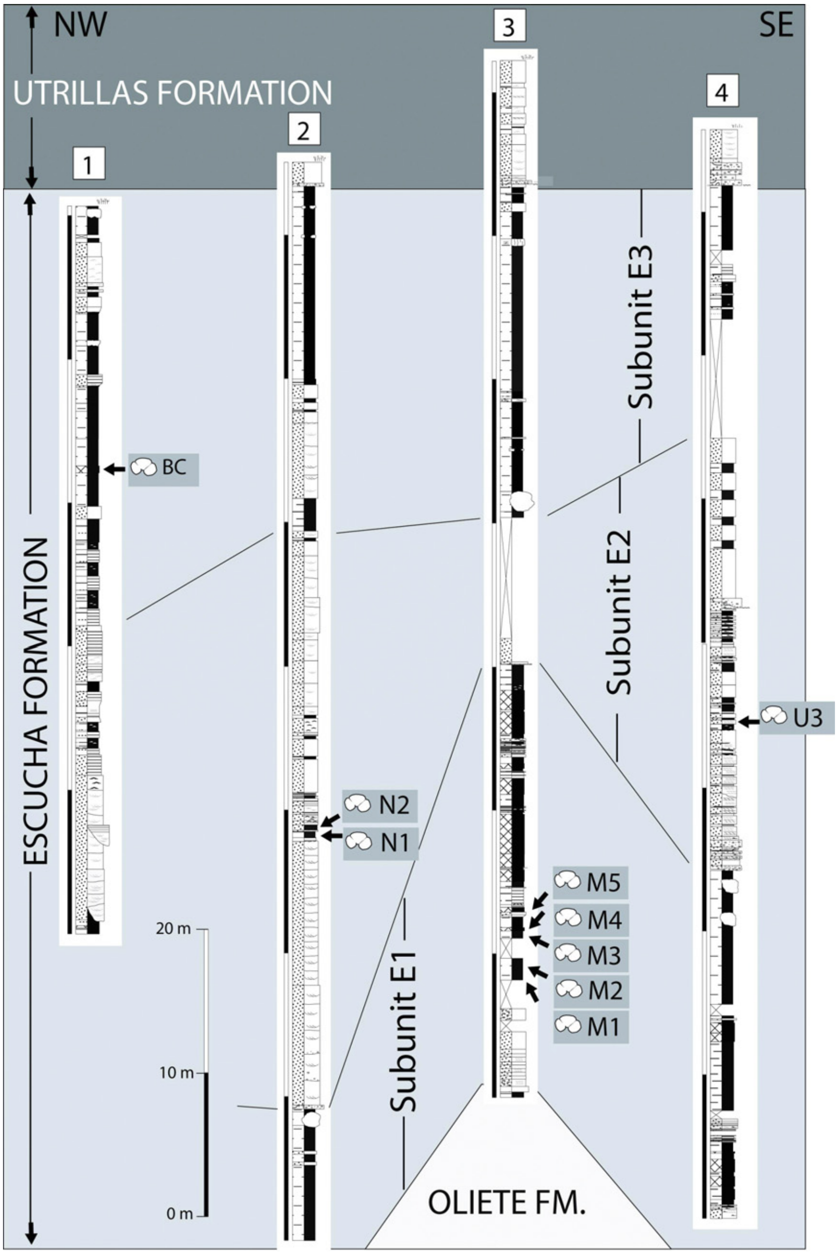

Fig. 2. Stratigraphic correlation of studied sections showing location of samples. The Escucha Formation is divided in three sub-units: E_1,$E_2$and E_3.
Fig. 2. Corrélation stratigraphique des sections étudiées et localisation des échantillons. La formation Escucha est divisée en trois sous-unités : E_1, E_2 et E_3.

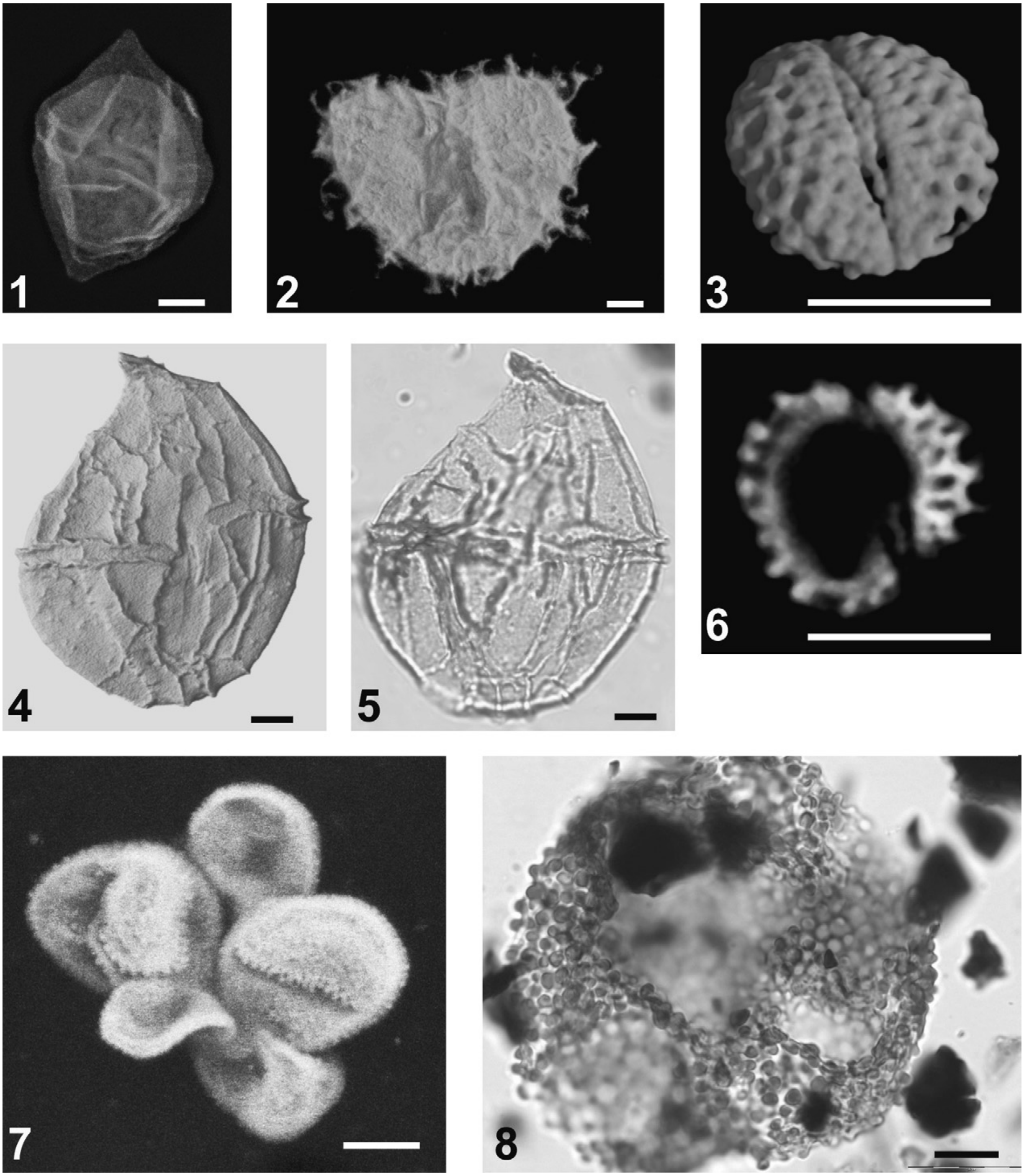

Fig. 3. **1**. *Subtilisphaera perlucida* (Alberti) Jain & Millepied, 1973. Confocal microscopy, maximum of projections, level M_1. **2**. *Cyclonephelium compactum* Deflandre & Cookson, 1955. Confocal microscopy, 3D-reconstruction, level M_1. **3**. *Brenneripollis/Pennipollis*. Confocal microscopy, 3D-reconstruction, level M_4. **4**. *Cribroperidinium orthoceras* (Eisenack) Davey, 1969. Confocal microscopy, 3D-reconstruction, level M_1. **5**. Same specimen as in **4**. Wide-field microscopy. **6**. Same specimen as in **3**. Confocal microscopy, section of the grain showing the non-columellate nature of the exine. **7**. *Clavatipollenites hughesii* Couper, 1958. Confocal microscopy, maximum of projections, level M_4. **8**. *Stellatopollis dejaxii* Ibrahim, 2002. Wide-field microscopy, level N_1. Scale bar: 10 μm.

2. Geological setting

The Oliete Sub-basin is located in the Iberian Range (eastern Central Spain, Figs. 1(a) and 1(b)). This extensional sub-basin was active from the Early Barremian to the Early–Middle Albian and it was infilled with sediments deposited in a variety of palaeoenvironments from continental to marine realms [35,50]. The stratigraphic record of this sub-basin (Fig. 1(c)) includes the Escucha Formation that has been dated back to the Early–Middle Albian in the Oliete Sub-basin based on ammonoids and palynological data [49]. However, new palynological data from this unit in the Oliete Sub-basin permits to consider an Upper Aptian–Lower Albian age for these deposits [41].

2.1. The Escucha Formation

The Escucha Formation is a heterolithic unit that lies on limestones and marls of the Urgonian Platforms (Aptian), and is covered by sandstones of the Utrillas Formation (Late Albian–Early Cenomanian) [3,11,39,44]. This unit has been interpreted as deposited in a deltaic [39] or deltaic-estuarine [44] setting. However, in the Oliete Sub-basin, at the lower part of this unit, more transgressive sedimentary systems have been recognized as barrier island systems with backbarrier marshes and flood-tidal deltas [47]. The formation can be divided into three sub-units named E_1, E_2, and E_3 from base to top (Fig. 2).

Sub-unit E_1 is composed of siltstones and mudstones usually organic-rich, some sandstone beds, and interbedded coal seams. It was deposited in a wide spectrum of coastal environments with strong marine influence, as evidenced by the presence of foraminifers and dinoflagellate cysts (Fig. 3: 1, 2, 4, 5).

E_2 is a predominantly sandy sub-unit with scarce siltstone levels. The marine influence is only present as sandy tidal deposits outcropping at the southern border of the sub-basin. In other areas, E_2 shows a clear continental influence and only restricted low-energy shallow coastal sub-environments, such as restricted lagoons and coastal ponds locally developed. In these sub-environments, grey organic-rich siltstones were deposited.

Sub-unit E_3 is composed of variegated mudstones and siltstones with common pedogenic features all over the sub-basin. Only a local black organic-rich bed, probably deposited in a confined pond, has been found.

3. Material and methods

3.1. Method of preparation and microscopy

Four stratigraphic sections of the Escucha Formation have been studied in the southern sector of the Oliete Sub-basin for palynological studies. Nine organic-rich beds from the three sub-units have been sampled for quantitative study (Fig. 2). Each sample has been prepared following the standard palynological techniques including acid treatments (HCl, HF, HNO_3) at high temperatures [60]. Microscopic analysis of residues, mounted in glycerine jelly, has been performed by a Leica Laborlux D microscope, and they produced pollen counts of at least 600 per sample. Problematic specimens and/or biostratigraphic key forms has been later analysed and imaged by a Biorad 1024 confocal laser scanning microscope driven by Leica Confocal Scanware (Centro de Microscopía y Citometría, Universidad Complutense de Madrid, Spain). VGStudio Max 1.2 (Volume Graphics GmbH, Heidelberg, Germany) was employed to process the image stacks and generate three-dimensional reconstructions of the whole grains.

3.2. Multivariate analysis

In order to extract the greatest variance of the pollen data set, multivariate analysis methods have been performed. Largely employed in Quaternary palaeoecology [42], the use of multivariate analytical approach remains scarce in Mesozoic studies [14,29,31,34]. To analyse the main gradients of changes of the levels according to changes in their taxa, a correspondence analysis [9] was performed based on the levels × taxa data matrix. The correspondence analysis (CA) has been successfully employed in many palynological [43] and palaeoecological studies [24,52]. Later, the chi-squared distance matrix was subjected to Q- and R-mode hierarchical cluster analysis using the Ward's method [58] as agglomerative algorithm, in order to group levels and taxa

Fig. 3. **1**. *Subtilisphaera perlucida* (Alberti) Jain & Millepied, 1973. Microscopie confocale, maximum de projections, niveau M_1. **2**. *Cyclonephelium compactum* Deflandre & Cookson, 1955. Microscopie confocale, reconstruction 3D, niveau M_1. **3**. *Brenneripollis*/*Pennipollis*. Microscopie confocale, reconstruction 3D, niveau M_4. **4**. *Cribroperidinium orthoceras* (Eisenack) Davey, 1969. Microscopie confocale, reconstruction 3D, niveau M_1. **5**. Même spécimen qu'en **4**. Microscopie optique traditionnelle. **6**. Même spécimen qu'en **3**. Microscopie confocale, section du grain montrant la nature non columellée de l'exine. **7**. *Clavatipollenites hughesii* Couper, 1958. Microscopie confocale, maximum de projections, niveau M_4. **8**. *Stellatopollis dejaxii* Ibrahim, 2002. Microscopie optique traditionnelle, niveau N_1. Barre d'échelle : 10 µm.

Table 1
List of palynomorphs identified in the Upper Aptian–Lower Albian of the Oliete Sub-basin, modified from [41]
Tableau 1
Liste des palynomorphes identifiés dans l'Aptien supérieur–Albien inférieur du sous-bassin d'Oliete, modifié d'après [41]

Miospores	Botanical affinity
Spores of vascular cryptogamma	
Aequitriradites spinulosus (Cookson & Dettmann 1958) Cookson & Dettmann 1961	Bryophyta
Appendicisporites spp.	Pteridophyta (Schizaeaceae)
Baculatisporites sp.	Pteridophyta (Osmundaceae)
Biretisporites sp.	Pteridophyta (Cyatheaceae/Dicksoniaceae/Dipteridaceae)
Camerozonosporites sp.	Lycophyta
Cibotiumspora jurienensis (Balme 1957) Filatoff 1975	Pteridophyta (Cyatheaceae/Dicksoniaceae)
Cicatricosisporites spp.	Pteridophyta (Schizaeaceae)
Cicatricososporites auritus Singh 1971	Pteridophyta (Schizaeaceae)
Cingutriletes sp.	Bryophyta
Concavissimisporites sp.	Pteridophyta (Cyatheaceae/Dicksoniaceae/Dipteridaceae)
Contignisporites sp.	Pteridophyta (Pteridaceae)
Converrucosisporites sp.	Pteridophyta (Cyatheaceae/Dipteridaceae)
Costatoperforosporites spp.	Pteridophyta (Schizaeaceae)
Deltoidospora spp.	Pteridophyta (Cyatheaceae/Dicksoniaceae/Dipteridaceae)
Densoisporites velatus Weyland & Krieger 1953	Lycophyta (Pleuromeiaceae/Selaginellaceae)
Dictyophyllidites harrisii Couper 1958	Pteridophyta (Dipteridaceae/Matoniaceae)
Echinatisporis sp.	unknown Pteridophyta
Foraminisporis asymetricus Dettmann 1963	unknown Pteridophyta
Foveotriletes spp.	unknown Pteridophyta
Gleicheniidites senonicus Ross 1949	Pteridophyta (Gleicheniaceae)
Ischyosporites spp.	Pteridophyta (Schizaeaceae)
Kraeuselisporites sp.	Lycophyta (Selaginellaceae)
Kuylisporites lunaris Cookson & Dettmann 1958	Pteridophyta (Cyatheaceae/Dicksoniaceae/Dipteridaceae)
Laevigatosporites sp.	Pteridophyta (Polypodiaceae)
Leptolepidites spp.	Lycophyta
Lycopodiumsporites crassimacerius Hedlund 1966	Lycophyta
Microreticulatisporites cf. *diatreus* Norris 1969	Pteridophyta (Botryopteridales)
Neoraistrickia sp.	Lycophyta
Nodosisporites sp.	Pteridophyta (Schizaeaceae)
Patellasporites tavaredensis Groot & Groot 1962	Pteridophyta
Phlebopterisporites globosus (Kimyai 1966) Juhász 1979	Pteridophyta (Matoniaceae)
Punctatisporites sp.	Pteridophyta (Osmundaceae)
Retitriletes spp.	Lycophyta
Rubinella sp.	unknown Pteridophyta
Staplinisporites caminus (Balme 1957) Pocock 1962	Bryophyta
Stereisporites spp.	Bryophyta (Sphagnaceae)
Taurucosporites cf. *segmentatus* Stover 1962	unknown Pteridophyta
Trachysporites sp.	unknown Pteridophyta
Trilobosporites sp.	Pteridophyta (Dicksoniaceae?)
Triporoletes reticulatus (Pocock 1962) Playford 1971	Bryophyta
Tuberositriletes sp.	unknown Pteridophyta
Todisporites major Couper 1958	Pteridophyta (Osmundaceae)
Undulatisporites sp.	unknown Pteridophyta
Uvaesporites sp.	Lycophyta (Selaginellaceae)
Verrucosisporites spp.	Pteridophyta (Botryopteridales/Zygopteridales/Marattiales)
Pollen grains (gymnosperms)	
Abietinaepollenites sp.	Coniferophyta (Pinaceae)
Alisporites spp.	Pteridospermophyta (Peltaspermales)
Araucariacites australis Cookson 1947	Coniferophyta (Araucariaceae)
Bennettiteapollenites sp.	Ginkgoales/Cycadales/Bennetitales
Cedripites sp.	Coniferophyta (Pinaceae)
Cerebropollenites spp.	unknown Coniferophyta
Classopollis spp.	Coniferophyta (Cheirolepidiaceae)
Cycadopites spp.	Ginkgoales/Cycadales/Bennetitales

Table 1 (*Continued*)

Miospores	Botanical affinity
Equisetosporites sp.	Gnetophyta
Eucommiidites spp.	Gnetales/Cycadales/Bennetitales
Exesipollenites tumulus Balme 1957	Bennetitales/Taxodiaceae
Inaperturopollenites spp.	Coniferophyta (Taxodiaceae–Cupressaceae)
Monosulcites minimus Cookson 1947 ex. Couper 1953	Ginkgoales/Cycadales/Bennetitales
Parvisaccites sp.	unknown Coniferophyta
Perinopollenites elatoides Couper 1958	Coniferophyta (Taxodiaceae)
Pinuspollenites sp.	Coniferophyta (Pinaceae)
Phyllocladidites sp.	Coniferophyta (Podocarpaceae)
Podocarpidites sp.	Coniferophyta (Podocarpaceae)
Rugubivesiculites sp.	unknown Coniferophyta
Spheripollenites sp.	unknown Coniferophyta
Undetermined bisaccate pollen grains	unknown Coniferophyta
Vitreisporites pallidus (Reissinger 1950) Nilsson 1958	Pteridospermophyta (Caytoniales)
Pollen grains (angiosperms)	
Afropollis sp.	Winteraceae?
Asteropollis sp.	unknown
Clavatipollenites spp.	Chloranthaceae?
Liliacidites spp.	Liliatae?
Brenneripollis–Pennipollis complex	Alismatidae?
Stellatopollis dejaxii Ibrahim 2002	Magnolidae?
Tricolpites sp.	unknown
Other palynomorphs	
Tasmanaceae	Prasinophyta
Dinoflagellate cysts	Dinophyceae
Michrystridium sp.	Acritarcha
Botryococcus	Chlorophyta
Organic lining	Foraminifera

The table highlights their botanical affinities in accordance with the data of Abbink [1], Abbink et al. [2], Balme [5], and Batten and Dutta [7].
Le tableau souligne leurs affinités botaniques, en accord avec les données d'Abbink [1], d'Abbink et al. [2], de Balme [5] et de Batten et Dutta [7].

according to their affinities. Eventually, to determine the grade of recruitment of groups of taxa among the different group of levels, a synthetic matrix (Fig. 7) has been elaborated based on frequencies of the groups of taxa in each group of levels. The statistical analyses were carried out with the computer programs PC-ORD 4.0 [33] and STATISTICA 6.0 (StatSoft Inc., 2001).

4. Results

The palynological study has yielded assemblages with high diversity of taxa. Terrestrial and marine palynomorphs (level M_1), including dinoflagellate cysts (Fig. 3: 1-2, 4-5), acritarchs and foraminifer linings, have been observed [41]. Concretely, 72 terrestrial palynomorphs (Table 1) have been identified here: 44 related to cryptogams, 21 to gymnosperms and seven to primitive angiosperms.

The palynological assemblages of the levels M_1 to M_5 corresponding to the sub-unit E_1, are dominated by pollen of gymnosperms such as *Classopollis*, *Araucariaceae*, *Taxodiaceae-Cupressaceae* and *Alisporites* (Fig. 4). By contrast, the levels U_3, N_1, N_2 and BC, corresponding to the Sub-units E_2 and E_3, are characterized by the high representation (levels N_1 and N_2) or dominance (levels U_3 and BC) of the spores of vascular cryptogams. The level BC stands out by the predominance of the genera *Deltoidospora* and *Dictyophyllidites*, which account for 94% of the total palynomorph sum. The Schizaeaceae (*Appendicisporites*, *Cicatricosisporites*, *Costatoperforosporites*, *Ischyosporites*, *Nodosisporites*) are particularly well diversified, especially in the levels of the Unit E_2.

The presence of pollen grains of primitive angiosperms (Fig. 3: 3, 6–8) is relevant in all the studied samples, except in the level BC. The tectate monosulcate pollen attributed to monocots and chloranthoid dicots are the most abundant. *Clavatipollenites* is the best represented, but pollen grains of the genus *Liliacidites* and *Brenneripollis–Pennipollis* complex [18,21,22,28] have been also recorded but in lower amounts. Scarce tricolpate grains (*Tricolpites*) have been noticed along the series. In addition, *Afropollis* and *Stellatopollis*, two genera related to angiosperms with

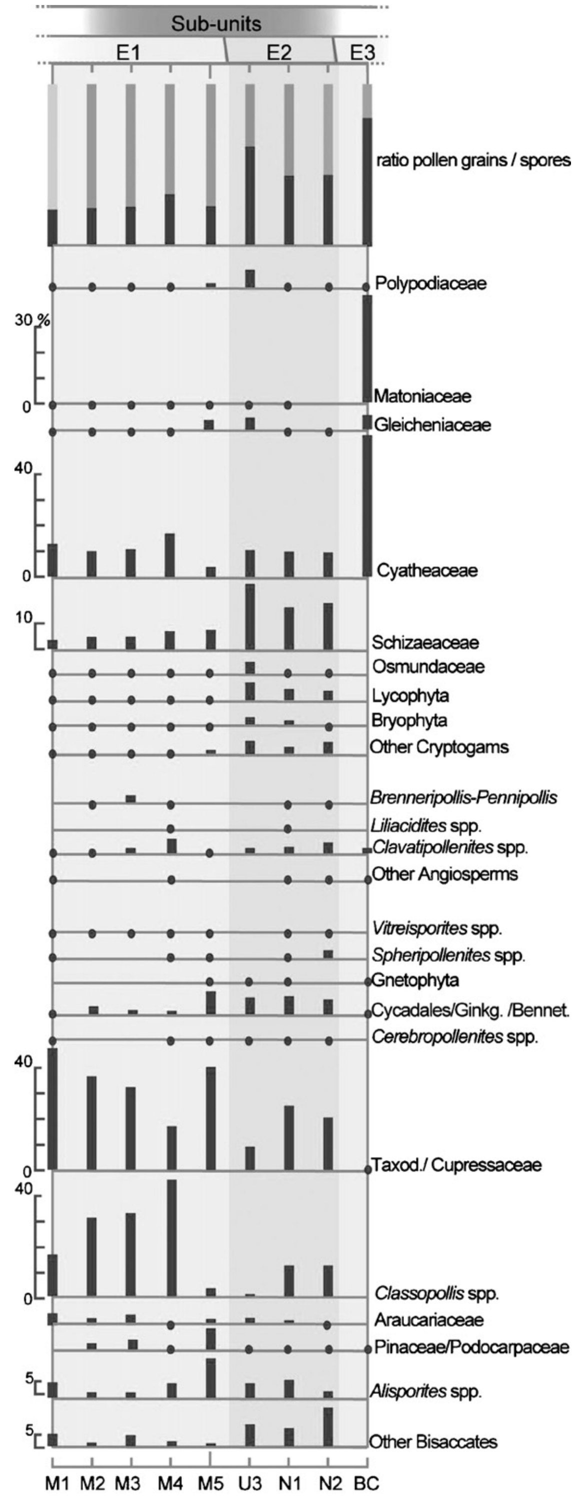

Fig. 4. Miospore percentage diagram of the Oliete Sub-Basin, illustrating the main groups of taxa classified according to their botanical affinities and abundance.

Fig. 4. Diagramme pollinique (en pourcentages) du sous-bassin d'Oliete, illustrant les principaux groupes de miospores, classifiés selon leurs affinités botaniques.

Gondwanan affinities, have been identified in various samples.

A first CA ordination carried out with the nine levels reveals a major direction of variation accounting for 55.5% of the total variance, and confirms the original pollen composition of the level BC compared with the other levels.

Omitting the level BC, a second CA presents a variance of 82.5% in the first two dimensions (Fig. 5). The first axis (48.1% of variance) explains a gradient between Schizaeaceae, Cycadales/Ginkgoales/Bennettitales, Lycophyta, *Alisporites* spp., Polypodiaceae, Gleicheniaceae and Osmundaceae in the negative extreme, and *Classopollis* spp., angiosperms and Cyatheaceae/Dicksoniaceae/Dipteridaceae in the positive one. In this dimension, the most representative levels are U_3 against M_4, M_3, and M_2. The second axis (34.4% of variance) explains a gradient between Taxodiaceae/Cupresaceae and Pinaceae/Podocarpaceae in the negative extreme, and Schizaeaceae, Lycophyta, Briophyta and Cyatheaceae/Dicksoniaceae/Dipteridaceae in the positive one. The most representative levels are M_5 and M_1 in the negative, and U_3 (but also N_1 and N_2) in the positive extreme. Cluster analysis reveals four groups of levels (Fig. 6(a)) and five groups of taxa (Fig. 6(b)). The matrix of Fig. 7 represents the percentages for each taxa group in every level-group.

5. Discussion and conclusions

Reconstructions of Early Cretaceous environments based on palynological studies are complex since fossil plants do not present modern counterparts. In these conditions, actualistic studies remain difficult to undertake.

The palynological analysis indicates the existence of highly diversified assemblages often dominated by spores attributed to different groups of vascular cryptogams. These plants are assumed to have grown under warm conditions (subtropical to tropical) in moist environments, although some inhabited drier locations [1,56]. High percentages of spores encountered in the levels corresponding to the sub-units E_2 and E_3 (Fig. 4) condition the composition of taxon-groups A and B (Fig. 6). Taxon-group A, including Bryophyta, Lycophyta, Gnetophyta and Polypodiaceae, may be associated with hygrophilous places related to understorey vegetation. Taxon-group B includes taxa that could be riparian such as Osmundaceae, Schizaeaceae and Cycadales/Ginkgoales/Bennettitales, and ferns of families Gleicheniaceae and Matoniaceae that were adapted to sunnier and drier places [17,56]. The palynomorphs that constitute Taxa groups A and B were

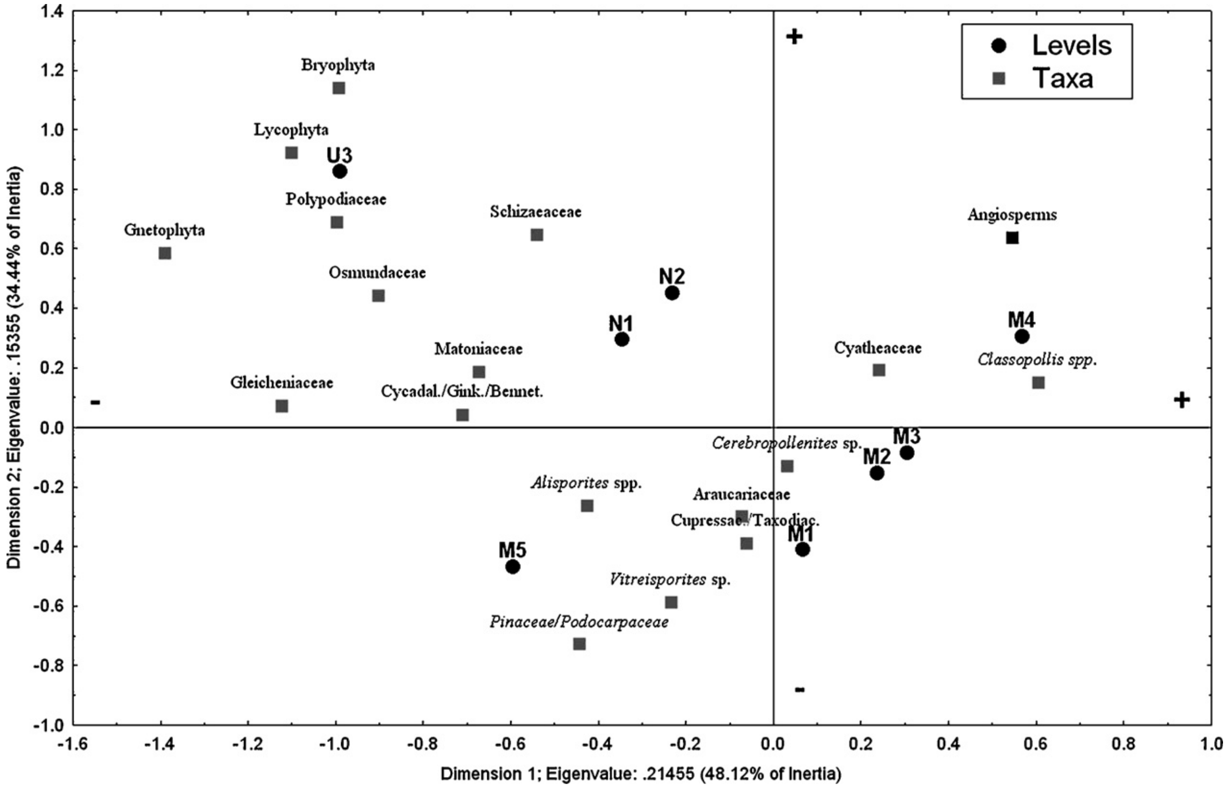

Fig. 5. Representation of the position of the levels and taxa in the two first dimensions of the correspondence analysis. Level BC was extracted from the analysis.

Fig. 5.Représentation de la position des niveaux et des taxa dans les deux premières dimensions de l'analyse factorielle des correspondances. Le niveau BC a été retiré de l'analyse.

mainly produced by local and parautochthonous elements, transported only over a small distance toward the deposition site [8]. Very likely, the spore-producers of taxon-groups A and B grew in back swamps, riverbanks or other freshwater-related environments.

Taxon group C is a miscellaneous group recruiting spores of Cyatheaceae/Dicksoniaceae/Dipteridaceae and pollen grains of *Classopollis* and angiosperms (Fig. 6). It is well represented in levels constituting the sub-unit E_1, except in the level M_5 (Figs. 4 and 7). *Classopollis* was produced by extinct anemophilous conifers of the Cheirolepidiaceae family. Traditionally, taxa attributed to this family are assumed drought-resistant and adapted to various environments, including saline ones [4,38,53]. On the contrary, representatives of the fern families Cyatheaceae, Dicksoniaceae, and Dipteridaceae are generally associated with wet places. Nevertheless, several taxa attributed to Dicksoniaceae and Dipteridaceae present a noteworthy protection of sporangia as well as coriaceous fronds, which may indicate adaptation to stressful environments like brackish areas [56]. Palaeoecological interpretations of fossil angiosperms [13,19,45,46] support the hypothesis of pioneer herbaceous plants or shrubs capable of colonizing frequently disturbed environments including riverbanks, floodplains and back swamps. Hence, the miscellaneous taxon-group C could integrate miospores of plants occupying both coastal forests with dry conditions and wetter environments, such as riverbanks, temporary ponds, and periodically flooded plains. Taxon-group C includes local and extra-local miospores of parautochthonous and allochthonous elements.

Taxon-groups D and E are constituted by pollen grains of different types of anemophilous gymnosperms (Fig. 6). Concretely, taxon-group D only includes bisaccate pollen grains and is well-represented in level M_5 of the sub-unit E_1 (Fig. 4). These pollens are related to pteridosperms (*Alisporites* and *Vitreisporites*) and conifers such as Pinaceae and Podocarpaceae. It appears highly probable that all these pollen grains were produced from diverse areas, since conifers inhabited environments of varied ecological conditions including dry, saline, or upland areas [2,55], whereas seed-ferns are assumed to grow in moist lush vegetation, mangroves and tidally

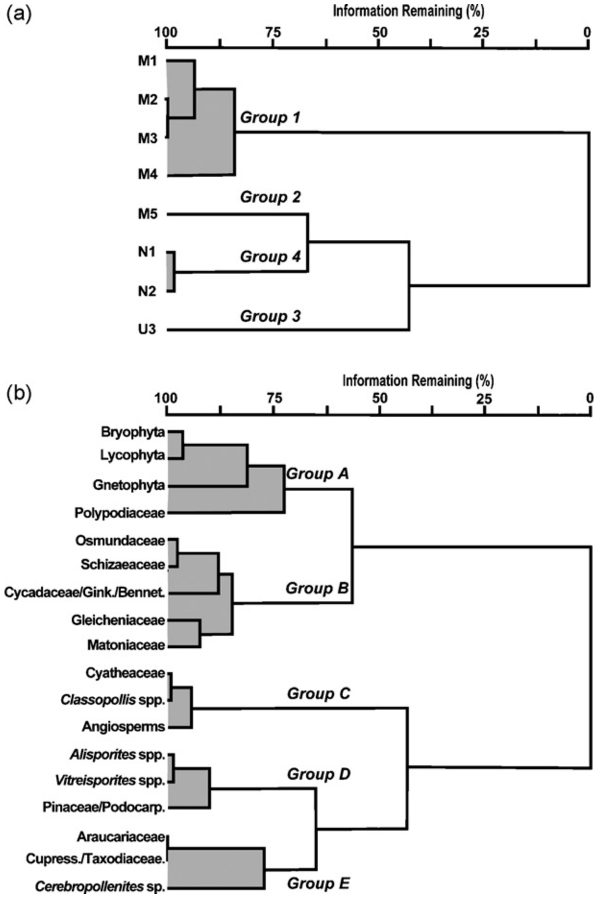

Fig. 6. Dendrograms of the Q-mode (a) and R-mode (b) cluster analysis using the Ward's method and the chi-squared distance matrix.

Fig. 6. Dendrogramme des modes Q (a) et R (b) de la classification ascendante hiérarchisée utilisant l'algorithme de Ward et la matrice de distance du chi^2.

influenced environments [26,57]. In a similar way, taxon-group E includes inaperturate forms such as pollen grains of Araucariaceae as well as pollen grains attributed to the genera *Inaperturopollenites* and *Cerebropollenites*. Pollen of this group is well represented along the succession, except in sub-unit E_3 (Fig. 4). Following an actualistic approach, it appears reasonable to attribute to this group environments of very diverse ecological conditions including saline coastal locations, but the exclusion of floodplains cannot be discarded. Contrarily, *Cerebropollenites*, pollen grains of uncertain filiation could be related to pioneer plants [1,36]. Hence, the components of taxon-groups D and E include local, extra-local, regional and surely extra-regional pollen of allochthonous elements. The grouping of these components may reflect a taphonomic bias.

		Taxa groups				
		A	B	C	D	E
Level groups	1	○	○	▲	●	△
	2	●	△	○	▲	△
	3	▲	●	○	○	○
	4	●	●	●	○	○

Fig. 7. Reduced data matrix calculated from the main clusters of the dendrograms in Fig. 5. Representation < 15%:○, 15–30%: ●, 30–50%: △ and > 50%: ▲.

Fig. 7. Matrice réduite calculée à partir des principales catégories des dendogrammes représentés sur la Fig. 5. Représentation < 15 % :○, 15–30 % : ●, 30–50 % : ▲ et > 50 % : ▲.

The quantitative study presented here permits to precise the environmental conditions of the successive levels. According to CA ordination (Fig. 5) and pollen diagram (Fig. 4), levels from sub-unit E_1 (M_1 to M_5) are mainly characterized by the high representation of gymnosperm pollen grains. To the contrary, the cluster analysis (Fig. 6(a)) clearly separates the level M_5 (level-group 2 of Fig. 6(a)) from levels M_1 to M_4, bunched together (level group 1 of Fig. 6(a)). The pollen diagram (Fig. 4) and the synthetic matrix (Fig. 7) indicate that level M_5 differs from the group formed by levels M_1 to M_4 (level-group 1 of Fig. 6(a)) by low percentages of spores of Cyatheaceae and pollen grains of *Classopollis* and angiosperms (taxon-group C of Fig. 6(b)) and a high representation of bisaccate pollen grains (taxon-group D of Fig. 6(b)). This could indicate the existence of forest communities widely distributed in the zone. Assemblages dominated by *Classopollis* pollen grains would represent forests integrated by Cheirolepidiaceae growing in more stressed conditions, while assemblages dominated by Araucariaceae, Taxodiaceae/Cupressaceae, and bissacate pollen grains (especially *Alisporites*, *Vitreisporites*), would correspond to forests occupying riverbanks or mangroves [1,2,4,13,38]. The availability of water could be one cause explaining the existence of these two different forest communities. Nevertheless, this hypothesis must be contrasted by taphonomic considerations, already mentioned concerning the wind-dispersed pollen grains that belong to taxon-groups D and E (and especially Pinaceae/Podocarpaceae).

The predominance of these pollen grains in levels from sub-unit E_1 indicates open environments of sedimentation, which can be subject to marine influence (level M_1). This evidence is probably related to the wide palaeoenvironmental differentiation characterizing the palaeogeography of the area during the deposition of the lower part of the Escucha Formation [47].

The levels U_3, N_1 and N_2 from sub-unit E_2 are characterized by the high representation of spores (Figs. 4 and 7). Considering the cluster analysis

(Fig. 6(a)), levels N_1 and N_2 appear bunched up and separated from level U_3. This separation may be explained by the sedimentological characteristics of the considered levels. Level U_3 arises from organic-rich sediments deposited under tidal conditions, whereas levels N_1 and N_2 come from grey organic-rich siltstone deposited in confined low-energy areas developed in more continental environments [47].

The high representation of spores of Bryophyta, Lycophyta and Polypodiaceae (taxon-group A) as well as of Osmundaceae and Schizaeaceae (taxon-group B) in level U_3 (Figs. 4 and 7) suggests the existence of a local humid vegetation. Levels N_1 and N_2 differ from level U_3 by the higher representation of extra-local elements such as *Classopollis* and Taxodiaceae/Cupressaceae pollen grains (Fig. 4). It could reflect humid environments recruiting parautochthonous and allochthonous elements such as opened ponds and back swamps. Nevertheless, the representation of wind-dispersed pollen grains is lower in sub-unit E_2 than in the sub-unit E_1. The sedimentological data clarified elsewhere [47] indicate that materials from sub-unit E_2 have been deposited in more restrictive and continental environments.

The low diversity of the assemblage exhibited in level BC, and especially its unusual percentage of fern spores (Fig. 4) could be related to very poorly diversified communities growing in stressed habitats. The palynological assemblage of level BC (sub-unit E_3) differs drastically from all other studied associations and supports original palaeoenvironmental conditions of deposition yet inferred by sedimentological evidences [47]. These ferns communities could be a possible case of recovery vegetation after crisis or represent a vegetation of replacement of more complex and diverse palaeoecosystems .

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References

[1] O.A. Abbink, Palynological investigations in the Jurassic of the North Sea region, Lab. Palaeobot. Palynol. Contrib. Ser. 8 (1998) 1–191.

[2] O.A. Abbink, J.H.A. Van Konijnenburg-Van Cittert, H. Visscher, A sporomorph ecogroup model for the Northwest European Jurassic–Lower Cretaceous: concepts and framework, Geol. Mijnbouw 83 (6) (2004) 17–31.

[3] M.J. Aguilar, J. Ramírez del Pozo, O. Ribas, Algunas precisiones sobre la sedimentación y paleontología del Cretácico Inferior en la zona de Utrillas-Villarroya de los Pinares, Estud. Geol. 27 (1971) 497–512.

[4] K.L. Alvin, Cheirolepidiaceae: biology, structure and paleoecology, Rev. Palaeobot. Palynol. 37 (1982) 71–98.

[5] B.E. Balme, Fossil in situ spores and pollen grains: an annotated catalogue, Rev. Palaeobot. Palynol. 87 (1995) 81–323.

[6] E.J. Barron, P.J. Fawcett, W.H. Peterson, A 'simulation' of mid-Cretaceous climate, Paleoceanography 105 (1995) 953–962.

[7] D.J. Batten, R.J. Dutta, Ultrastructure of exine of gymnospermous pollen grains from Jurassic and basal Cretaceous deposits in Northwest Europe and implications for botanical relationships, Rev. Palaeobot. Palynol. 99 (1997) 25–54.

[8] A.K. Behrensmeyer, R.W. Hook, Paleoenvironmental contexts and taphonomic modes in the terrestrial fossil record, in: A.K. Behrensmeyer, J.D. Damuth, W.A. DiMichele, R. Potts, H.-D. Sues, S.L. Wing (Eds.), Terrestrial Ecosystems through Time. Evolutionary Paleoecology of Terrestrial Plants and Animals, University of Chicago Press, Chicago, 1992, pp. 15–38.

[9] J.-P. Benzécri, L'analyse des correspondances, in: L'analyse des Données, 2, Dunod, Paris, 1973.

[10] R.A. Berner, Z. Kothavala, GEOCARB. III: a revised model of atmospheric CO_2 over Phanerozoic time, Am. J. Sci. 301 (2001) 182–204.

[11] A. Cervera, G. Pardo, J. Villena, Algunas precisiones litoestratigráficas sobre la formación 'Lignitos de Escucha', Tecniterrae 14 (1976) 25–33.

[12] L.J. Clarke, H.C. Jenkyns, New oxygen isotope evidence for long-term Cretaceous climatic change in the Southern Hemisphere, Geology 27 (1999) 699–702.

[13] C. Coiffard, B. Gomez, J. Kvaček, F. Thévenard, Early Angiosperm ecology: evidence of Albian-Cenomanian of Europe, Ann. Bot. 98 (2006) 495–502.

[14] B. Courtinat, B. David, Analyse multivariée de trois populations de *Corollina* du Jurassique moracain, Rev. Palaeobot. Palynol. 41 (1984) 39–50.

[15] P.R. Crane, Vegetational consequences of angiosperm diversification, in: E.M. Friis, W.G. Chaloner, P.R. Crane (Eds.), The Origins of Angiosperms and their Biological Consequences, Cambridge University Press, Cambridge, 1987, pp. 107–144.

[16] P.R. Crane, S. Lidgard, Angiosperm diversification and palaeolatitudinal gradients in Cretaceous floristic diversity, Science 246 (1989) 675–678.

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

[18] J.A. Doyle, The rise of Angiosperms as seen in the African Cretaceous pollen record, in: K. Heine, A. Scott, A. Cadman, R. Verhoeven (Eds.), Palaeoecology of Africa and the Surrounding Island, 3rd Conf. Afr. Palynol., Johannesburg, Republic of South Africa, 1999, pp. 3–29.

[19] T.S. Feild, N.C. Arens, J.A. Doyle, T.E. Dawson, M.J. Donoghue, Dark and disturbed: a new image of early angiosperm ecology, Paleobiology 30 (2004) 82–107.

[20] F. Fluteau, G. Ramstein, J. Besse, R. Guiraud, J.-P. Masse, Impacts of palaeogeography and sea level changes on mid-Cretaceous

climate, Palaeogeogr. Palaeoclimatol. Palaeoecol. 247 (2007) 357–381.

[21] E.M. Friis, K.R. Pedersen, P.R. Crane, Fossil floral structures of a basal angiosperm with monocolpate, reticulate-acolumellate pollen from the Early Cretaceous of Portugal, Grana 39 (2000) 226–239.

[22] E.M. Friis, K.R. Pedersen, P.R. Crane, Cretaceous angiosperm flowers: innovation and the evolution in plant reproduction, Palaeogeogr. Palaeoclimatol. Palaeoecol. 232 (2006) 251–293.

[23] A. Hallam, Phanerozoic Sea Level Changes, Columbia University Press, New York, 1992.

[24] O. Hammer, D.A.T. Harper, Paleontological Data Analysis, Blackwell Publishing, Malden, MA, USA, 2006.

[25] B.U. Haq, J. Hardenbol, P.R. Vail, Chronology of fluctuating sea levels since the Triassic, Science 235 (1987) 1156–1166.

[26] T.M. Harris, The stem of *Pachypteris papillosa* (Thomas and Bose) Harris, Bot. J. Linn. Soc. 86 (1983) 149–159.

[27] G.F.W. Herngreen, M. Kedves, L.V. Rovnina, S.B. Smirnova, Cretaceous palynofloral provinces: a review, in: J. Jansonius, D.C. McGregor (Eds.), Palynology: principles and applications, Am. Assoc. Stratigr. Palynol. Found. 1996, pp. 1157–1188.

[28] M. Hesse, R. Zetter, The fossil pollen record of Araceae, Plant Syst. Evol. 263 (2007) 93–115.

[29] R.N.L.B. Hubbard, M.C. Boulter, Mid Mesozoic floras and climates, Palaeontology 40 (1997) 43–70.

[30] B.T. Huber, D.A. Hodell, C.P. Hamilton, Middle–Late Cretaceous climate of the southern high latitudes: Stable isotopic evidence for minimal equator-to-pole thermal gradients, Geol. Soc. Am. Bull. 107 (1995) 1164–1191.

[31] W.L. Kovach, D.J. Batten, Association of palynomorphs and palynodebris with depositional environments: quantitative approaches, in: A. Traverse (Ed.), Sedimentation of Organic Particles, Cambridge University Press, Cambridge, 1994, pp. 391–407.

[32] R. Lupia, S. Lidgard, P.R. Crane, Comparing palynological abundance and diversity: implications for biotic replacement during the Cretaceous angiosperm radiation, Paleobiology 25 (1999) 305–340.

[33] B. McCune, M.J. Mefford, PC-ORD. Multivariate Analysis of Ecological Data. Version 4.0, MjM Software Design, Gleneden Beach, OR, USA, 1999.

[34] J. Médus, C. Ipert, Introduction de l'analyse multifactorielle dans le traitement de données palynofloristiques santoniennes (Crétacé supérieur), Rev. Palaeobot. Palynol. 24 (1977) 141–154.

[35] A. Meléndez, A.R. Soria, N. Meléndez, A coastal lacustrine system in the Lower Barremian from the Oliete Sub-basin, central Iberian Range, northeastern Spain, in: E. Gierlowski-Kordesch, K. Kelts (Eds.), Lake Basins through Space and Time, 46, AAPG Mem., 2000, pp. 279–284.

[36] B.A.R. Mohr, New palynological information on the age and environment of Late Jurassic and Early Cretaceous vertebrate localities of the Iberian Peninsula (eastern Spain and Portugal), Berl. Geowiss. Abh, Reihe A. Geol. Palaeontol. 106 (1989) 291–301.

[37] J.R. Morley, Interplate dispersal paths for megathermal angiosperms, Perspect. Plant Ecol. Evol. Syst. 6 (2003) 5–20.

[38] T.T. Nguyen Tu, H. Bocherens, A. Mariotti, F. Baudin, D. Pons, J. Broutin, S. Derenne, Cl. Largeau, Ecological distribution of Cenomanian terrestrial plants based on $^{13}C/^{12}C$ ratios, Palaeogeogr. Palaeoclimatol. Palaeoecol. 145 (1999) 79–93.

[39] G. Pardo, Estratigrafía y sedimentología de las formaciones detríticas del Cretácico Inferior terminal del Bajo Aragón Turolense, Tesis Doctoral, Universidad de Zaragoza, Spain, 1979.

[40] D. Peyrot, J.P. Rodríguez-López, E. Barrón, N. Meléndez, A.R. Soria, Nuevas aportaciones a la Palinología del Cretácico Inferior de la Subcuenca de Oliete (Fm. Escucha, Teruel), Fundamental 6 (2005) 165–168.

[41] D. Peyrot, J.P. Rodríguez-López, E. Barrón, N. Meléndez, Palynology and biostratigraphy of the Escucha Formation in the Early Cretaceous Oliete Sub-basin, Teruel, Spain, Rev. Esp. Micropaleontol. 39 (2007) 135–154.

[42] I.C. Prentice, Multidimensional scaling as a research tool in Quaternary palynology: a review of theory and methods, Rev. Palaeobot. Palynol. 31 (1980) 71–104.

[43] I.C. Prentice, Multivariate methods for data analysis, in: B.E. Berglund (Ed.), Handbook of Holocene Palaeoecology and Palaeohydrology, Wiley, New York, 1986, pp. 775–797.

[44] X. Querol, Distribución de la materia mineral y azufre en los carbones de la Fm. Escucha. Relación con los factores geológicos, sedimentológicos y diagenéticos, Tesis Doctoral, Universidad de Barcelona, Spain, 1990.

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

[46] G. Retallack, D.L. Dilcher, Cretaceous angiosperm invasion of North America, Cretaceous Res. 7 (1986) 227–252.

[47] J.P. Rodríguez-López, N. Meléndez, A.R. Soria, Arquitectura estratigráfica de la Fm. Escucha (Albiense) en el flanco sur del sinclinal de Cueva Foradada. Subcuenca de Oliete (Teruel), Cuenca Ibérica Central, Geo-Temas 8 (2005) 95–98.

[48] D.L. Royer, R.A. Berner, D.J. Beerling, Phanerozoic atmospheric CO_2 change: evaluating geochemical and paleobiological approaches, Earth-Sci. Rev. 54 (2001) 349–392.

[49] N. Solé de Porta, X. Querol, R. Cabanes, R. Salas, Nuevas aportaciones a la palinología y paleoclimatología de la formación Escucha (Albiense inferior-medio) en las cubetas de Utrillas y Oliete, Cordillera Ibérica Oriental, Cuad. Geol. Iber. 18 (1994) 203–215.

[50] A.R. Soria, La sedimentación en las cuencas marginales del Surco Ibérico durante el Cretácico Inferior y su control tectónico, Tesis Doctoral, Universidad de Zaragoza, 1997.

[51] R.A. Spicer, A.B. Herman, The Albian-Cenomanian flora of the Kukpowruk River, western North Slope, Alaska: stratigraphy, palaeofloristics, and plant communities, Cretaceous Res. 22 (2001) 1–40.

[52] R.A. Spicer, C.R. Hill, Principal components and correspondance analyses of quantitative data from a Jurassic plant bed, Rev. Palaeobot. Palynol. 28 (1979) 273–299.

[53] F. Thévenard, B. Gomez, V. Daviero-Gomez, Xeromorphic adaptations of some Mesozoic gymnosperms. A review with palaeoclimatological implications, C. R. Palevol 4 (2005) 67–77.

[54] G. R. Upchurch, J.A. Wolfe, Cretaceous vegetation of the Western Interior and adjacent regions of North America. Evolutions of the Western Interior Basin, in: E.G. Kauffman, W.G.E. Caldwell (Eds.), Cretaceous evolution of the Western Interior Basin, Geol. Assoc. Can. Spec. Pap., 1993, pp. 243–281.

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

[56] J.H.A. Van Konijnenburg-Van Cittert, Ecology of some Late Triassic to Early Cretaceous ferns in Eurasia, Rev. Palaeobot. Palynol. 119 (2002) 113–124.

[57] J.H.A. Van Konijnenburg-Van Cittert, J. Van der Burgh, The flora from the Kimmeridgian (Upper Jurassic) of Culgower, Sutherland, Scotland, Rev. Palaeobot. Palynol. 78 (1993) 235–267.

[58] J.H. Ward, Hierarchical grouping to optimize an objective function, J. Am. Stat. Assoc. 58 (1963) 236–244.

[59] P.A. Wilson, R.D. Norris, Warm tropical ocean surface and global anoxia during the mid-Cretaceous period, Nature 412 (2001) 425–429.

[60] G.D. Wood, A.M. Gabriel, J.C. Lawson, Palynological techniques processing and microscopy, in: J. Jansonius, D.C. McGregor (Eds.), Palynology: Principles and Applications, 1, American Association of Stratigraphic Palynologists Foundation, 1996, pp. 29–50.