

A new uppermost Albian flora from Teruel province, northeastern Spain

Luis Miguel SENDER

Universidad de Zaragoza, Departamento Ciencias de la Tierra (Paleontología),
c/ Pedro Cerbuna 12, E-50009 Zaragoza (Spain)
lsender@unizar.es

Uxue VILLANUEVA-AMADOZ

Instituto de Geología, UNAM, Departamento de Paleontología,
Ciudad Universitaria, Coyoacan 04510 México D.F. (Mexico)
Uxuevillanueva@yahoo.es

Jose Bienvenido DIEZ

Raquel SANCHEZ-PELLICER

Universidad de Vigo,
Departamento Geociencias Marinas y Ordenación del Territorio,
Campus Lagoas-Marcosende, E-36200 Vigo, Pontevedra (Spain)
jbdiez@uvigo.es
sanchezpellicer@uvigo.es

Antoine BERCOVICI

Lund University, Department of Geology,
Sölvegatan 12, SE-223 62 Lund (Sweden)
antoine.bercovici@geol.lu.se

Denise PONS

Université Pierre et Marie Curie, UMR 7207,
Muséum national d'Histoire naturelle,
Centre de Recherche en Paléobiodiversité et Paléoenvironnements
case postale 48, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
denise.pons@snv.jussieu.fr

Javier FERRER

Universidad de Zaragoza, Departamento Ciencias de la Tierra (Paleontología),
c/ Pedro Cerbuna, 12, E-50009 Zaragoza (Spain)
joferrer@unizar.es

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ABSTRACT

This paper reports a new Early Cretaceous flora discovered recently near the village of Estercuel (Teruel province, northeastern Spain). The plant bearing beds belong to the uppermost part of the Early Cretaceous succession, at the top of the fluvial deposits of the Utrillas Formation. The site has yielded a diverse assemblage of plant compressions including lycopods and ferns, various gymnosperms as well as terrestrial and aquatic angiosperms. Leaves of aquatic lycopods (*Isoetites* sp.) constitute a minor component of the palaeobotanical assemblage. Filicales are not very common, with Dicksoniales (*Onychiopsis* sp.) and a few specimens of *Cladophlebis* type fronds. The gymnosperms are represented by fragmented remains of long parallel veined *Desmiophyllum* leaves as well as a great abundance of conifer axis corresponding to the form-genus *Pagiophyllum* and female cones. Terrestrial angiosperms include pinnately lobed leaves of the genus *Myricompia*, simple leaves with spatulate lamina and some petiolate leaves both corresponding to angiosperms of uncertain affinity. Aquatic angiosperms consist of *Nelumbo*-like floral receptacles (Nelumbonaceae, Proteales) and *Aquatifolia* cf. *fluitans* (Nymphaeales). The palynological assemblage is dominated by pollen of gymnosperms (mainly *Taxodiaceapollenites hiatus*, *Classopollis major* and *Araucariacites australis*). It also includes many angiosperm grains (*Afropollis jardinus*, *Clavatipollenites* spp., *Dichastopollenites* spp., *Liliacidites doylei*, *Monosulcites chaloneri*, *Penetetrapites mollis*, *Pennipollis* spp., *Phimopollenites augathellaensis*, *Retimonocolpites textus*, *Rousea* spp., *Senectotetradites varireticulatus*, *Stellatopollis barghoornii*, *Striatopollis* spp., *Transitoripollis* sp. cf. *T. similis*, *Tricolpites* spp., *Tricolporoidites* sp.) and records the first occurrence of tricolporate forms in the uppermost part of the Utrillas Formation. Both macroflora and microflora assemblages present taxa similar to those of the uppermost Albian Shaftesbury Formation in northwestern Alberta in Canada, the uppermost Albian Denton Shale Member of Bokchito Formation in southern Oklahoma, the lower part of the Upper Albian Dakota Formation from the mid-west of North America, and Subzone II C of the Potomac Group, eastern United States. Both macro- and microflora assemblages display boreal influence with some similar taxa to those of the Upper Albian Kome Formation in western Greenland and some taxa as *Afropollis jardinus* and *Stellatopollis barghoornii* more frequently found in the tethyan and gondwanan realms. A gondwanan affinity is also indicated by the presence of *Klitzschophyllites* leaves.

KEY WORDS

Palaeobotany,
palynology,
angiosperms,
Utrillas Formation,
Late Albian,
Spain.

RÉSUMÉ

Une nouvelle flore de l'Albien supérieur terminal de la province de Teruel, nord-est de l'Espagne.

Ce travail met l'accent sur la découverte d'une nouvelle flore d'âge crétacé inférieur près du village d'Estercuel (province de Teruel, nord-est de l'Espagne). Les niveaux fossilifères, situés au sommet des dépôts fluviaux de la formation Utrillas, sont surmontés par les grès marins peu profonds de la formation Mosqueruela. Le site a livré des assemblages diversifiés de plantes en compression incluant des lycopodes et des fougères, des gymnospermes variées ainsi que des angiospermes terrestres et aquatiques. Les feuilles de lycopodes aquatiques (*Isoetites* sp.) constituent un composant mineur de l'assemblage floristique. Les filicales sont peu communes, avec des dicksoniales (*Onychiopsis* sp.) et quelques spécimens de type *Cladophlebis*. Les gymnospermes sont représentées par de longues feuilles fragmentaires à nervures parallèles (*Desmiophyllum*), par une grande abondance d'axes de conifères correspondant au morphogène *Pagiophyllum*, ainsi que par des cônes

femelles. Les angiospermes terrestres incluent des feuilles pennées lobées (*Myricom-pia*), des feuilles spatulées et quelques feuilles pétiolées d'affinités incertaines. Les Angiospermes aquatiques consistent en réceptacles floraux semblables à ceux de *Nelumbo* (Nelumbonaceae, protéales) et de *Aquatifolia* cf. *fluitans* (nymphéales). La palynoflore est dominée par des grains de pollen de gymnospermes (principalement *Taxodiaceapollenites hiatus*, *Classopollis major* et *Araucariacites australis*). Sont également inclus de nombreux grains d'angiospermes comprenant *Afropollis jardinus*, *Clavatipollenites* spp., *Dichastopollenites* spp., *Liliacidites doylei*, *Monosul-cites chaloneri*, *Penetetrapites mollis*, *Pennipollis* spp., *Phimopollenites augathellaensis*, *Retimonocolpites textus*, *Rousea* spp., *Senectotetradites varireticulatus*, *Stellatopollis barghoornii*, *Striatopollis* spp., *Transitoripollis* sp. cf. *T. similis*, *Tricolpites* spp. et *Tricolporoidites* sp. Les deux assemblages (macro- et palynoflores) sont similaires à ceux de l'Albien terminal de la formation Shaftesbury du NE de l'Alberta (Canada), de l'Albien terminal du membre Denton Shale de la formation Bokchito au sud de l'Oklahoma (USA), de la partie inférieure de l'Albien supérieur de la formation Dakota du centre-ouest de l'Amérique du Nord et de la sous-zone II C du groupe Potomac (est des USA). Les deux assemblages présentent des influences à la fois boréales et gondwaniennes, avec quelques taxons comparables à ceux de l'Albien supérieur de la formation Kome à l'ouest du Groenland. La présence de feuilles du genre *Klitzschophyllites* montre des affinités gondwaniennes.

MOTS CLÉS

Paléobotanique,
palynologie,
angiospermes,
formation Utrillas,
Albien supérieur
terminal,
Espagne.

INTRODUCTION

The Albian-Cenomanian transition represents a key-period in the diversification of eudicot angiosperms. During this period of time, the fossil records show a major change in the systematic composition of angiosperms assemblages with a marked increase in abundance and complexity of angiosperm leaves (Hickey & Doyle 1977; Lidgard & Crane 1988; Vakhrameev 1991; Upchurch & Wolfe 1993; Friis *et al.* 2010). Associated with the changes in the angiosperm macrofossil assemblages, there is also a change in the palynological assemblage worldwide with an increase in tricolpate and other triaperturate pollen in the Late Cretaceous (Singh 1975; Doyle & Robbins 1977; Hickey & Doyle 1977; Wingate 1980; Villanueva-Amadoz *et al.* 2011).

Several rich macrofossil floras corresponding to the Albian-Cenomanian transition have been described from western Europe (Gomez *et al.* 2004), central Asia (Vakhrameev 1952, 1976, 1991; Samylina 1988) and also in the North-American mid-west Dakota Formation (Lesquereux 1883, 1892; Berry

1922; Rushforth 1971; Hickey & Doyle 1977; Upchurch & Dilcher 1990; Schwarzwaldner & Dilcher 1991; Skog & Dilcher 1992, 1994; Skog *et al.* 1992; Wang 2002, 2008; Wang & Dilcher 2006a, b). More recently, Gomez *et al.* (2009) and Sender *et al.* (2010) described fossil leaves from the Albian-Cenomanian of Spain focusing exclusively on the aquatic elements, because of their relatively rare occurrence. The plant fossils described in this paper are important in documenting higher diversity of different groups of plants than previously known in the Albian-Cenomanian deposits of Spain.

GEOLOGICAL SETTING AND STRATIGRAPHY

The site is located in the west of the Aragonese Branch of the Iberian Chain, near the village of Esteruel (Teruel province, northeastern Spain) (Fig. 1), in the Oliete subbasin (Soria 1997). The plant bearing beds belong to the uppermost part of the Early Cretaceous succession at the top of

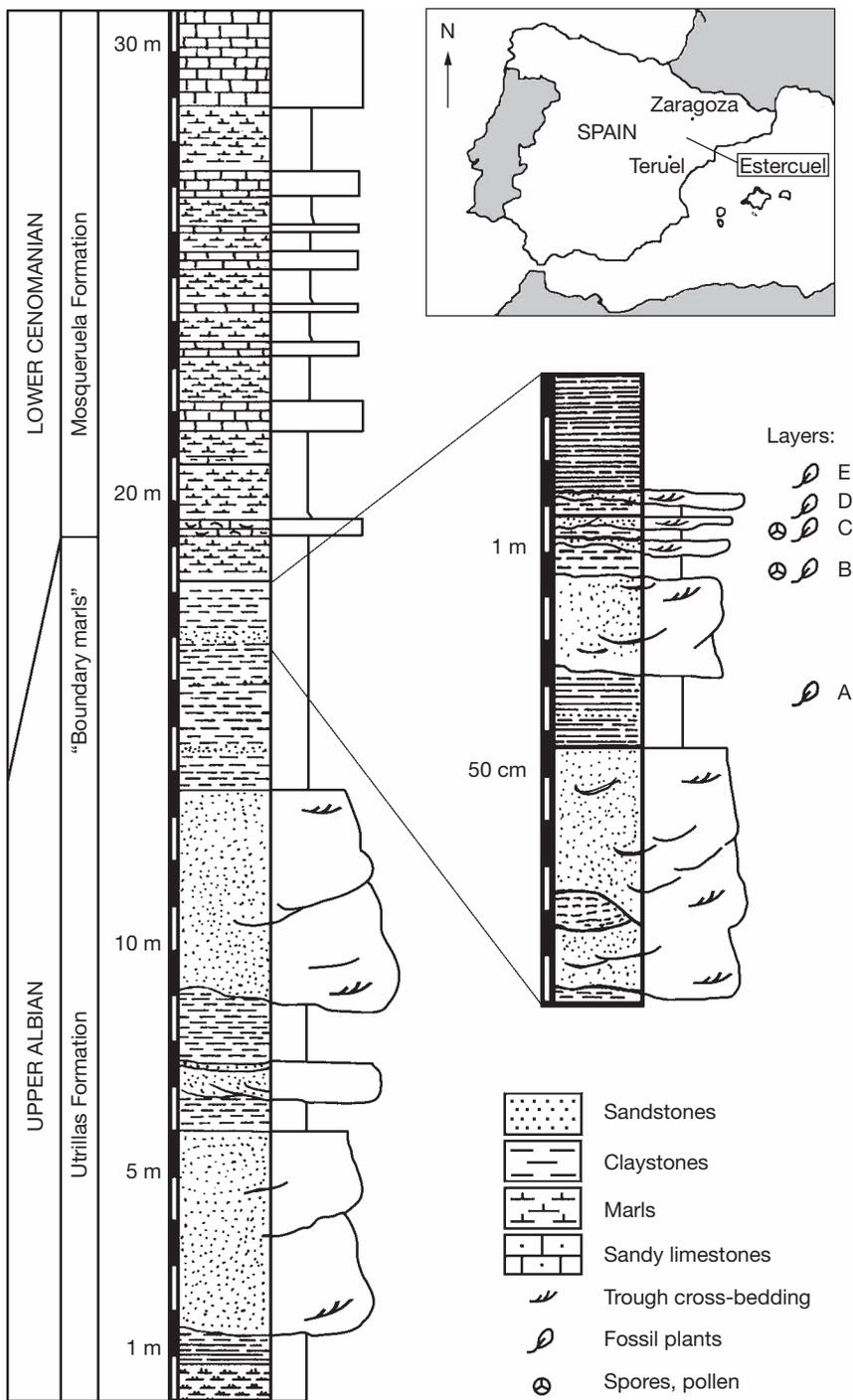


FIG. 1. — Location and stratigraphic section of the fossil site of Esterciel (Teruel province, northeastern Spain) and position of the fossil plants levels within the Boundary Marls Unit (modified from Pardo 1979).



FIG. 2. — General view of the outcrop in the Estercuel quarry (Teruel province, northeastern Spain).

the fluvial deposits of the Utrillas Formation. The Utrillas Formation is composed of sandstone bodies with intercalations of coloured silty claystones with increasing occurrence upward. The upper part represents a finning upward sequence of grey to dark coloured marls constituting the “Boundary Marls” unit (named as “Margas de Transición” unit by Aguilar *et al.* 1971). The “Boundary Marls” contains the flora studied here and represents the transitional layers between the fluvial deposits of the Utrillas Formation and the overlying shallow marine deposits of the Mosqueruela Formation (Fig. 1). The fossil plants and palynological assemblages were collected from five layers indicated in the stratigraphic log (Fig. 1[A-E]).

The age of the “Boundary Marls” unit was previously established as latest Albian and the underlying Utrillas Formation as middle-latest

Late Albian on the basis of the palynological assemblage in other localities of the same basin (Villanueva-Amadoz 2009). Moreover, the overlying Mosqueruela Formation has been dated in several sections nearby the Estercuel site on the basis of the assemblage of benthic foraminifera: Cenomanian in Huesa del Común and Puerto de Rudilla localities (Lendínez *et al.* 1989), Lower Cenomanian in the Puerto de San Just (Neumann & Schroeder 1985; Calonge 1989) and Upper Albian next to Fortanete village (Canérot 1974).

Two different floral assemblages preserved in different lithologies and different stratigraphic levels can be distinguished: the basal stratigraphic level is composed of grey claystones intercalated with fine to coarse grained yellow sandstones, which were deposited in a tidally influenced

fluvial sedimentary environment (Fig. 2). This level contains both abundant and diverse and exceptionally well-preserved macrofloral and microfloral assemblages.

The upper stratigraphic level consists of dark grey to black laminated claystones deposited in a swampy environment with lower diversity of floral elements (Fig. 2).

MATERIAL AND METHODS

The samples were collected during fieldwork associated to programs 223/2008 and 081/2009 of the Diputación General de Aragón (Government of Aragón, Spain).

The plant macrofossils are preserved mainly as compressions, and some specimens have a thin coaly surface. The plant macrofossils were prepared under a stereomicroscope by removing the matrix with a percussion hammer and mounted needles.

A total of 267 plant macrofossils were studied. They are for the moment housed in the Museo Paleontológico de Universidad de Zaragoza (Spain) with the denominations MPZ 2010/910 to MPZ 2010/1175 and MPZ 2009/342.

Five samples were processed for palynological study using standard technique (Erdtman 1943): 20 g of each sample were crushed in a mortar, carbonates were dissolved with 10% HCl and the silicates removed with 70% HF and 10% HCl; later, the organic residue was oxidized with 30% HNO₃, then washed three times with water and centrifuged. The residue was filtered through a 100 µm mesh sieve, but in order to keep the smallest angiosperm pollen grains (<10 µm), no other sieving operation was undertaken. The residue was permanently mounted for observation in Loctite 350.

The slides were analyzed at the Muséum national d'Histoire naturelle (Paris). A total of 143 individual palynomorphs were photographed. Several separate optical section images were taken for each palynomorph and depth of field was reconstructed using the free image stacking program CombineZM (Hadley 2006; Bercovici *et al.* 2009). Scanning electron micrographs were taken at Vigo University using a Phillips XL 30 SEM.

SYSTEMATIC PALAEOBOTANY

Division LYCOPHYTA Scott, 1909
Class LYCOPSIDA Scott, 1909
Order ISOETALES Prantl, 1874
Family ISOETACEAE Reichenb., 1828
Genus *Isoetites* Munster, 1842

Isoetites sp.

Layers B to D (Fig. 4B, D)

SPECIMENS. — MPZ 2010/910 to MPZ 2010/926.

DESCRIPTION

Leaves simple, elongated to lanceolate, up to 4 cm long and 5 mm wide. Margin entire, base slightly expanded and apex acute. Leaves preserved as longitudinal sections showing a gross mid vein up to 2 mm wide. Leaves are lacunate, with trabeculae inter-distance measuring 1 mm. Only a single specimen shows preserved fertile parts, bearing an enlarged sporangial region at the base and containing clumps of microspores. For an accurate description and detailed palynological analysis of this particular specimen see Villanueva-Amadoz *et al.* 2012.

Division PTERIDOPHYTA Schimper, 1879
Class POLYPODIOPSIDA
Cronquist, Takht. & Zimmerm., 1966
Order CYATHEALES A. B. Frank, 1877
Family DICKSONIACEAE M. R. Schomb., 1848
Genus *Onychiopsis* Yokoyama, 1889

Onychiopsis sp.

Layers A to D (Fig. 4C)

SPECIMENS. — MPZ 2010/927 to MPZ 2010/935.

DESCRIPTION

Fragments of bipinnate fronds. Secondary pinna subtriangular up to 6.3 cm long and 2 cm wide. Pinnules alternate, lanceolate, highly lobed. Lobules lanceolate to triangular acute which are best developed at the base of pinnules. Venation consists of several thin veins which enter the pinnule from the base forking several times to end in the margins.

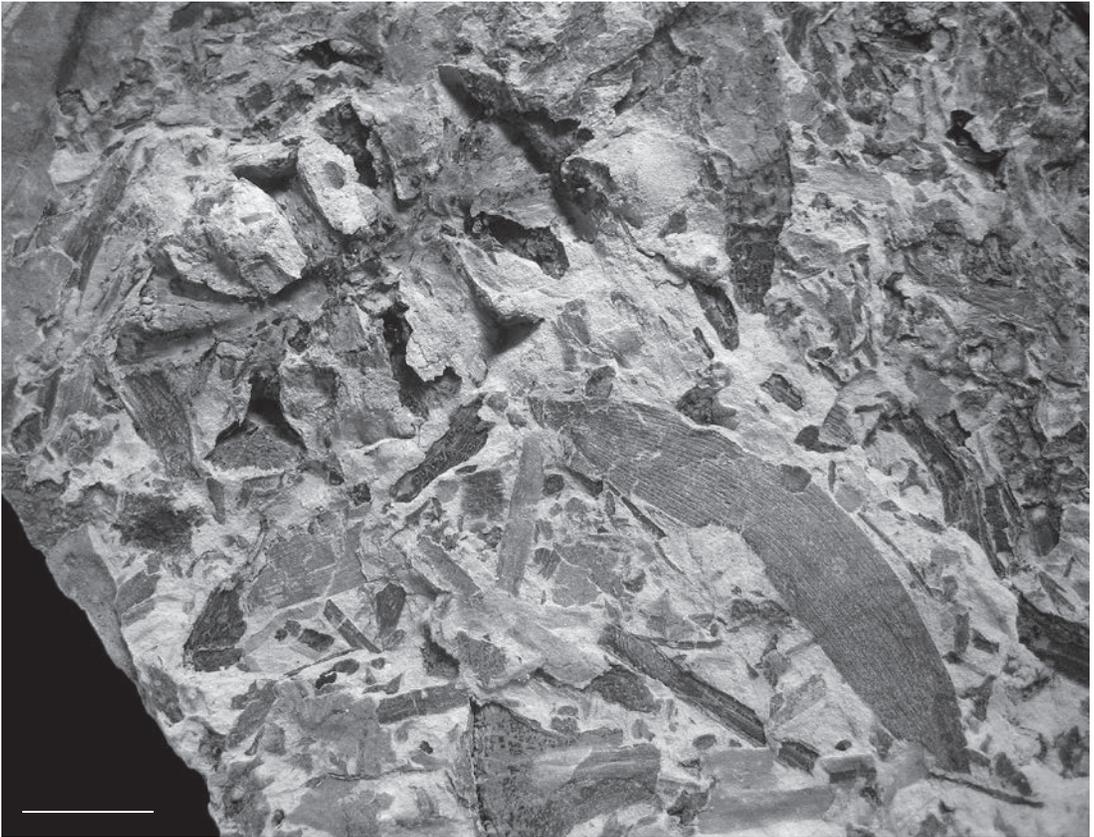


FIG. 3. — Concentration of fossil plant remains (conifer female cone and scales fragments, one *Podozamites* (Brongniart) Braun, 1843 leaf and fragments of angiosperm leaves type 1) and comminuted plant debris on a slab from the lowermost fossiliferous level. Scale bar: 1 cm.

Family indet.

Form-genus *Cladophlebis* Brongniart, 1849

Cladophlebis sp.

Layer E (Fig. 4A)

SPECIMEN. — MPZ 2010/936.

DESCRIPTION

Fragments of penultimate pinnae up to 4.5 cm long and 2.5 cm wide bearing ultimate pinnae alternate and lanceolate, slightly decurrent at base. Pinnules opposite to sub-opposite, ovoidal. Margin of pinnules entire, joined to the rachis by the entire base. Apex rounded. Venation is difficult to distinguish, but apparently comprises one medial vein with diverging alternate secondary veins which fork up to the margins.

Division PINOPHYTA

Cronquist, Takht. & Zimmerm., 1996

Class PINOPSIDA Burnett, 1835

Family indet.

Form-genus *Pagiophyllum* Heer, 1881

Pagiophyllum sp.

Layers A to E (Fig. 5D, F)

SPECIMENS. — MPZ 2010/937 to MPZ 2010/1024.

DESCRIPTION

Fragments of twigs up to 12 cm long, branched up to three times and bearing spirally arranged scale-like leaves (up to 4 mm long and 1.5 mm wide). Leaves are rhombic, slightly decurrent at the base, appressed proximally and separated from the axis just in the

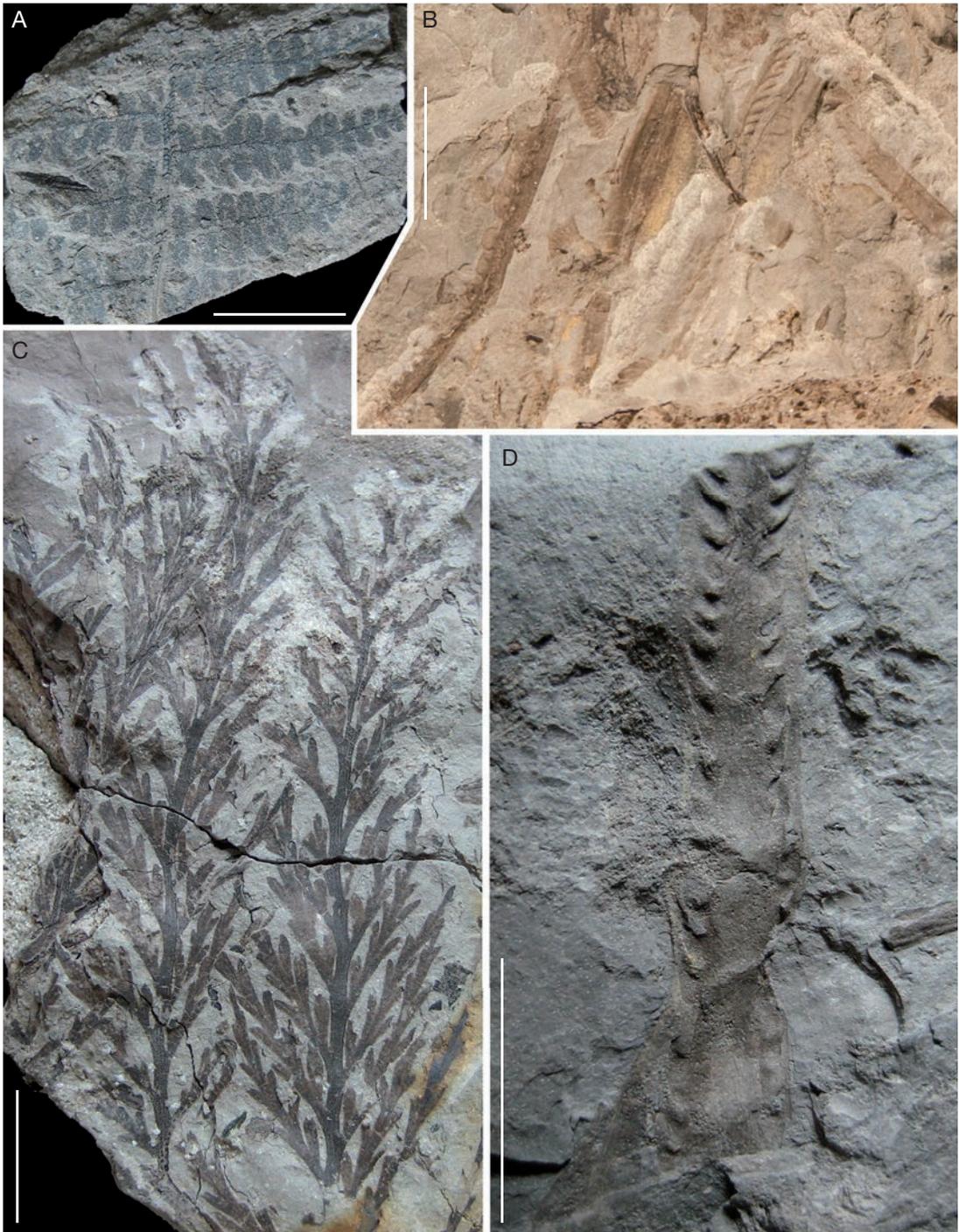


FIG. 4. — Lycopsids and ferns: **A**, fern *Cladophlebis* sp., fragment of secondary pinna; **B**, accumulation of *Isoetites* leaves (Lycopsida); **C**, fern *Onychiopsis* sp., secondary pinnae; **D**, *Isoetites* sp., isolated leaf showing trabeculae. Scale bars: 1 cm.



FIG. 5. — Gymnosperms of the Estercuel plant fossil site (Teruel province, northeastern Spain): **A**, *Desmiophyllum* sp.; **B**, fragments of *Podozamites* (Brongniart) Braun, 1843 leaves; **C**, conifer seed cones; **D**, *Pagiophyllum* sp., branched shoots; **E**, *Podozamites* sp.; **F**, *Pagiophyllum* sp. shoots. Scale bars: 1 cm.

first 1/3 of their length. A medial keel is present on the abaxial face of the leaves and a medial groove present on the adaxial face. Apex of leaves sharply acute.

Family indet.

Form-genus *Podozamites* (Brongniart) Braun, 1843

Podozamites sp.

Layers A to E (Fig. 5 B, E)

SPECIMENS. — MPZ 2010/1025 to MPZ 2010/1034.

DESCRIPTION

Leaves lanceolate up to 7 cm long and 1 cm wide. Lamina tapers at the base into a narrow wing. Apex rounded to obtusely pointed. Venation composed of numerous parallel veins (*c.* 30 veins per cm) equally spaced, which diverge from a point at base and fusing apparently at apex.

Conifer seed cones

Layer B (Fig. 5 C)

SPECIMENS. — MPZ 2010/1035 to MPZ 2010/1039.

DESCRIPTION

Cones seen in longitudinal sections up to 4.5 cm long and 2.5 cm wide. Scales robust and woody, spirally arranged, semicircular to trapezoidal in section up to 1 cm long and 7.5 mm wide. Surface of scales shows numerous thin veins running parallel from the base up to the apex.

Family indet.

Form-genus *Desmiophyllum* Lesquereux, 1878
Layers A to E (Fig. 5 A)

SPECIMENS. — MPZ 2010/1040 to MPZ 2010/1052.

DESCRIPTION

Fragments of elongate strap-like leaves up to 12 cm long and 2 cm wide. Margins straight and reinforced. Base and apex not preserved. Venation consists of numerous

gross veins, *c.* 25 veins per cm, running parallel to leaf margins. Another four thin veins extended between two gross veins making a total of *c.* 125 veins per cm.

REMARKS

Similar leaves were also found in the Aptian-Albian of western Europe (Coiffard *et al.* 2007), Canada (Bell 1956) and in Albian-Cenomanian deposits of Alaska (Spicer & Herman 2001) and Russia (Spicer *et al.* 2002).

Class ANGIOSPERMAE Lindley, 1830

Order NYMPHAEALES

Salisb. ex Bercht. & J. Presl, 1820

Family cf. NYMPHAEACEAE Salisb., 1805

Genus *Aquatifolia* Wang & Dilcher, 2006

Aquatifolia cf. *fluitans*

Layers B to D (Fig. 6B, C)

SPECIMENS. — MPZ 2010/1130 to MPZ 2010/1134 and MPZ 2009/342.

DESCRIPTION

Leaf orbicular to ovate, petiolate. Base cordate. Base angle wide obtuse. Petiole stout with an expanded fusiform float in its lower part. Float length is 60 mm long and 17 mm wide in its central part. Leaf blade up to 39 mm long and 45 mm wide (no complete specimens). Margin crenate with tooth type convex-convex. Primary venation basal actinodromous with one medial vein branching up to the margin and four lateral primary veins which fork several times, gradually decreasing in thickness toward the margin. Angle between primary veins 45°. Branches from primary veins join to form polygonal large meshes. Secondary venation apparently craspedodromous. Tertiary and quaternary veins forming small polygonal meshes.

REMARKS

The unique combination of spherical to fusiform floats and foliar lamina with Nymphaeaceae-like venation together with other characteristics is characteristic for the genus *Aquatifolia* Wang & Dilcher from the Hoisington III locality, Kansas, USA (Wang & Dilcher 2006a). The Spanish fossils are closely similar to the



FIG. 6. — Fertile and sterile structures of aquatic plants: **A**, floral receptacles of presumable Nelumbonaceae floral receptacle showing internal moulds of achene cavities; **B**, *Aquatifolia* cf. *fluitans*, aquatic plant with foliar lamina, petiole and fusiform float organ at base; **C**, almost complete lamina of *Aquatifolia* cf. *fluitans* showing venation. Scale bars: 1 cm.

type species *Aquatifolia fluitans* (Wang & Dilcher 2006a), but because leaf margin and endings of veins are not well preserved, we hesitate to include the Spanish material in the same species. Currently the genus has only been recovered from the Estercuel outcrop and the Hoisington III locality.

Order PROTEALES

Juss. ex Bercht. & J. Presl, 1820

Family NELUMBONACEAE A. Rich., 1827

Layer B (Fig. 6A)

REPRODUCTIVE STRUCTURES. — Floral receptacles.

SPECIMENS. — MPZ 2010/1135 and MPZ 2010/1136.

DESCRIPTION

Structures circular in outline, about 3.5 cm in diameter, containing up to 10 smaller, protuberant and circular units, about 0.45 cm in diameter. The smaller units are surrounded by a circular ridge and groove. The apex of each unit possesses a central sunken pit with several grooves radiating from the center.

REMARKS

The characters of the fossil suggest that they are floral receptacles with moulds of cavities containing achenes, probably related to the Nelumbonaceae. They closely resemble fossils from the Upper Albian Potomac Group in the Quantico locality (Virginia, USA), described by Upchurch *et al.* (1994) as *Nelumbites*.

They are also similar to the *Nelumbo*-like structures from the Campanian-Maastrichtian La Colonia Formation from Patagonia, Argentina (Gandolfo & Cúneo 2005) and to the receptacles of extant *Nelumbo* Nelumbonaceae (Proteales) (Hayes *et al.* 2000; Miller *et al.* 2009).

Other angiosperms of uncertain placement

Incertae sedis

Angiosperm type 1

Layers A to E (Figs 7A-E; 8A)

SPECIMENS. — MPZ 2010/1137 to MPZ 2010/1172.

DESCRIPTION

Leaves simple, up to 25 cm long and 5 cm wide, elliptical to spatulate in shape with marked decurrent lamina at base. Margin entire and reinforced. Base probably rounded but not totally preserved. Apex rounded or slightly emarginate in some specimens. Mid-vein strong. Secondary veins semicraspedodromous, alternate, very dense at base. Vein spacing decreasing toward base with secondary veins very closely spaced at the basal lamina tissue. Vein angle increasing toward base with veins disposed at right angles in the base of lamina and at acute angles from the medial part up to the apex. Intersecondaries weak, two to four. Tertiary veins alternate percurrent. Quaternary veins alternate percurrent to polygonal reticulate. Quinary veins regular polygonal reticulate. Areoles well developed.

REMARKS

The leaves resemble some extent that of *Jaramillophyllum celatus* (Lesquereux) Wang (*nomen nudum*) in size and spatulate-shaped lamina, reinforced margin, strong by decurrent lamina and craspedodromous secondary venation described from the Dakota Formation of the Hoisington III locality in Kansas (USA), Late Albian in age (Wang 2002).

Angiosperm type 2

Layers A to C

(Fig. 8B)

SPECIMENS. — MPZ 2010/1173 to MPZ 2010/1175.

DESCRIPTION

Fragments of leaves up to 7 cm long and 3 cm wide, simple, elliptical to lanceolate in shape. Margin entire. Base cuneate. Apex not preserved. Petiole straight and narrow (1.5 cm long and 2 mm wide). Mid-vein stout and strong. Secondary veins craspedodromous to weak brochidodromous disposed at acute angles from primary vein. Intersecondaries weak. Tertiary veins alternate percurrent. Quaternary veins apparently alternate percurrent.



FIG. 7. — Angiosperms type 1 leaf morphology and venation pattern: **A**, detail of insect feeding holes in the surface of a leaf; **B**, complete leaf apical fragment showing feeding holes and fungi black marks; **C**, nearly complete leaf with characteristic spatulate morphology; **D**, detail of venation pattern in the apical part of an angiosperm type 1; **E**, detail of venation pattern in the central part of a leaf. Scale bars: 1 cm.

Genus *Myricompia* Boyd, 1998

Myricompia sp.

Layers A and B

(Fig. 9C)

SPECIMENS. — MPZ 2010/1053 to MPZ 2010/1056.

DESCRIPTION

Fragments of pinnately lobed leaves up to 4 cm long and 1 cm wide. Lobes are short and pointed, with entire margin and acute apex. They are connected by a narrow lamina parallel to the primary vein. Primary vein straight and narrow. Numerous secondary veins are disposed at acute angles from the base of lobes. Two secondary veins enter into each lobe and fork almost twice before ending freely at the margins.

REMARKS

This genus was erected by Boyd (1998) for specimens from west Greenland deposits of the Albian Kome Formation., West Greenland.

Genus *Klitzschophyllites* Lejal-Nicol, 1987 emend. Gomez, Coiffard, Sender, Martín-Closas, Villanueva-Amadoz & Ferrer (2009)

Klitzschophyllites choffatii

(Saporta) Teixeira, 1948

emend. Gomez, Coiffard, Sender, Martín-Closas, Villanueva-Amadoz & Ferrer (2009)

Layers B to D

(Fig. 9A, B)

SPECIMENS. — MPZ 2010/1057 to MPZ 2010/1129.

DESCRIPTION

Leaves simple and small, semicircular to ovoidal in shape, up to 2 cm long and 1.5 cm wide. They are bilateral symmetrical and petiolate. Petiole straight and robust (4 mm wide) preserved in some specimens. Leaf margin dentate with up to 15 teeth. Primary venation flabellate. Secondary veins straight, running from the primary veins. Tertiary veins alternate percurrent. Intramarginal

vein present. Numerous primary veins diverging from the upper part of petiole and ending apically in the sinuses between teeth. Secondary veins ending in the tooth apex. Teeth retroflexed/retroflexed, apex mucronate. Tooth sinus glandular, bearing a circular gland.

REMARKS

The genus is based on material from Portugal (Teixeira 1948). Later it was suggested that the Tunisian (Barale & Ouaja 2001) and Brazilian material (Mohr & Rydin 2002; Mohr *et al.* 2006) was conspecific with material from Portugal. More recently Gomez *et al.* (2009) emended the genus with new material recovered from a fossil site in northeastern Spain (nearby the Esterciel plant fossil site) extending the temporal distribution of genus up to the Upper Albian. Nevertheless, Friis *et al.* (2010) indicate that figured specimens of *Klitzschophyllites* in the publications cited here-above are different from the original description and drawings of the type species *Protorrhypis choffatii* erected by Saporta (1894). This authors suggest that the portuguese material is related to the aquatic fern *Ceratopteris* Brong.

PALYNOLOGY

The five samples from the uppermost part of the Utrillas Formation yielded rich and well-preserved palynological assemblages. Taxa identified are summarized in Table 1 (Figs 10; 11). The presence of *Concavisporites punctatus* and *Converrucosisporites platyverrucosus* that are not known to extend above the Albian-Cenomanian boundary, *Afropollis jardinus*, distributed from the middle Albian to Cenomanian and *Stellatopollis barghoornii* from the middle Albian to middle Cenomanian, together with *Senectotetradites varireticulatus*, which is restricted to the latest Albian-Cenomanian interval in Laurasia indicates a Late Albian age (Figs 10; 11).

The assemblage shows high diversity of palynomorphs, and particularly great abundance of gymnosperm pollen (mainly represented by *Taxodiaceapollenites hiatus*, *Araucariacites australis* and *Classopollis* spp., followed in abundance

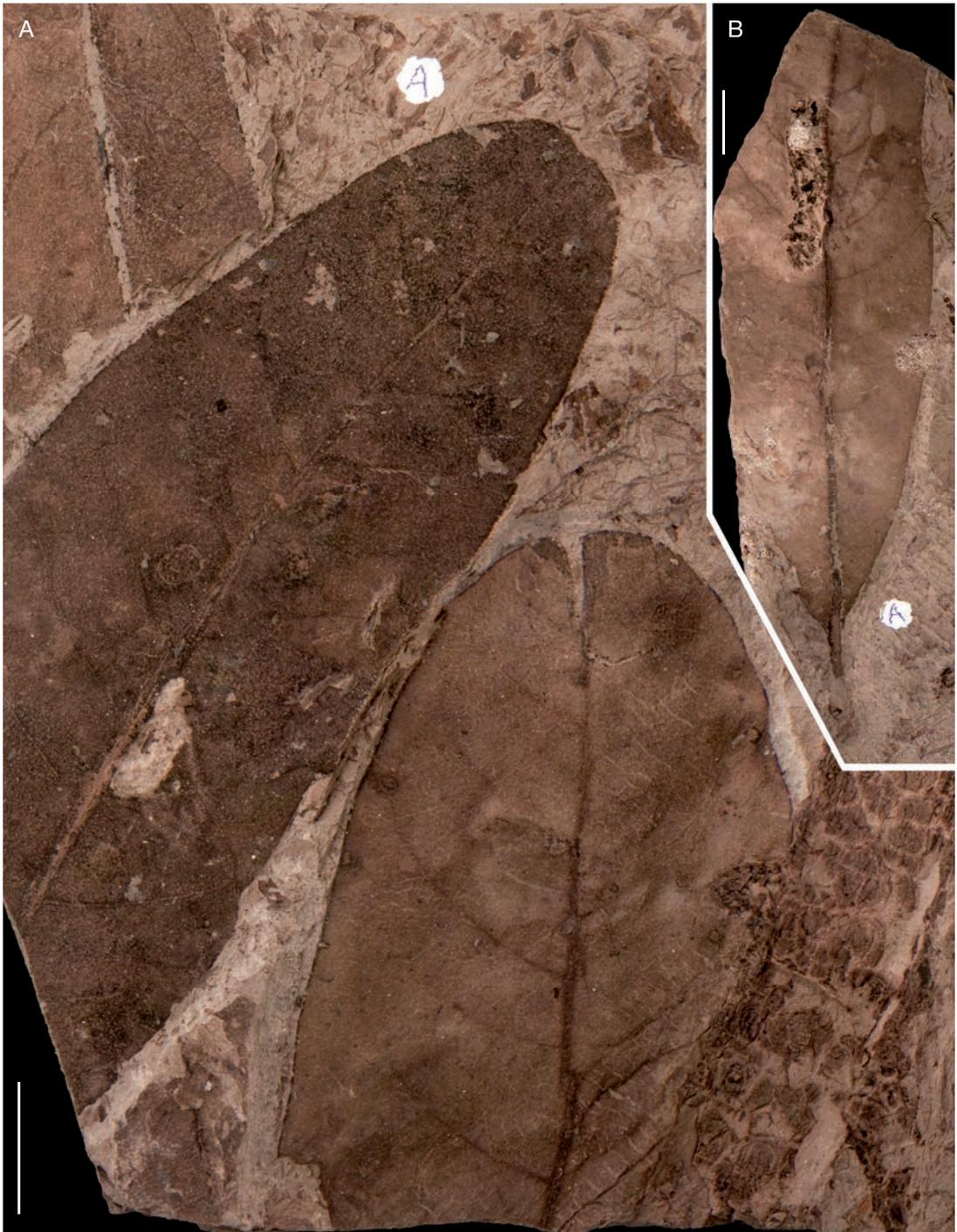


FIG. 8 — Angiosperms leaves: **A**, apical fragments of leaves of Angiosperms type 1; **B**, Angiosperm type 2 leaf with petiole. Scale bars: 1 cm.

TABLE 1. — List of palynomorphs from Estercuel fossil plant site (Teruel province, Spain). *, reworked palynomorphs.

Continental-origin palynomorphs

Microspores, macrospores, pollen grains

Spores

- Camarozonosporites* sp.*
Cicatricosisporites hallei Delcourt & Sprumont, 1955*
Cicatricosisporites sp.
Concavisporites punctatus Delcourt & Sprumont, 1955
Concavissimisporites verrucosus (Delcourt & Sprumont) Delcourt, Dettmann & Hugues, 1963*
Converrucosisporites platyverrucosus Brenner, 1963
Crybelosporites sp.*
Cyathidites australis Couper, 1953
Cyathidites minor Couper, 1953
Deltoidospora psilostoma Rouse, 1959
Gabonisporis sp.
Matonisporites equiexinus Couper, 1958
Microfoveolatosporis baconicus Juhász, 1977
Patellasporites tavadarensis Groot & Groot, 1962*
Peromonolites sp.
Plicatella sp. cf. *P. potomacensis* (Brenner) Davies, 1985*
Plicatella robusta (Kemp) Davies, 1985*
Reticulosporis sp.
Stereisporites antiquasporites (Wilson & Webster) Dettmann, 1963
Triporoletes sp. cf. *T. radiatus* (Dettmann) Playford, 1971*

Gymnosperm pollen

- Araucariacites australis* (Cookson) Couper, 1953
Balmeiopsis limbata (Balme) Archangelsky, 1977
Cedripites canadensis Pocock, 1962
Classopollis major Groot & Groot, 1962
Classopollis sp.
Cycadopites sp.
Ephedripites sp. cf. *E. dudarensis* Deák, 1964
Ephedripites sp. cf. *E. multicostatus* Brenner, 1963
Eucomiidites troedsonii (Erdtman) Potonié, 1958
Exesipollenites scabrosus Norris, 1969
Perinopollenites halonatus Phillips & Felix, 1971
Singhia sp.
Spheripollenites sp.
Taxodiaceapollenites hiatus (Potonié) Kremp, 1949

Angiosperm pollen

- Afropollis jardinus* Doyle, Jardiné & Doerenkamp, 1982
Clavatipollenites hughesii Couper, 1958
Clavatipollenites minutus Brenner, 1963
Clavatipollenites tenellis Phillips & Felix, 1971
Clavatipollenites sp.
Dichastopollenites sp. cf. *D. reticulatus* May, 1975
Liliacidites doylei Ward, 1986
Monosulcites chaloneri Brenner, 1963
Penetetrapites mollis Hedlund & Norris, 1968
Pennipollis sp. cf. *P. reticulatus* (Brenner) Friis, Pedersen & Crane, 2000
Pennipollis escuchensis Villanueva-Amadoz, Pons, Diez, Ferrer & Sender, 2010
Pennipollis sp.
Phimopollenites augathellaensis (Burger) Dettmann, 1973
Retimonocolpites textus (Norris) Singh, 1983
Rousea sp.
Senectotetradites varireticulatus Dettmann, 1973
Stellatopollis barghoornii Doyle, 1975
-

TABLE 1. — Continuation.

Angiosperm pollen
<i>Striatopollis</i> sp. cf. <i>S. paraneus</i> (Norris) Singh, 1971
<i>Striatopollis trochuensis</i> (Srivastava) Ward, 1986
<i>Striatopollis</i> sp.
<i>Transitoripollis</i> sp. cf. <i>T. similis</i> Góczán & Juhász, 1984
<i>Tricolpites crassimurus</i> (Groot & Penny) Singh, 1971
<i>Tricolpites</i> sp.
<i>Tricolporoidites</i> sp.
Other palynomorphs
Algae
<i>Schizophacus parvus</i> (Cookson & Dettmann) Pierce, 1976
Marine-origin palynomorphs: dinoflagellate cysts
<i>Oligosphaeridium</i> sp.

by *Perinopollenites halonatus*, *Spheripollenites* sp., *Ephedripites* spp., *Exesipollenites scabrosus*, *Balmeiopsis limbata*, *Cycadopites* spp., *Cedripites canadensis*, *Eucommidites troedsonii* and *Singhia* sp.) and, to a lesser extent, angiosperm pollen grains and spores. Spores are scarce, mainly represented by *Cyathidites* spp., *Gabonisporis* sp., *Matonisporites equixinus* and *Peromonolites* sp., and in very low percentages *Cicatricosisporites* sp., *Concavisporites punctatus*, *Convruccosisporites platyverrucosus*, *Deltoidospora psilostoma*, *Microfoveolatosporis baconicus* and *Stereisporites antiquasporites*. The angiosperm assemblage consists of relative high percentage of *Clavatiipollenites* spp. and *Afropollis jardinus* while other monoaperturate types such as *Stellatopollis barghoornii*, *Dichastopollenites* spp., *Liliacidites doylei*, *Monosulcites chaloneri*, *Pennipollis* spp., *Retimonocolpites textus* and *Transitoripollis* sp. cf. *T. similis* are less abundant. Tricolpates, mainly *Tricolpites* spp. followed by *Phimopollenites augathellaensis*, *Rousea* spp., *Senectotetradites varireticulatus* and *Striatopollis* spp., and multiporates, *Penetrapites mollis*, are also less abundant. The first appearance of tricolporate pollen grains (*Tricolporoidites* sp.) is in the “Boundary Marls”, but they are presented in a scarce number. The earliest evidence of this morphological type in northeastern Spain is suggested to be coincident in age with that of subzone II-C of the Potomac Group (Doyle & Robbins 1977) in the Atlantic Coastal Plain (USA).

DISCUSSION

BIOSTRATIGRAPHY

The earliest tricolporates appeared in different areas at the Albian-Cenomanian transition. The stratigraphic levels showing the first occurrence of tricolporates in the latest Albian are: 1) Canada: below the Fish-Scale Marker in Shaftesbury Formation, Peace River area (Singh 1975); and 2) USA: Denton Shale Member of the Bokchito Formation, southern Oklahoma and northern Texas (Wingate 1980); near the base of Huntsman Shale and in the uppermost beds of the Dakota Sandstone, Denver basin, Colorado (Pannella 1966). Moreover, the first occurrence in Cenomanian stratigraphic levels are: 1) Canada: Dunvegan Formation, Alberta (Singh 1983); and 2) USA: Dakota Sandstone, northeastern Arizona (Agasie 1969); Red Branch Member of the Woodbine Formation, Oklahoma (Hedlund 1966); Raritan fire clay of the Raritan Formation, New Jersey (Groot *et al.* 1961); lower part of the Raritan Formation, Delaware (Brenner 1967), and near the top of the Patapsco Formation (beds at Elk Neck), Maryland (Doyle 1969).

The gondwanan influences are also evident from the palynological assemblage with the presence of high proportions of *Afropollis jardinus*, together with tethyan *Stellatopollis barghoornii* and some ephedralean pollen grains (*Ephedripites* spp. and *Singhia* sp.). Such taxa present a peak of abundance in the uppermost Albian-lowermost Cenoma-

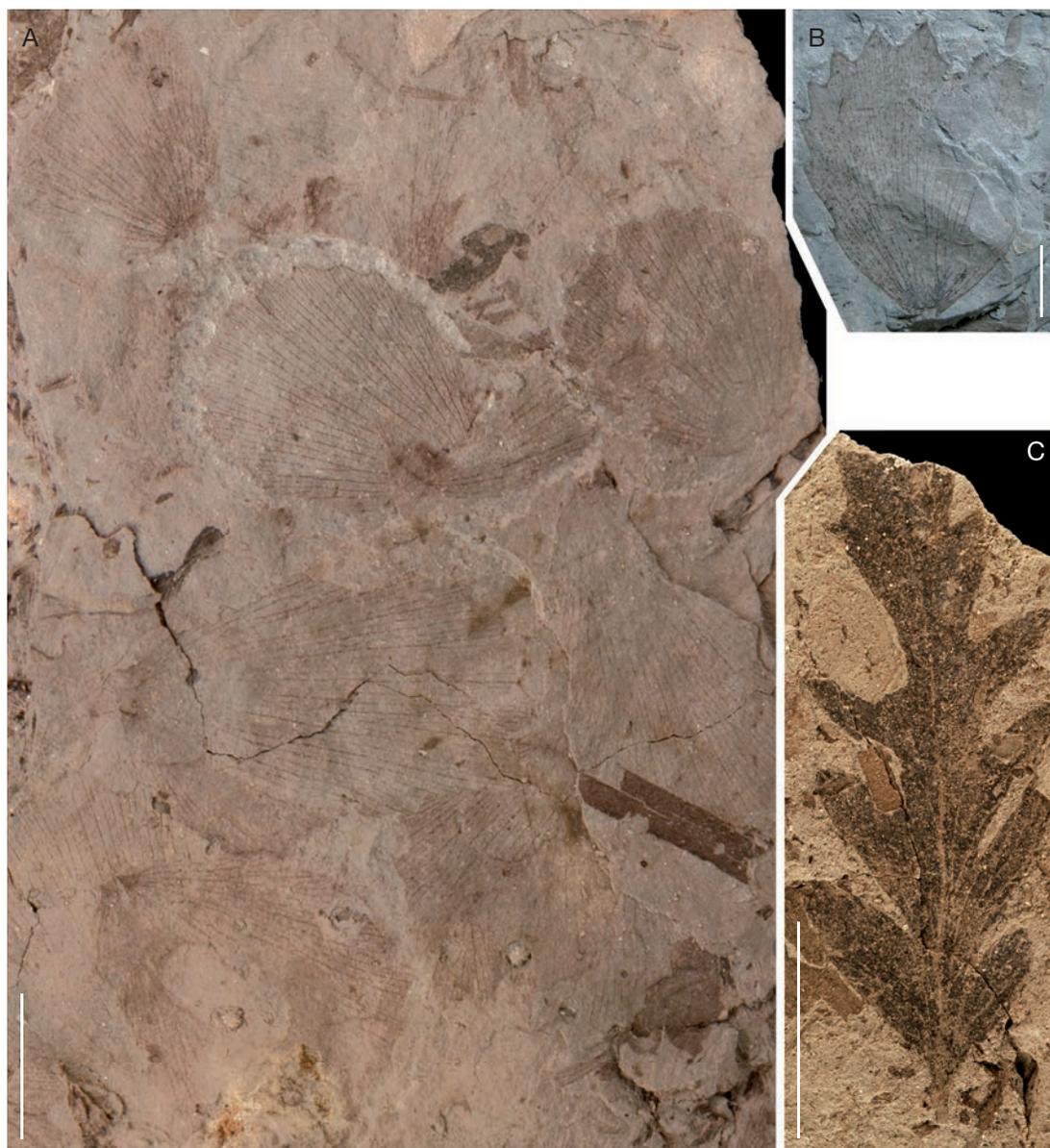


FIG. 9 — **A**, accumulation of *Klitzschophyllites choffatii* young leaves with poorly developed teeth; **B**, nearly complete leaf of *Klitzschophyllites choffatii* showing well-developed teeth; **C**, pinnately lobed leaf of *Myricompia* sp. Scale bars: 1 cm.

nian deposits of the Iberian Plate as discussed in Villanueva-Amadoz *et al.* 2011.

The majority macrofossils of the Esteruel site are known to have a large distribution in the continental deposits of Late Albian-Early Cenomanian

age. Nevertheless, it is the first time that the unique aquatic angiosperm *Aquatifolia* is recorded outside of the Dakota Formation deposits from the mid-west of North America (United States), where it was first described by Wang & Dilcher (2006a). Besides,

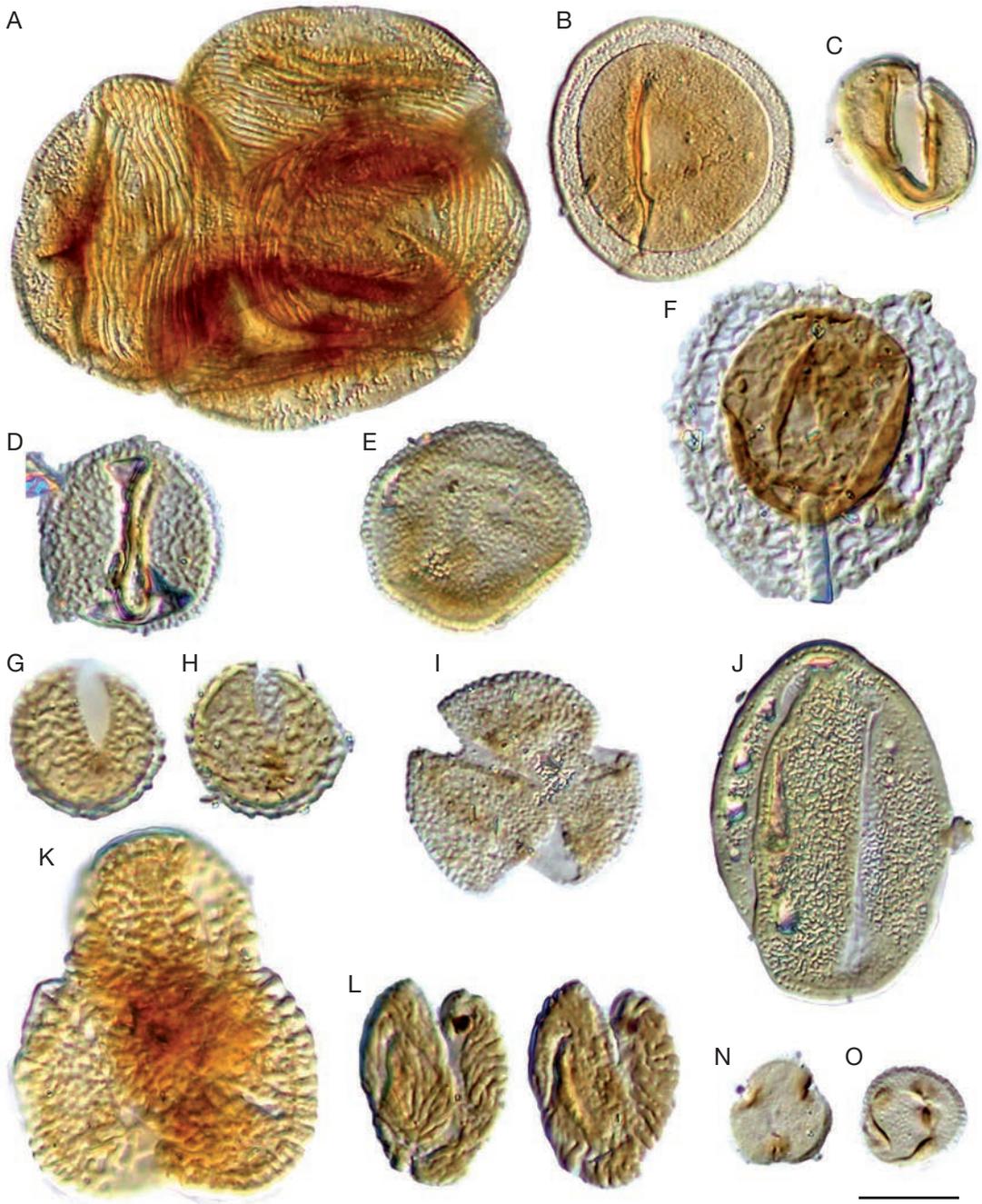


FIG. 10. — Photographs of some selected sporomorphs from the Esteruel section (Teruel province, northeastern Spain): **A**, *Classopollis major*; **B**, *Perinopollenites halonatus*, mid focus; **C**, *Transitoripollis* sp. cf. *T. similis*, distal face; **D**, *Retimonocolpites textus*, distal face; **E**, *Clavatipollenites* sp., mid focus; **F**, *Afropollis jardinus*, mid focus; **G**, **H**, *Pennipollis* sp. cf. *P. reticulatus* in distal (**G**) and proximal (**H**) faces; **I**, *Rousea* sp., polar view; **J**, *Phimopollenites augathellaensis*, equatorial view; **K**, *Senectotetradites varireticulatus*, equatorial view; **L**, **M**, *Striatopollis* sp., equatorial view; **L**, high focus; **M**, same specimen, low focus; **N**, **O**, *Tricolporoidites* sp.; **N**, polar view; **O**, equatorial view. Scale bar: 10 μ m. Full taxa names are given in Table 1.

the genus *Myricompia* observed in the present work has only been recovered from the sediments of the Upper Albian Kome Formation from west Greenland (Boyd 1998). The aquatic *Klitzschophyllites* with gondwanan affinities (see references in the systematic palaeobotany part) is well represented within the Esterciel site floral assemblages.

TAPHONOMY, PALAEOECOLOGY AND PALAEOENVIRONMENTS

The rich plant bearing beds of the Esterciel fossil site include a number of different lithologies with a wide variety of floristic elements. The macrofloras occurring in the silty claystones and in the lower level corresponding to the laminated claystones (layers A to D) are very similar despite the different lithology. They consist mostly of semi-complete leaves of angiosperms type 1, a small number of leaves of angiosperms type 2 and *Myricompia*, abundant ramified shoots of the conifers *Pagiophyllum*, detached *Podozamites* leaves, long fragments of *Desmiophyllum* leaves, occasional pinnae of the fern *Onychiopsis*, centimeter to decimeter long moulds of stems and trunks and a massive concentration of fragments of plants of irregular shape as well as comminuted plant debris (Fig. 3). They are composed of millimeter to centimeter-sized remains of leaves, fragments of conifer axis and scales of conifers female cones, fragments of angiosperm leaves and occasionally fragments of charcoaled wood, some of them with angular shape. The lithologies and characteristics preservation of the plant remains may be related to deposition in a nearshore fluvial environment.

The main difference between the lower and the upper stratigraphical levels is based on the accumulations of *Klitzschophyllites hoffatti* leaves, remains of *Aquatifolia* cf. *fluitans* and *Isoetites* sp. corresponding to the finest grained lithologies (laminated claystones of layers B, C and D) related to quiet water environments, possibly small ponds.

The flora of the upper level of dark laminated and bioturbated claystones (layer E) consists of numerous large ramified shoots of *Pagiophyllum*, leaves of *Podozamites*, fragments of strapped leaves of the gymnosperm *Desmiophyllum* and leaves of angiosperms type 1 and the presence of *Cladophlebis*

type fern. All plant remains at this stratigraphical level are preserved as stained impressions with a coaly thin layer present, and the shoots of *Pagiophyllum* are always coalified. These characteristics might indicate the deposit of plants in a swampy environment.

It is noteworthy that a great number of terrestrial angiosperm leaves and a number of aquatic leaves, occurring in all layers, are affected by galls, mines, circular holes and other structures indicating several kinds of insect-plant interactions (Figs 6A, B; 7A; 8C; 9A).

According to the palynological analysis, the algae *Schizophacus parvus*, nowadays indicating stagnant, shallow, and more or less mesotrophic freshwater habitats (Van Geel & Van der Hammen 1978), would be associated to nearby freshwater environment. This suggestion is corroborated by the presence of *Gabonispuris* sp. (Marsileaceae) and *Peromonolites* sp. (Isoetaceae). These palynomorphs would reflect the composition of the local flora surrounding the subaquatic depositional environments.

Highly abundant gymnosperm pollen such as *Araucariacites australis* is interpreted as allochthonous representatives of a relatively nearby upland vegetation, whereas pollen of *Taxodiaceapollenites hiatus* and *Ephedripites* probably represents nearby lowland coastal environments. These taxa were possibly transported to the depositional area as wind-borne particles as for extant representatives. Cheirolepidiaceae pollen was probably also wind dispersed (Srivastava 1976), however, the good preservation and the presence of tetrads of *Classopollis major* (Fig. 10A) indicate short transport. The latter taxon has also been interpreted as being produced by xeromorphic coastal plants, adapted to halophytic and riparian habitats from brackish marshes and fluvio-lacustrine freshwater environments (Watson 1977; Upchurch & Doyle 1981; Alvin 1982; Pons & Koeniguer 1985; Watson 1988; Gomez *et al.* 2002).

Among angiosperm pollen, *Clavatipollenites* appears to be abundant and well preserved indicating short transport, possibly by wind. These pollen grains have compared to *Ascarina* of the Chlorantaceae (Walker & Walker 1984), which is wind-pollinated.

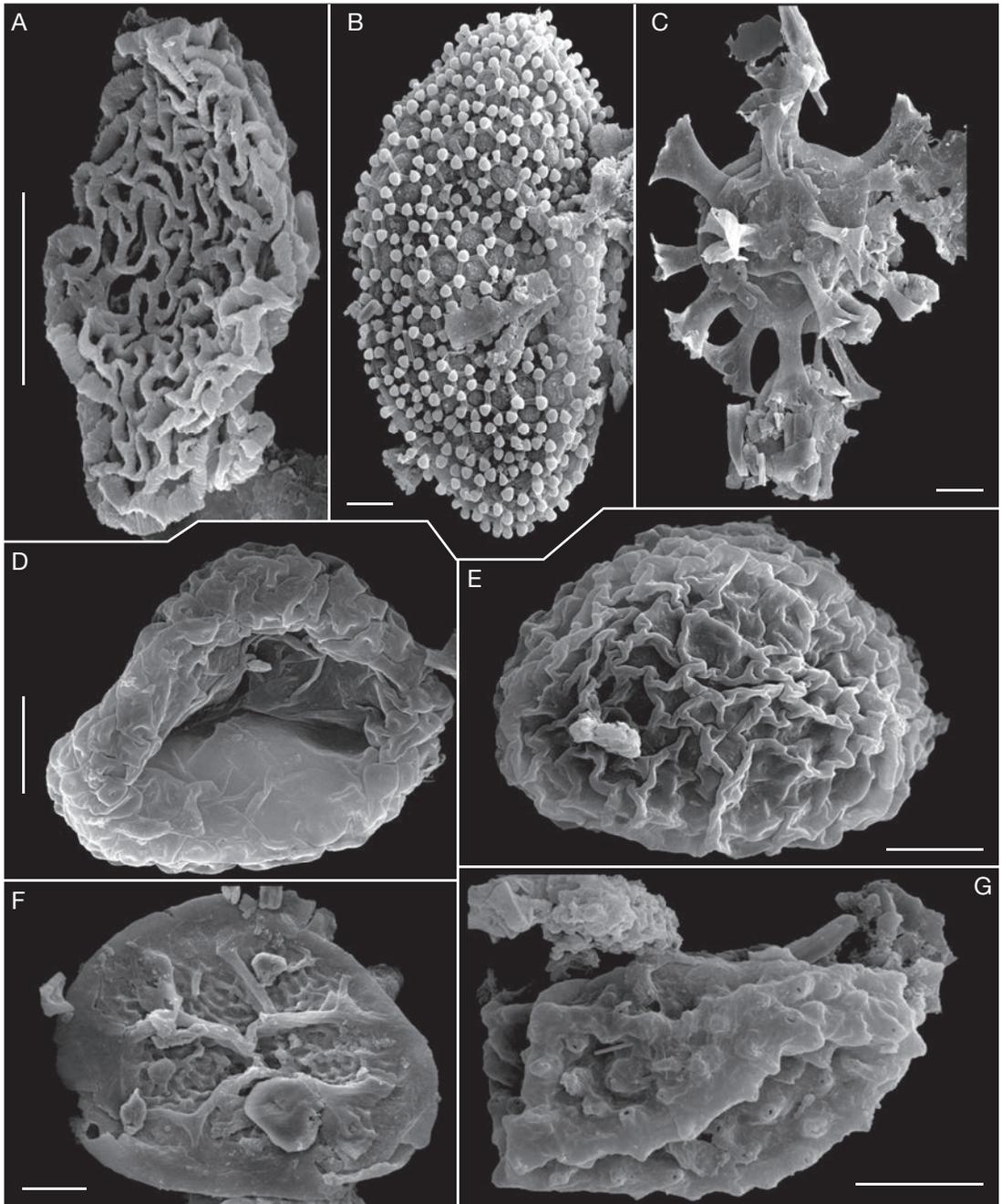


FIG. 11 — SEM images of sporomorphs from the Estercuel section (Teruel province, northeastern Spain): **A**, *Afropollis jadinus*; **B**, *Steliatopollis barghoornii*, lateral face; **C**, dinoflagellate cyst *Oligosphaeridium* sp.; **D**, *Gabonisporites* sp., proximal face; **E**, *Gabonisporites* sp., distal face; **F**, reworked *Triporoletes* sp. cf. *T. radiatus*, proximal face showing damage in the exine; **G**, *Peromonolites* sp., distal face. Scale bars: 10 μ m. Full taxa names are given in Table 1.

There are few well-preserved dinoflagellate cysts (*Oligosphaeridium* sp.) indicating a marine influence. However, their low abundance would indicate relative proximity to a coastal floodplain environment.

In addition, there are some reworked elements that appear eroded and with a higher thermal degree of organic maturation within the assemblage such as the spores *Camarozonosporites* sp., *Cibotiumspora juncta*, *Cicatricosisporites* spp., *Concavissimisporites verrucosus*, *Patellasporites tavadarensis* and *Plicatella* spp., together with the freshwater elements *Crybelosporites* sp. (related to Marsileaceous ferns) and *Triporoletes* sp. cf. *T. radiatus* (related to bryophytes). From this, it can be inferred that reworking and redepositing of older pollen and spores occurred because of fluvial influence.

According to the fossil fauna from Estercuel locality, moulds of mytilid bivalves (order Mytiloida, family Mytilidae) (Dr. Graciela Delvene, pers. comm.) up to 2 cm long and 1 cm wide in the finest grained lithology are noteworthy. At this fossil site the bivalves are usually preserved with the two valves still articulated (in connection) indicating little or no transport prior to deposition. The presence of this group of marine and brackish-water bivalves together with dinoflagellate cysts indicate some marine input into the depositional environment where the fossil plants were deposited.

CONCLUSIONS

The rich fossil floras recently discovered from the "Boundary Marls" unit of the Utrillas Formation at the Estercuel site, Teruel province, northeastern Spain, include diverse assemblages of green algae, aquatic lycopsids, pteridophytes, gymnosperms as well as terrestrial and aquatic angiosperms. The fossils include both allochthonous and parautochthonous elements deposited in swampy and fluvial sedimentary environments with tidally influence. The palynological data indicate a latest Albian age. The plant assemblage of the Estercuel site shows a mixture of Laurasian and Gondwanan floristical elements in the uppermost Albian deposits from northeastern Spain.

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