

Systematic Palaeontology (Palaeobotany)  
Middle Albian gymnosperms from the  
Río Martín Valley (Teruel, Spain)

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## Abstract

The fossil-rich site within the Albian Escucha Formation in the Oliete Sub-basin, located in the Northeast of Spain, has provided a great abundance of impressions, including leaf remains and seed cones of Coniferales (*Sphenolepis kurriana*, *Sphenolepis sternbergiana*, *Elatides curvifolia*, *Brachyphyllum* sp. and *Geinitzia* sp. cf. *G. rigida*), leaves of Caytoniales (*Sagenopteris elliptica*), Ginkgoales (*Ginkgoites pluripartita*, and *Sphenobaiera* sp. cf. *S. longifolia*), Bennettitales (*Ptilophyllum* sp. cf. *P. pecten* and aff. *Zamites* sp.), Cycadales (*Nilssonia tenuinervis* and *Ctenozamites* with entire and denticulate pinnae margins), Czekanowskiales, and reproductive structures of Gnetales. The gymnosperm remains are fairly abundant in the upper member, built up of sediments deposited in fluvial and swamp environments without marine influence. The different gymnosperm associations in this outcrop indicate a wide variety of environments in a subtropical climate, and a mixture of North American and European taxa in the Iberian plate during the Middle Albian. **To cite this article:** L.M. Sender et al., C. R. Palevol 7 (2008).

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## Résumé

**Les gymnospermes de l'Albien moyen de la vallée du río Martín (Teruel, Espagne).** La vallée du río Martín (Nord-Est de l'Espagne) renferme une riche flore fossile d'âge Albien moyen, découverte dans la formation Escucha. Ce site a livré une grande diversité d'empreintes foliaires et d'inflorescences de Coniférales (*Sphenopteris kurriana*, *Sphenolepis sternbergiana*, *Elatides curvifolia*, *Brachyphyllum* sp. et *Geinitzia* sp. cf. *G. rigida*), de folioles de Caytoniales (*Sagenopteris elliptica*), de feuilles de Ginkgoales (*Ginkgoites pluripartita*, et *Sphenobaiera* sp. cf. *S. longifolia*), de Bennettitales (*Ptilophyllum* sp. cf. *P. pecten* et aff. *Zamites* sp.), de Cycadales (*Nilssonia tenuinervis* et *Ctenozamites* avec des folioles à bords entiers et denticulés), de Czekanowskiales, ainsi que des inflorescences de Gnétales. Les Gymnospermes sont plus abondantes dans le membre supérieur de la formation Escucha, constitué de sédiments fluviaux et palustres sans influence marine. Les différentes associations floristiques suggèrent

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des environnements variés sous un climat subtropical et un mélange de taxons européens et nord-américains sur la plaque Ibérique durant l'Albien moyen. **Pour citer cet article :** L.M. Sender et al., C. R. Palevol 7 (2008).

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**Keywords:** Gymnosperms; Middle Albian; Escucha Formation; Spain; Potomac Group; Euro-Sinian and Siberian-Canadian Provinces

**Mots clés :** Gymnospermes ; Albien moyen ; Formation Escucha ; Espagne ; Groupe Potomac ; Provinces euro-sinienne et sibéro-canadienne

## 1. Introduction

The present paper deals with the gymnosperm component of a rich Middle Albian flora from Teruel province (Spain), obtained from several bands with plant impressions which include also a wide variety of angiosperms and pteridophytes [32]. This is part of a study undertaken for a doctoral thesis by the first author (L.M.S.). All plant remains occur as transported elements in quiet waters, associated with a fluvatile environment. Identifiable plants are associated with abundant comminuted plant debris (CPD) in different proportions. Each band displays a somewhat different assemblage and the local nature of the water bodies represented, as well as the appreciable size of identifiable plant remains suggest a local origin. Some of the gymnosperm remains show remnants of a coaly layer, but this is structureless. No cuticles are available, almost certainly because of adverse weathering conditions. Earliest works [10,14–18] also gave more incidental results regarding the gymnosperms of the Teruel province.

## 2. Geographic and geologic setting

The Lower Cretaceous sediments of the Escucha Formation [1], which have been sampled for the present investigation, occur in the Oliete Sub-basin [34] within the Maestrazgo basin in the Aragonian sector of the Iberian Range (Fig. 1). The overall succession of the Escucha Formation has been interpreted as a regressive megasequence produced by progradation of a deltaic-estuarine system [29].

This formation overlies disconformably the Aptian Oliete Formation [5]. Whereas the latter is entirely marine, the Escucha Formation ranges from shallow marine/estuarine to non-marine. The Utrillas Formation, which follows in succession also disconformably, consists of fluvatile sandstones with shale intercalations, and it is dated as Late Albian in this area. Three members have been recognised in the Escucha Formation on lithological and sedimentological criteria [7]: Barriada, Regachuelo, and La Orden (Fig. 1).

In the studied outcrop, the Escucha Formation is represented by 130 m of sandstones and shales with inter-

bedded coal seams and calcarenites in the lower part. Six fossiliferous horizons in the La Orden Member have yielded gymnosperm remains (Fig. 1). A lower locality (RU-2) did not yield gymnosperms. The lower part of the La Orden Member, in which these plant-bearing horizons occur, consists of alternating fine sandstones and shales with increasing shale content upwards. The fossiliferous horizons vary in thickness between a few centimetres and more than two metres. A lacustrine facies is involved and the plant fragments represent floated remains that settled on the bottom of what seems to have been shallow ponded areas.

## 3. Taxonomic descriptions

All specimens from the Río Martín valley are impressions without cuticle. Therefore, some of the taxa can only be described as form genera with tentative species identification. Specimens have been lodged in the collections of the Palaeontological Museum, University of Zaragoza, with numbers MPZ 2007/1477 to MPZ 2007/1762.

Order Coniferales

Genus *Sphenolepis* Schenk, 1871

*Sphenolepis sternbergiana* (Dunker, 1846) Schenk emend. Harris, 1953

Plate 1 (B and C) shows 98 specimens, from MPZ 2007/1477 to MPZ 2007/1574.

Fragments of twigs up to 10 cm long and 0.3 cm wide. The best specimens preserve up to three orders of alternate axes. Leaves spirally disposed, adpressed, scale like, rhomboidal, tapering in acute apex. Dimensions of leaves: 3.5 to 1 mm in length and 1.5 to 0.75 mm in width in the basal parts of the longer shoots, and 2.5 mm long and 1 mm wide, on the average, in the basal parts of the smaller ones. The leaves possess a marked dorsal keel. Leaf base slightly constricted; leaf apex slightly tilted outwards at 40° to 45°, with a falcate tip.

Seed cones are spherical to ovoid in shape, with diameters or main length ca 1.5 cm. They are terminally attached. All specimens are preserved as transversal or longitudinal sections, so it is not possible to determine

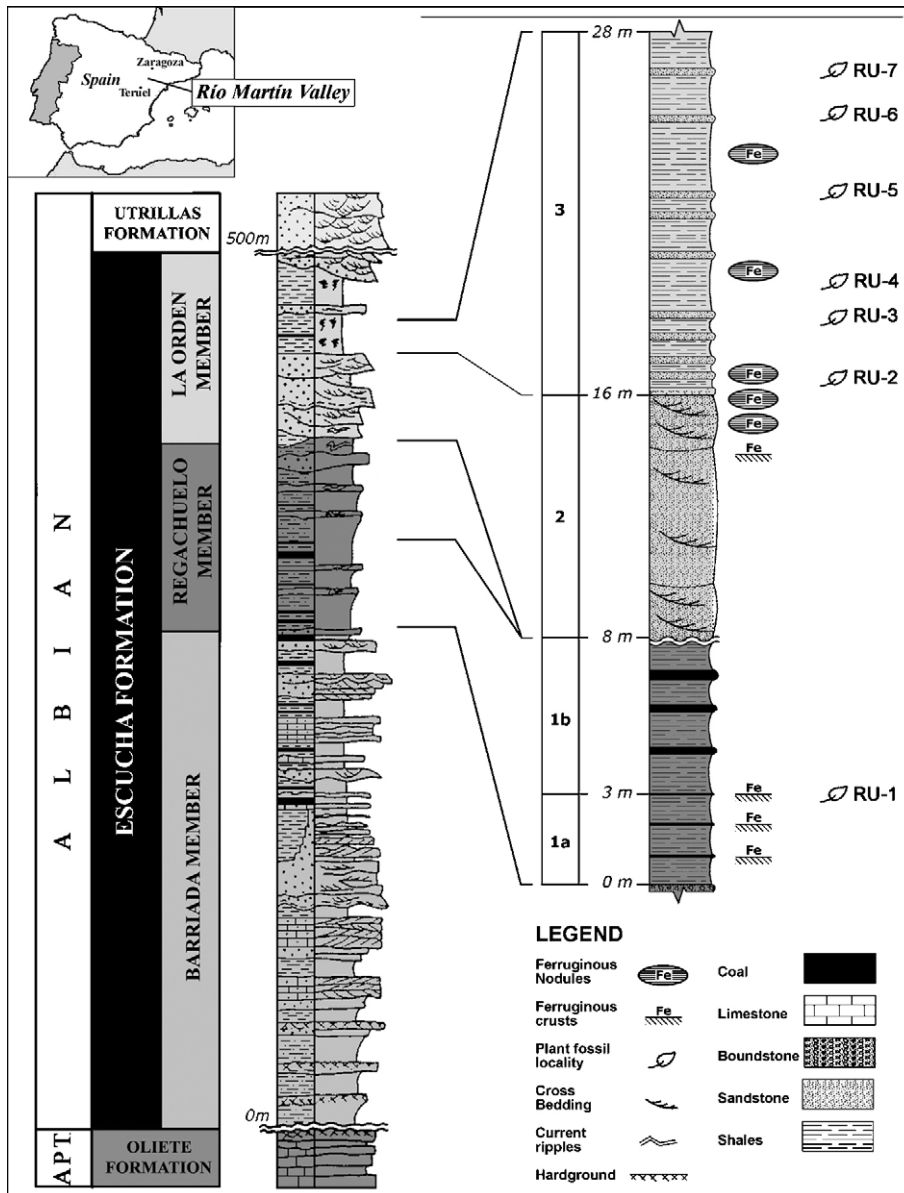


Fig. 1. Geographic location of the outcrop and stratigraphic succession at the fossiliferous site (right) in relation to the general section of the Escucha Formation (left). Modified from [29].

Fig. 1. Localisation géographique du gisement et succession des niveaux fossilifères (à droite), replacés sur une section générale de la formation Escucha (à gauche). Modifié d'après [29].

the original shape of cone scales, which are spirally arranged, peltate, and with a distinct stalk. Head of cone scales elliptical; inner part of scales channelled by thin parallel grooves. Best-preserved specimens show at least two oval impressions on the surface of bracts, which apparently correspond to the position of seeds.

This species has also been found in the Potomac Group of the USA [36] and from the Aptian–Albian of western Canada [3].

*Sphenolepis kurriana* (Dunker, 1846) Schenk emend. Harris, 1953

Plate 1 (A) shows 55 specimens, from MPZ 2007/1575 to MPZ 2007/1629.

Fragments of twigs up to 25 cm long and 0.15 cm wide. Some specimens preserve up to four orders of branched shoots. Leaves spirally disposed, imbricate and adpressed, elongate, oval to asymmetrically rhomboidal,

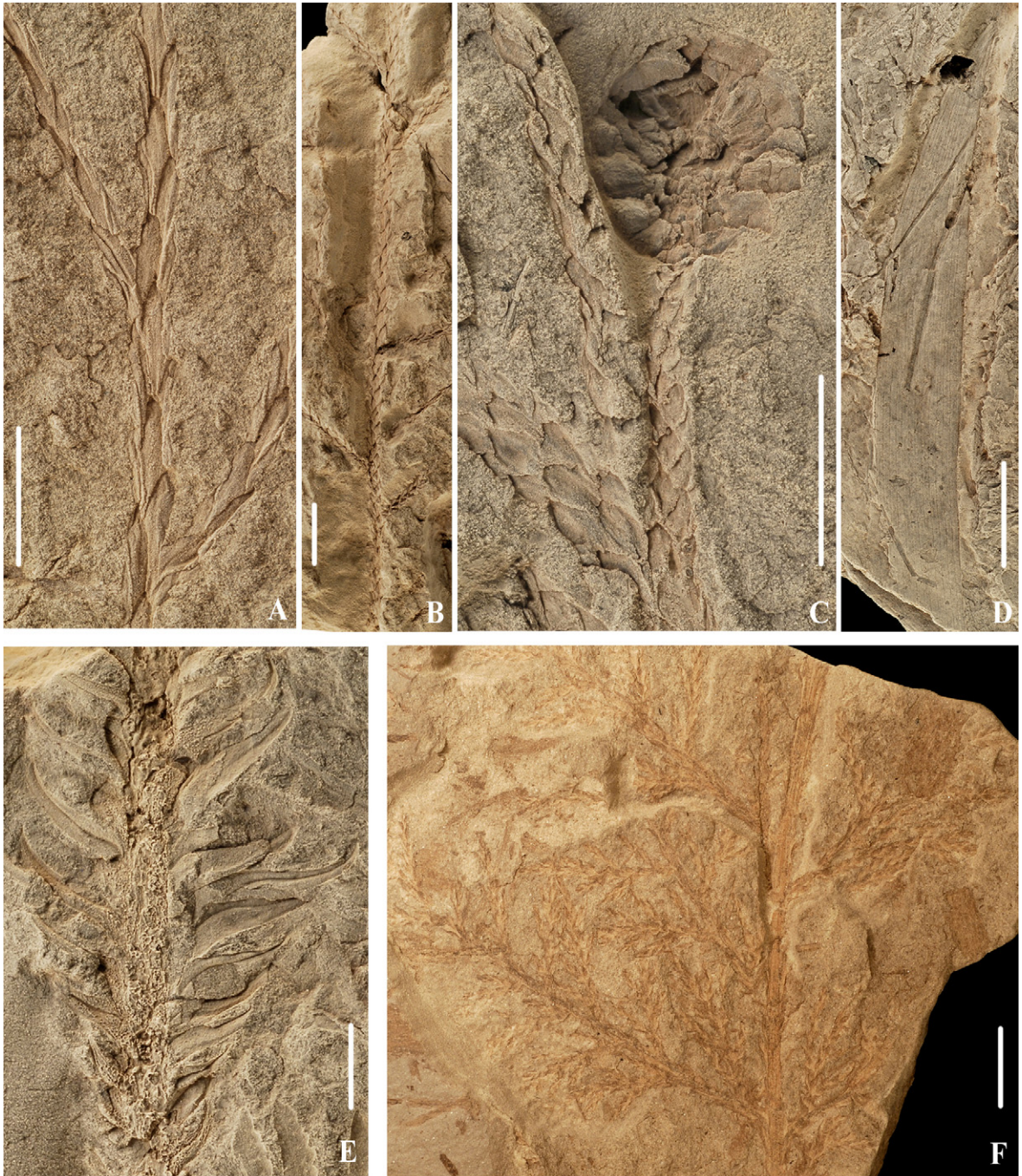


Plate 1. (A) MPZ 2007/1575. Branched shoot of *Sphenolepis kurriana*. (B) MPZ 2007/1477. Twig with alternate axes of *Sphenolepis sternbergiana*. (C) MPZ 2007/1478. Section of a seed cone attached terminally to a shoot of *Sphenolepis sternbergiana*. (D) MPZ 2007/1642. Detached leaf of *Podozamites* sp. (E) MPZ 2007/1639. Fragment of axis with falcate leaves corresponding to *Elatides curvifolia*. (F) MPZ 2007/1638. Great main branched complex of *Geinitzia* sp. cf. *G. rigida*, branching up to four times. Scale bars: A, C and E: 0.5 cm, B, D and F: 1 cm.

Planche 1. (A) MPZ 2007/1575. Axe ramifié de *Sphenolepis kurriana*. (B) MPZ 2007/1477. *Sphenolepis sternbergiana*: ramille portant des axes alternes. (C) MPZ 2007/1478. Cône observé en section à la partie supérieure d'un axe de *Sphenolepis sternbergiana*. (D) MPZ 2007/1642. Feuille isolée de *Podozamites* sp. (E) MPZ 2007/1639. *Elatides curvifolia*: fragment d'axe avec des feuilles falquées. (F) MPZ 2007/1638. *Geinitzia* sp. cf. *G. rigida*: fragment d'axes ramifiés jusqu'au quatrième ordre. Échelle : A, C and E: 0,5 cm, B, D and F: 1 cm.

tapering in acute apex. Dimensions of leaves: 4 to 2.5 mm long and 1.5 to 0.75 mm wide from the lower to the upper parts of longer shoots. The leaves possess a marked dorsal keel. Only a small part of apex is free, and it is slightly arched adaxially. The free leaf portions of leaves spread angles less than 10°.

This European species is also reported in the late Early Cretaceous of Canada [3], Portugal [35], Tunisia [4], and Czech Republic [27].

Form-genus *Brachyphyllum* Lindley et Hutton ex Brongniart, emend. Harris, 1979

*Brachyphyllum* sp.

Plate 2 (A) shows eight specimens, from MPZ 2007/1630 to MPZ 2007/1637.

Fragments of twigs preserve up to three orders of axes. Shoots disposed at 30–40°. Leaves triangular to rhomboidal, spirally arranged, very adpressed and imbricated. The leaves possess a marked and bulky abaxial keel. Leaf apex prominent, elongate, and cuneate. Several thin and parallel grooves channel the whole surface of leaves.

The marked abaxial keel and the parallel grooves of leaves are two main characteristics of both fossil and extant Araucariaceae and Taxodiaceae families [37].

Form-genus *Geinitzia* Endlicher, 1847

*Geinitzia* sp. cf. *G. rigida* (Phillips) Harris, 1979

Plate 1 (F) shows one specimen, MPZ 2007/1638.

The single specimen found corresponds to a branch 13 cm long and 0.4 cm wide, showing leaf bases and dividing up to four times into small, alternate to subopposed branchlets. Last and penultimate shoots are proportionally short. Complete penultimate ones are 3 cm long and 0.4 cm wide. Rhomboidal scale-like leaves spirally arranged. Leaves up to 5 mm in length and 2 mm in width, at about 45° to axis, and inclined outwards. Leaf margins straight.

This taxon is widely reported from Middle Jurassic strata in Europe [12,22] and the lower part of the Cretaceous in Australia [6]. It resembles *Geinitzia rechenbachi*, but differs by its longer and thinner leaves, with a different angle of attachment.

Form-genus *Elatides* Endlicher, 1847

*Elatides curvifolia* (Dunker) Nathorst, 1897

Plate 1 (E) shows three specimens, from MPZ 2007/1639 to MPZ 2007/1641.

Fragments of isolated shoots up to 10.7 cm long and 1.4 cm wide. Leaves spirally arranged, 0.9 cm to 0.7 mm long and 0.15 cm wide, falcate, needle-like, with a marked and wide midrib, attached at basal non-contracted cushions. Leaves at about 90° to 65° to axis, curving adaxially from medial part. Apex acute and pointed.

The species was identified by Bell [3] in the Blairmore Group of Alberta (Canada). This author put on synonymy *Elatides curvifolia* with *Geinitzia* sp. and with *Sphenolepis sternbergiana*. We agree with the first comparison, but not with the second one, because leaves of *S. sternbergiana* species are triangular in shape, lacking of both curved apex and marked midrib.

*Elatides curvifolia* species is represented from Jurassic and Early Cretaceous in North America, Europe, and Asia [22,26].

Conifer *incertae sedis*

*Podozamites* sp. (Brongniart) Braun, 1843

Plate 1 (D) shows four specimens, from MPZ 2007/1642 to MPZ 2007/1645.

Fragments of leaves up to 6.4 cm long and 0.85 cm wide, lanceolate to falcate, with straight margins. Leaves taper to the base and end in an acute apex. Venation consists of several marked and parallel veins (up to 14) equally spaced, which run parallel one to another and parallel to the margins, and join together at the apex.

Order Ginkgoales

Genus *Ginkgoites* Seward, 1919

*Ginkgoites pluripartita* (Schimper) Seward, 1926

Plate 2 (B) shows ten specimens, from MPZ 2007/1646 to MPZ 2007/1655

Detached leaves and fragments. Best preserved leaves up to 3 cm long and 2.4 cm wide. Petiole up to 1.8 cm long and 0.2 cm wide, which tapers adaxially and enlarges abruptly at its top to form a lamina up to 3.3 cm long. The lamina consists of up to 14 lanceolate segments (with dimensions up to 2 cm long and 0.3 cm wide), which develop radially from the distal end of the petiole. The segments are narrow at the base and increase in width adaxially. Apices of segments are acute, rounded, or irregular. Lateral margins entire or slightly sinuous. Venation composed of 2 to 3 veins per millimetre, which dichotomize towards the apex.

Krassilov [23] and Watson et al. [42] indicate that *Ginkgoites* could be used as a generic name for *Ginkgo*-like leaves that cannot be attributed to any established



Plate 2. (A) MPZ 2007/1630. Branched shoot of *Brachyphyllum* sp. (B) MPZ 2007/1646. Leaf of *Ginkgoites pluripartita*. (C) MPZ 2007/1656. Small leaf of *Sphenobaiera* sp. cf. *S. longifolia*? with two teeth at the end of segments. (D) MPZ 2007/1693. Seed cone of a gnetalean with ovules protected by scales. (E) MPZ 2007/1661. Leaflet of *Sagenopteris elliptica* showing anastomosed venation. (F) MPZ 2007/1695. *Czekanowskia* sp. cf. *C. rigida*. (G) MPZ 2007/1698. Detached leaf of *Nilssonia tenuinervis*. (H) MPZ 2007/1700. Three pinnae of *Ctenozamites* aff. *leckenbyi*. Scale bars: A, B, and C: 0.5 cm, E, F, G and H: 1 cm, D: 1 mm.

Planche 2. (A) MPZ 2007/1630. Axe ramifié de *Brachyphyllum* sp. (B) MPZ 2007/1646. Feuille de *Ginkgoites pluripartita*. (C) MPZ 2007/1656. Petite feuille de *Sphenobaiera* sp. cf. *S. longifolia*? avec deux dents à l'extrémité des segments. (D) MPZ 2007/1693. Cône fructifère de Gnétale, avec ovules protégés par des écailles. (E) MPZ 2007/1661. Foliote de *Sagenopteris elliptica* montrant la nervation anastomosée. (F) MPZ 2007/1695. *Czekanowskia* sp. cf. *C. rigida*. (G) MPZ 2007/1698. Feuille isolée de *Nilssonia tenuinervis*. (H) MPZ 2007/1700. Trois pinnes de *Ctenozamites* aff. *leckenbyi*. Échelle A, B, et C : 0,5 cm, E, F, G et H : 1 cm, D : 1 mm.

genus. *G. pluripartita* species has been found in the Lower Cretaceous of western Greenland [33], USA [25], western Canada [3], Germany, and eastern Siberia [30]. Watson et al. [42] show that leaves of *G. pluripartita* species possess a wide range of morphological varia-

tion. These authors also point out the possibility that several specimens of the Potomac Flora, which were previously attributed by Fontaine [13] to other taxa, could correspond to *G. pluripartita* species.

Genus *Sphenobaiera* Florin, 1936

*Sphenobaiera* sp. cf. *S. longifolia*? (Pomel) Florin, 1936

Plate 2 (C) shows five specimens, from MPZ 2007/1656 to MPZ 2007/1660.

Leaves wedge-shaped, triangular, without a distinct petiole and tapering strongly towards the base. Dimensions: up to 2.6 cm long and 0.9 cm wide. Basal undivided portion of the leaf about 0.9 cm long, widening gradually towards the apex. Lamina forking dichotomously three times, giving elongate segments with entire margins. Segments diverging at an angle of about 5°. The distal segments (which resemble small denticles) are quite shorter than proximal ones, and they end in an acute apex. Veins parallel, two per lobe, forking repeatedly at base, and ending at the apex of each segment.

The studied leaves are similar to apical parts of *Czekanowskia microphylla* species [21] in having dichotomous apices of leaf segments (divided in two sharp acute teeth). Nevertheless, in *C. microphylla* species, the leaves have a single vein, but the leaves from Río Martín valley possess segments channelled by several dichotomic veins.

#### Order Caytoniales

Genus *Sagenopteris* Presl, 1838

*Sagenopteris elliptica* Fontaine, 1889

Plate 2 (E) shows 32 specimens, from MPZ 2007/1661 to MPZ 2007/1692.

Detached leaflets up to 11 cm long and 3.5 cm wide, oval to lanceolate shaped, lateral and apical margins entire, sometimes slightly undulate in apical part. Cuneate base with a short petiole up to 0.7 cm long and 0.3 cm wide in the best-preserved remains. The apex is rounded, acute or only slightly pointed. Some leaflets are slightly asymmetric because of inward curving. Venation composed of a central and distinct midrib (0.1 cm wide), which narrows abruptly near the apex. Secondary veins very thin and numerous, at 20° to 35° from the midrib, curving towards the leaf margin, and which curve outward to the lateral margins. These secondary veins anastomose to form a dense reticulum. The meshes are rhomboidal and elongate hexagonal, diminishing near the leaf margins without forming an exmedial vein.

*S. oregonensis* is a similar species which shows a less persistent midrib ([39] p. 235). According to Fontaine [13], *Sagenopteris* is a minority element in the Potomac Flora. Likewise, it is uncommon in the Río Martín valley localities as it is in the lower Cretaceous deposits in Spain generally.

#### Order Gnetales

Plate 2 (D) shows two specimens, MPZ 2007/1693 and MPZ 2007/1694.

Spike-shaped female cones, preserved as a longitudinal section. Dimensions: 0.8 cm long and 0.3 cm wide. Alternate reproductive units disposed at both sides of a thin axis and attached at 35° from it. The units have minute spherical to subovoidal seeds (0.8 mm in length), surrounded by at least two triangular bracts.

Reproductive structures of Gnetales occur also in the Barremian deposits of China [43], but they are bigger than our specimens are, and their morphology is quite different. Some similarities could be pointed out in relation to reproductive spikes of Gnetales species defined by [9] from the Albian Potomac Group.

#### Order Czekanowskiales

Genus *Czekanowskia* Heer, 1876

*Czekanowskia* sp. cf. *C. rigida* Heer

Plate 2 (F) shows three specimens, from MPZ 2007/1695 to MPZ 2007/1697.

Dimensions of the best-preserved specimen: 7.7 cm long and 4.2 cm wide. Basal part constitutes by a small shoot (0.4 cm long), which bears bud scars of leaves spirally arranged. Eight preserved needle-like leaves are situated in bundle at the upper part of the shoot. Leaves entire or slightly curved, up to 7.5 cm in length, and 0.5 mm to 1 mm in width, adapically. Most part of leaves fork once dichotomically. Venation consists of a marked midrib that channelled the leaf longitudinally.

Several species of *Czekanowskia* genus have been grouped into two formal morphological groups by Samylinina [31], in relation to the width of their leaves. Therefore, leaves of *Czekanowskia* cf. *G. rigida* are 0.5 to 1.5 mm wide. These measures agree with the dimensions of the leaves of our specimen.

Some kinds of fossil *Pinus*-like short shoots could be compared with our specimen. However, they only possess up to five spirally arranged needle-like leaves, attached at a central point. Leaves from Río Martín valley are dissected, single-veined, dichotomous, and they are attached to a dwarf shoot, which are characteristics typical of *Czekanowskia* genus [21].

Bell [3] reports *Czekanowskia rigida* species from the Aptian Kootenay Formation of western Canada. Up to now, for Albian times, this order has only been found in sediments of the Siberian-Canadian floristic province.

## Order Cycadales

Genus *Nilssonia* Brongniart, 1825*Nilssonia tenuinervis* Seward, 1900

Plate 2 (G) shows two specimens, MPZ 2007/1698 and MPZ 2007/1699.

Fragments of detached leaves, strip-shaped, which narrow slightly towards the apex. Dimensions of leaves: up to 6 cm long and 0.6 cm wide. Margins of leaves entire to slightly undulated, which show several constrictions on their surface. Leaves possess a marked midrib (0.75 mm wide); secondary veins are simple, thin and numerous (ca 30 veins per centimetre), at 80° or 90° from the midrib, ending in margins freely.

Harris [19] pointed that specimens of *Nilssonia parvula* Fontaine, from the Jurassic of Oregon in the United States [39], resemble the smallest forms of *N. tenuinervis* cycadalean foliage. Specimens from the Río Martín valley show very similar characteristics to those reported by Harris ([19] Plate XVII, Figs. 1–7). Nevertheless, Cleal et al. [8], in their revision of the basynonymy between *Nilssoniopteris* and *Nilssonia* types, concluded that *Nilssonia tenuinervis* could be used as the foliage morphospecies.

Genus *Ctenozamites* Nathorst, 1886 (ex *Ctenopteris* Saporta)

Genus *Ctenozamites* Brongniart ex Saporta 1873 non *Ctenopteris* Blume ex Kunze 1846

Substitute name *Ctenozamites* Nathorst, 1886. ([12], p. 456).

*Ctenozamites* aff. *C. leckenbyi* (Leckenby) Nathorst, 1886

Plate 2 (H) shows two specimens, MPZ 2007/1700 and MPZ 2007/1701.

Upper parts of pinnae up to 6 cm long and 1.6 cm wide. Pinnules, subopposed to alternate, distinctly falcate, which curve strongly adapically. Dimensions: 1.2 cm in length and 0.4 cm in width (3 times as long as broad), asymmetrical; basisopic zone of pinnules bigger than acroscopic one. Margins of pinnules entire. Base contracted, expanded downwards, which is connected to the base of adjacent pinnules by a thin foliar tissue. Apex acute. Venation of leaves composed of a marked midrib (0.8 mm in width), which tapers progressively towards the apices. Five sinuous secondary veins entering the basisopic part of the base of every pinnula, forking once or twice to end in margin. Several secondary veins pinnately arranged at 20° from the midrib. They divide dichoto-

mically, ending in margins at both sides of it. Pinnae possess a distal expanded leaflet, with asymmetrical base.

Characteristics of the Río Martín valley specimens fit well in those corresponding to *Ctenozamites leckenbyi* species. Nevertheless, our specimens possess asymmetrical leaves channelled by a distinct midrib. Harris [19] described an unusual specimen (p. 92, text–fig. 39B) that shows pinnules with midribs and contracted bases, which he considered as pinnae from a leaf apex of *Ctenozamites leckenbyi*.

*Ctenozamites insignis*

*Ctenopteris insignis* Fontaine, 1899

*Ctenopteris integrifolia* Berry, 1911

Plate 3 (A,B) shows 31 specimens, from MPZ 2007/1702 to MPZ 2007/1732.

Fragments of leaves up to 5.7 cm long and 3 cm wide. Rachis stout, pinnae alternate, at 40° to 50° from the rachis, and attached to it by their entire base, which is slightly decurrent. Pinnae lanceolate, lobated and toothed. They show two subopposite and acute teeth in each side at the medial zone of the pinna, and two smaller ones at the distal part of it. Apex acute, ending in two small subopposed and triangular teeth. Venation consists of six to seven thin veins that develop parallel from the base and diverge flabelately towards the apex. They fork up to four times, reaching the apex of the lobes and the margins of pinnae to end freely.

This taxon has only been found previously in the Albian deposits of the Potomac Group in Fredericksburg (USA) [13] and tentatively in the Aptian of the Blairmore Group from western Canada [3] and in the Upper Albian–Lower Cenomanian from Madrid (Spain) [11] at the moment. *Ctenozamites insignis* species was originally described as a bennettitalean, but now is accepted as a cycadalean, because of its foliage characteristics [28].

*Ctenozamites virginienensis*

*Ctenopteris virginienensis* Fontaine, 1899

*Ctenopteris integrifolia* Berry, 1911

Plate 3 (C) shows ten specimens, from MPZ 2007/1733 to MPZ 2007/1742.

Fragments of leaves up to 7.7 cm long and 3.3 cm wide. Pinnae opposed to alternate, at 40° to 45° from the rachis. Pinnae attached to the rachis by their whole base, which is expanded abapically. They are ovoidal





Plate 3. (A) MPZ 2007/1702. Apical fragment of a leaf of *Ctenozamites insignis*. (B) Detail of some pinnae from A. (C) 2007/1733. Leaf fragment of *Ctenozamites virginiensis*. (D) MPZ 2007/1743. Leaf fragment of *Zamites* sp. cf. *Z. carruthersii*. (E) Detail of a single pinna of aff. *Zamites* sp. from G. (G) MPZ 2007/1750. Fragment of leaf of aff. *Zamites* sp. Note the well-developed teeth of the pinnae. (H) MPZ 2007/1761. Leaf fragment of *Ptilophyllum* sp. cf. *P. pecten*. Scale bars: A–D and G–H: 1 cm, E–F: 0.5 cm.

Planche 3. (A) MPZ 2007/1702. Fragment d'une penna terminale de *Ctenozamites insignis*. (B) Détail de quelques pinnules de A. (C) MPZ 2007/1733. Fragment d'une penna de *Ctenozamites virginiensis*. (D) MPZ 2007/1743. *Zamites* sp. cf. *Z. carruthersii*. (E) Détail d'une pinnule de D. (F) Détail d'une pinnule de G. (G) MPZ 2007/1750. Fragment de penna de aff. *Zamites* sp. observer les pinnules plus ou moins dentées. (H) MPZ 2007/1761. Penna de *Ptilophyllum* sp. cf. *P. pecten*. Échelle A–D et G–H: 1 cm, E–F: 0,5 cm.

to lanceolate, with entire margins. Only two subopposed lobes are present, located at both sides of the pinna apex; the adaxial lobe is larger than the abaxial one. Pinna apex acute, ending in two small triangular teeth. Venation consists of six to seven thin veins that develop from a common point from the base, forking up to three times and ending free in the margins of lobes.

We have separated *Ctenopteris virginensis* and *Ctenopteris insignis* species in their original denomination by Fontaine [13] because we have found neither the similarities in shape nor the venation to join them in a single species.

Order Bennettitales

Genus *Zamites* Brongniart, 1828

*Zamites* sp. cf. *Z. carruthersii* Seward, 1917

Plate 3 (D,E) shows seven specimens, from MPZ 2007/1743 to MPZ 2007/1749.

Fragments of leaves up to 8.5 cm long and 3.4 cm wide. Pinnae opposite at 70° to 90° from the midrib, lanceolate to oblong. Dimensions of pinnae: up to 2 cm long and 0.5 cm wide. Margins entire; base rounded, slightly and symmetrically contracted. Apex acute, slightly pointed. Veins very thin, which diverge from the point of attachment of the pinna. Veins fork several times, ending freely at the margins.

*Zamites* genus was defined to distinguish those leaves of bennettitales that possess pinnae with rounded apices and slightly contracted symmetrical bases. It has become a typical form–genus of Cretaceous cycadopsid foliage around the world. In their monographs of the Bennettitales of the English Wealden, Watson and Sincok [40] make a revision of the genus and present a key to the main characteristics of the different species from England.

aff. *Zamites* sp.

Plate 3 (F,G) shows 11 specimens, from MPZ 2007/1750 to MPZ 2007/1760.

Fragments of leaves up to 5.5 cm long and 3.7 cm wide. Pinnae lanceolate, subopposed and strongly toothed. Dimensions of the largest detached pinnae: up to 2.9 cm long and 0.8 cm wide. Lobes alternate, slightly cuneate; the two medial ones are the biggest. Base of pinna rounded and contracted. Apex acute; in some specimens it is divided in two small, acute, and asymmetrical teeth. Venation consists of 6 to 8 veins, diverging from the base and forking almost once to end in the apex of teeth or in their surroundings. A well-marked midrib is present in some specimens. This vein runs from the

insertion point of the pinna to its middle part, narrowing towards the apex. Secondary veins pinnate, at variable angles from the midrib, ending at the margins.

Pinnae with similar characteristics have been found in sediments from the Aptian Kootenai Formation in Montana. They were assigned to an unidentified fern by [25], and these authors also pointed the similarities of these pinnae with some Cretaceous Cycadales. The specimens from the Río Martín valley differentiate from the Montana pinnae in having a distinct mid vein. We classify our specimens as *Zamites* sp. because of the contracted bases of pinnae, the divergent venation, and the attachment to the rachis.

Genus *Ptilophyllum* Morris, 1840

*Ptilophyllum* sp. cf. *P. pecten* (Phillips) Morris, 1841

Plate 3 (H) shows two specimens, MPZ 2007/1761 and MPZ 2007/1762.

Fragments of leaves 6.7 cm long and 2.9 cm wide. Pinnae alternate to subopposed, lanceolate, at 53° and 70° from rachis. Pinnae 17 mm to 8 mm long and 3 mm to 1.5 mm wide. Base basiscopically expanded and slightly decurrent. Apex obtuse to slightly acute. Venation consists of five to six thick veins that develop from the base, forking once adapically, to end at the margins.

This species is a common element in Jurassic and Cretaceous floras both from Eurasia and Gondwana [2,20].

#### 4. Plant–fossil assemblages and the corresponding depositional environments

The lithology of locality RU-3 consists of two metres of light-grey sandy shales with planar cross lamination, and intercalations of thin-bedded fine-grained white sandstones. A large quantity of Comminuted Plant Debris (CPD = 80%) of variable sizes is present.

Locality RU-4 is represented by alternating white and yellow sandy shales with brown ferruginous patches, and centimetre-thick planar beds of white fine-grained sand with planar cross lamination in the upper part. Bioturbation occurs in the highest part of this unit, which displays inclined perforations. Small plant fragments diminished in importance (CPD = 40%) but are generally larger in size than in the previous locality. Both RU-3 and RU-4 horizons display branched shoots of conifers *Sphenolepis sternbergiana* and *Sphenolepis kurriana* species, the latter with attached seed cones, and fragments of leaves with variable size up to 8 cm corresponding to Cycadales and Bennettitales, with their apical parts already preserved.

Locality RU-5: the basal part consists of less than a metre of grey laminated sandy shales with cross lamination and very abundant white sand lenticules on the millimetre scale. Gymnosperm remains corresponding to *Sphenolepis sternbergiana* conifer are rare, and are only a few centimetres in length. In this horizon, some leaves of Caytoniales (*Sagenopteris elliptica*) and a scarce number of leaves of *Ginkgoites pluripartita* species occur. About 50% of CPD is present. The higher part of this horizon is represented by a little over 2 metres of laminated shales devoid of sand content; they show millimetric coal intercalations. The surface of laminae is specked by minute plant fragments (less than 1 millimetre in diameter), interspersed with centimetric plant fragments. Scarce but complete conifers shoots of *Brachyphyllum* sp. and *Elatides curvifolia* species, leaves of *Ginkgoites pluripartita*, as well as a moderate quantity of leaflets of the caytoniale *Sagenopteris elliptica* are preserved at this level.

Locality RU-7 consists of an alternation of grey laminated shales and light brown fine-grained sand layers with cross lamination. Both lithologies occur in thin beds, between 1 and 12 cm thick. At this level occur scarce leaves of Czekanowskiales and Gnetales species, leaves of *Sphenobaiera* sp, and the largest specimens of gymnosperms remains corresponding to *Sphenolepis kurriana* and *Geinitzia* cf. *rigida* species are found up to 20 cm. The amount of CPD increases to about 40%.

The sedimentological characterization of the different fossil horizons suggests that different plant assemblages correspond to different areas of a fluvial plain within a general fluvial-estuarine environment.

## 5. Palaeogeographical discussion

The Río Martín valley site presents several different gymnosperms (Coniferales, Ginkgoales, Caytoniales, Gnetales, Czekanowskiales, Cycadales and Bennettitales), most of which are known from classical European localities [38], representing the subtropical belt of the Northern hemisphere in Early Cretaceous times [24].

Similar gymnosperm assemblages belonging to the same climatic belt are known from other places, such as the Lower Cretaceous Wealden in England [41] and several localities in Portugal [35] and in the eastern USA [13], Aptian–Albian in age. However, North American *Ctenozamites insignis* and *Ctenozamites virginensis* species are recorded for the first time in the Middle Albian of Europe.

During Aptian and Albian times, *Czekanowskia* genus was restricted to the Siberian–Canadian palaeofloristic region [38] and to the transitional zone between the

latter and the Euro–Sinian region [31] (which was located in the middle part of China). Therefore, the occurrence of *Czekanowskia* cf. *C. rigida* in the Río Martín valley (eastern of Spain) represents the first mention of a representative of this order found in the Albian of western Europe (Euro–Sinian region).

According to [26], the Sibero–Canadian province was characterized by the absence of *Ptilophyllum*, *Zamites* and *Elatides curvifolia* species and the abundance of *Ginkgoites*, *Sphenobaiera*, and *Czekanowskia* species. All these taxa have also been found in the Río Martín valley, so the data could point to a possible mixture of elements from Siberian–Canadian, Potomac, and Euro–Sinian provinces [38].

## 6. Conclusions

The Río Martín valley site provides the most widespread representation of genera and species of gymnosperms never ever found in the late Early Cretaceous of Spain. It is the first time that *Ctenozamites insignis* and *C. virginensis* species are referenced outside North America. In this site has also been found the first Czekanowskiale from the Albian in western Europe. The presence of this taxon in the western boundary of the Euro–Sinian region, where it was thought to be extinct in Albian times, provides a longer range of distribution of this genus. All these data could point to a possible mixture of elements from Siberian–Canadian, Potomac and Euro–Sinian provinces in the eastern zone of Spain during Middle Albian times. These new data give support to the idea of Vakhrameev [38] in relation to the possibility of union of European and Potomac provinces during Early Cretaceous, and its continuation in time up to the terminal Early Cretaceous.

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