

## A new species of *Nehvizdya* (Ginkgoales) from the Lower Cretaceous of the Iberian Ranges (Spain)

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### Abstract

A new species of the formerly monospecific genus *Nehvizdya* Hluštík, *Nehvizdya penalveri* sp. nov. is described from the Albian of the Escucha Formation (Eastern Iberian Ranges, Teruel, Spain). The type species *Nehvizdya obtusa* Hluštík was first found in the Lower–Middle Cenomanian Peruc Member of the Peruc–Korycany Formation (Bohemian Massif, Czech Republic). Both taxa closely resemble each other, not only in leaf shape and venation pattern, but also in their epidermal structures and the occurrence of resin bodies. The Spanish species, however, is notable for its marked amphistomatic leaves with stomatal apparatus, which have inner folds inside the stomatal pits. Comparison with *Eretmophyllum andegavense* Pons et al. from the Cenomanian of the Baugeois Clays (Maine-et-Loire, France) allows us to transfer this species to the genus *Nehvizdya* Hluštík. The new combination proposed is *Nehvizdya andegavense* (Pons et al.) comb. nov. A taphonomic analysis in this layer appears to characterise a biocoenosis formed from *N. penalveri* sp. nov. and *Frenelopsis alata* (K. Feistmantel) Knoblock. Similar associations have been described in the Czech and French Cenomanian. In all three cases, the associations grew around coastal lagoons and ponds where they formed a shrubby halophyte vegetation. © 2000 Elsevier Science B.V. All rights reserved.

**Keywords:** Albian; Ginkgoales; new species; Spain

### 1. Introduction

The gymnospermous leaf genus *Nehvizdya* Hluštík was until now known by only one species found in various places of the Cenomanian in the Peruc Member of the Peruc–Korycany Formation

(Velenovský, 1885; Hluštík, 1977; Uličný et al., 1997). *Nehvizdya obtusa* (Velenovský) Hluštík found in the Bohemian Massif (Czech Republic) was attributed to the Ginkgoales because of its *Ginkgo*-like ovules and megasporangiophores (cupules), the resin bodies inside the mesophyll of very thick leaves, as well as sharing several epidermal features in common (Hluštík, 1986). Hluštík considered *Nehvizdya* to be a distinct taxon of the extinct Ginkgoales, which formed part of the evolutionary lineage of the Glossophyllaceae *sensu* Tralau (1968), whereas according to Zhou (1997)

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the leaves of the *Eretmophyllum*-type which include the genus *Nehvizdya* were attributed to the family Karkeniaceae.

Leaf compressions were collected in clays intercalated with coarse, cross-bedded sands of the Lower Cretaceous of the Escucha Formation in the Lower to Middle Albian of the Rubielos de Mora (Teruel, Spain). Detailed morphological and anatomical studies conducted on the cuticles demonstrate that they actually belong to a second species of the same genus. The results presented here led us to a comparison and a subsequent re-examination of the *Eretmophyllum*-like leaves of *Eretmophyllum andegavense* Pons et al. (1976) from the Cenomanian of Anjou (Maine-et-Loire, France).

The leaves of *Nehvizdya penalveri* sp. nov. described here were more clearly amphistomatic than the French species *Eretmophyllum andegavense* and, furthermore, were quite unlike the strict hypostomatic leaves of the Czech species *Nehvizdya obtusa*. The stomatal structure of the Spanish material, lacking free and well-defined papillae inside the stomatal pits, closely resembles those of the Czech and the French cuticles. This characteristic clearly distinguishes them from the leaf species of the genus *Eretmophyllum* (Thomas) emend. Harris et al. As suggested by Pons (1979), Pons et al. (1980) and Hlušík (1980), and as demonstrated here with the new data from the Spanish material, *Eretmophyllum andegavense* should be formally transferred to the genus *Nehvizdya* Hlušík. Unlike Hlušík (1986), who subdivided the type species into two subspecies, *obtusa* and *andegavensis*, we consider the differences between the three taxa to be sufficient to raise them to the species level. Moreover, our point of view diverges from Kvaček (1999) who joined the both taxa *Nehvizdya obtusa* and *Eretmophyllum andegavense* within the genus *Eretmophyllum* considering that their stomatal structures were similar. However, the presence of free and well-defined papillae in *Eretmophyllum* and their absence in *Nehvizdya* enables distinction between both genera. Now, if we include the newly described species, the stratigraphic range of the genus extends from Lower–Middle Albian to Cenomanian.

The Spanish species as well as the species found

in the Czech Republic and France are associated with *Frenelopsis alata* (K. Feistmantel) Knobloch which has been identified as a shrubby halophyte plant (Uličný et al., 1997). *Nehvizdya penalveri* sp. nov. may have shared a similar habitat as indicated by sedimentological, taphonomic and palaeoecological data.

## 2. Geological and stratigraphical setting

The leaf-bed bearing *Nehvizdya penalveri* sp. nov. is found in the ravine known as El Paso, which flows into the stream Arroyo de la Pascueta, near the village Rubielos de Mora, Teruel Province, Spain. From the geological point of view the locality belongs to the northern margin of the Penyalgosa sub-basin (Fig. 1A and B). This is one of the Mesozoic sub-basins described by Salas and Guimerá (1997) in the Maestrat Basin. The Penyalgosa sub-basin is roughly triangular in shape and is bounded to the north-east by the Cedrillas Fault, whereas the south-western border is constituted by the south-western Iberian Chain threshold. The Mesozoic basins of the Iberian Ranges originated during the Late Oxfordian–Albian rifting cycle, which was linked to the opening of the North Atlantic sea-floor (Salas and Casas, 1993). During the Lower Cretaceous the sedimentation in the Iberian Basin (Iberian Ranges) was mainly formed by shallow marine and freshwater limestones and marls. However, during the Lower and Middle Albian, at the end of the rifting cycle, significant inputs of siliciclastics developed as a result of the formation of deltaic systems (Fig. 2). In the regional literature these systems are referred to as the Escucha Formation.

The series studied belongs to this formation and consists of up to 250 m of white, well-sorted and cross-bedded sands intercalated with grey clays and silts including abundant limonitic crusts. Lutites bear abundant plant remains (Fig. 3). The upper part of the series includes some calcareous oolitic bars. The top of the series is covered, in angular unconformity, by grainstones of the marine Cenomanian (Godoy et al., 1986). This stratigraphic log fits well within the vertical evolution and the stacking pattern of the Escucha

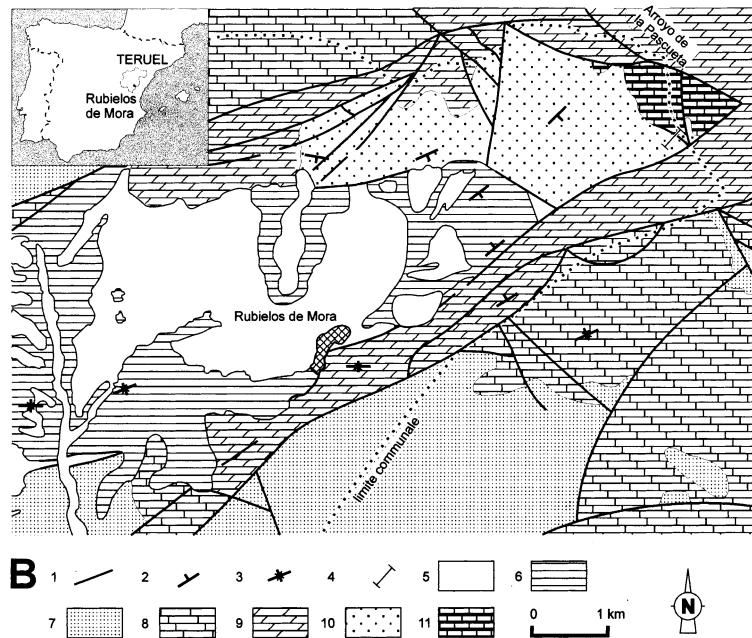
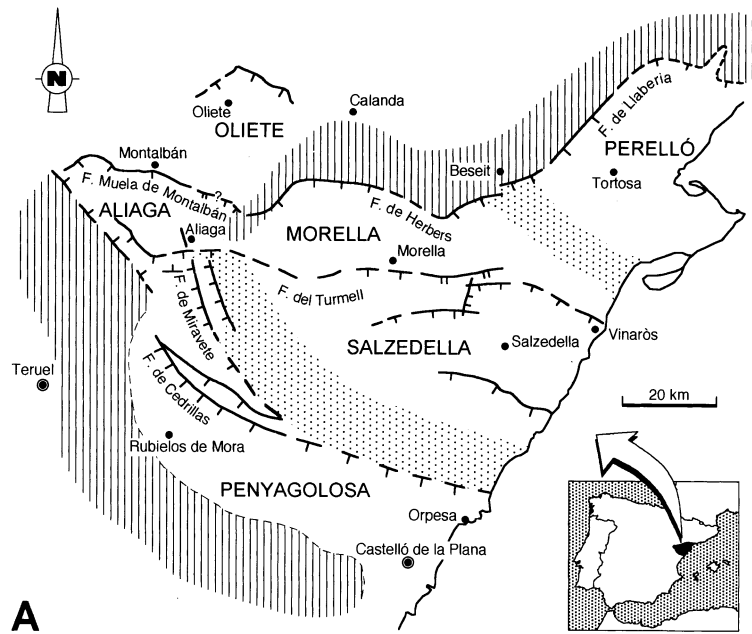


Fig. 1. (A) Situation of Rubielos de Mora in the Penyalgolesa Basin, Eastern Iberian Ranges. Basins are separated by lystric faults (F). Palaeogeographic thresholds are dotted. (B) Geological map of the area around Rubielos de Mora with location of the outcrop studied. Legend: 1, Major fault; 2, dip direction; 3, syncline; 4, studied section; 5, Quaternary; 6, Miocene; 7, Neocomian (Wealden facies); 8, Barremian limestones; 9, Aptian limestones and dolostones; 10, sands and lutites of the Escucha Formation; 11, Cenomanian limestones (modified from Godoy et al., 1986)

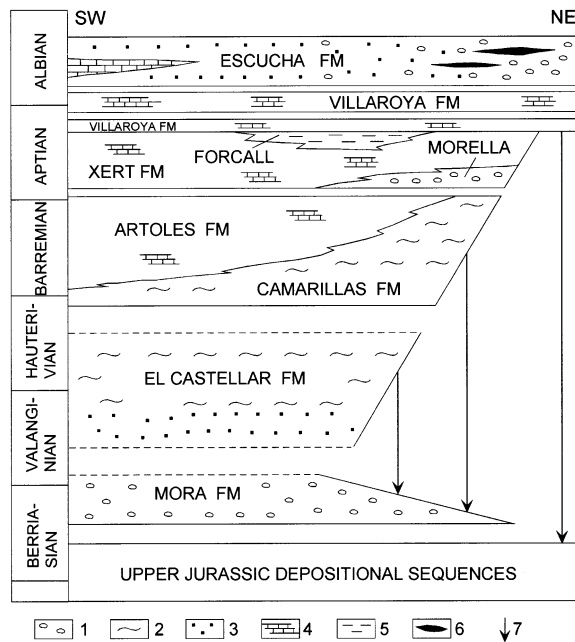


Fig. 2. Stratigraphic framework of the Lower Cretaceous Depositional Sequences in the Aliaga-Penyagolosa Subbasin showing the deposition of the Escucha Formation at the end of the Lower Cretaceous sedimentary cycle. Legend: 1, continental clastics; 2, Lacustrine limestones and marls; 3, deltaic, coastal and marine clastics; 4, shallow marine and transitional limestones and marls; 5, deeper marine marls and shales; 6, coals; 7, sedimentary gap (modified from Salas et al., 2000).

Formation as described by Querol (1990). The lower part of the series, formed by an alternation of white sandstones and grey lutites, corresponds to the basal progradation of the Escucha Fm. delta (Lowstand Systems Tract). The calcareous oolitic bars found in the central part of the series correspond to the marine incursion related to the Transgressive Systems Tract. Above these marine layers the series is once more formed by continental facies, which records the second progradation of the Escucha Fm. delta during the development of the Highstand Systems Tract. The Escucha Fm., which was deposited as a single depositional sequence during the rifting stage, is often found in angular unconformity below different units of the post-rift stage, including the Cenomanian. Martínez et al. (1993) attributed the Escucha Fm. to the Lower and Middle Albian according to the ammonite fauna found in the neighbouring

Morella sub-basin. In the series of El Paso-Arroyo de la Pascueta the formation appears to have the same age according to the presence of *Mesorbitolina* gr. *subconca* (LEYMERIE) at 150 m above the base (R. Schroeder, personal communication).

From a sedimentological point of view, the series records an interaction between the lower delta plain and the delta front in the vicinity of Rubielos de Mora. Sandy layers and the oolitic limestones at the top of the series correspond to tidal sand bar progradation sequences described by Querol et al. (1992) in the delta front of the Escucha Fm. The lutitic intervals, bearing plant remains and including the leaf-bed studied, correspond to brackish water swamp sequences of the lower delta plain as described by the same authors. The presence of mixed marine and freshwater algae, that is, zygnetalean spores and marine dinocysts respectively, in the leaf-bed (N. Solé de Porta, personal communication) confirms that these swamps received marine and freshwater inputs. These data supply significant palaeo-environmental information to the palaeoecology of the new species *Nehvizdya penalveri*.

### 3. Material and methods

Plant remains are dominated by *Sciadopitys*-like leaves (ex. *Pseudocycas* Gomez et al., 1999), *Frenelopsis* (Coniferales) and *Nehvizdya* (Ginkgoales). These authors also mentioned a number of other conifer leaves, including *Pagiophyllum*, male cones of *Classostrobus* and the wood *Agathoxylon*. New field-collections and light microscope preparations have recently revealed the occurrence of *Weichselia reticulata* (Matoniaceae) and *Pseudotorellia* (Coniferales?) (unpublished data).

Cuticles were obtained by bulk maceration in hydrogen peroxide ( $H_2O_2$ ) followed by washing in water through a fine mesh sieve (0.5 mm). After sorting under the microscope, isolated cuticles were macerated in Schulze's solution [the duration depending on the degree of carbonisation and preservation; cf. Kerp (1990)]. The products of oxidation were rinsed with water and neutralised

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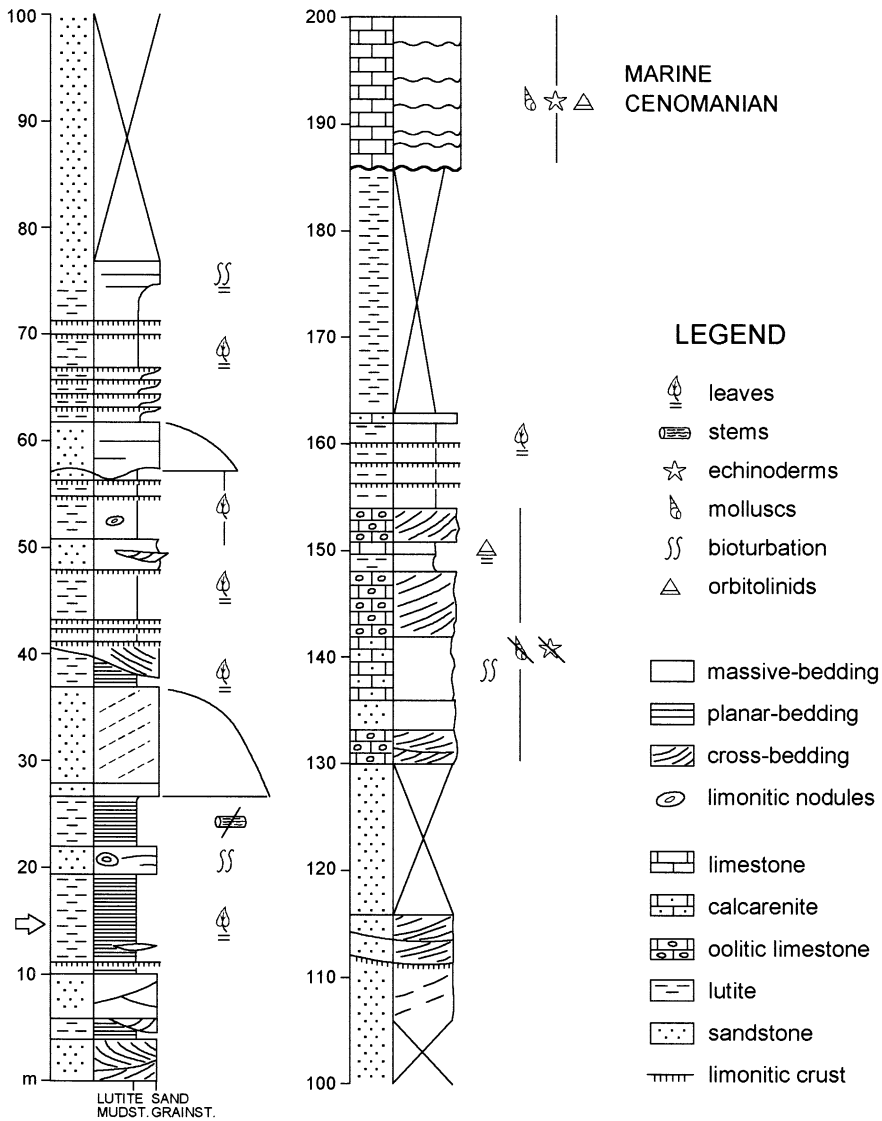


Fig. 3. Stratigraphic log of the siliciclastic series probably belonging to the Escucha Formation near Rubielos de Mora, leaf-bed studied marked with an arrow.

in a diluted solution of ammonia (3%). It was sometimes necessary to use hydrofluoric acid (HF) to eliminate siliceous remnants. Then the abaxial and adaxial cuticles were separated and mounted on glass slides for light microscope preparations in glycerine. A few specimens were stained with

safranine before mounting, and others were prepared for electron microscopy. Specimens for light microscopy (LM) were observed with a Leitz Aristoplan microscope. Photomicrographs were taken with a Wild Photoautomat MPS 45-51S, in the Université Claude Bernard Lyon-1,

Villeurbanne (Rhône, France). Samples for scanning electron microscopy (SEM) were coated with 100% gold and observed with a Hitachi S2300 SEM instrument in the Serveis Científico-Tècnics of the University of Barcelona.

The material will be housed in the collections of the Museo Paleontológico de Zaragoza (Zaragoza, Spain).

#### 4. Taxonomy

Order: GINKGOALES

Family: KARKENIACEAE Krassilov (1970, p. 18)

Form-genus: *Nehvizdya* Hlušík, 1977

**Type species:** *Nehvizdya obtusa* (Velenovský) Hlušík, 1977

*Original diagnosis* of *Nehvizdya* Hlušík, 1977:

Coriaceous oblanceolate single leaves with petiolar base and round apex. Veins dichotomously branched forming longitudinal parallel venation in the leaf lamina, slightly convergent in the apex. Epidermal cells polygonal, heavily cutinised. Stomata of haplocheilic type, sunken, evenly distributed between veins. Guard cells in stomatal pits forming irregularly orientated stomatal apertures (Hlušík, 1977, p. 174).

*Emended diagnosis* of *Nehvizdya* Hlušík, 1977 emend. Gomez: Single leaves, coriaceous, oblanceolate to lanceolate, straight or S-shaped to sickle shaped; rather long petiolar tapering base; retuse, rounded or mucronate apices; entire slightly undulating margins. Venation dichotomously branched in several dichotomies with narrow angle from one or two veins at the base; regularly spaced and forming longitudinal parallel venation towards the top of the lamina; veins, more or less parallel in the proximal and middle parts, slightly converging to the centre or the apex and ending without fusing just before the apical margin. Leaves hypostomatic to amphistomatic. Stomata of the haplocheilic type, monocyclic or incompletely dicyclic; subsidiary cells without free and well-developed papillae but with inner folds of the outer periclinal walls inside the stomatal pits, often partly overhanging

the guard cells; subsidiary cells forming an elevated rim around the stomatal pits and projecting above the cuticle surface; guard cells sunken and symmetrically arranged; stomatal apertures irregularly oriented; heavily cutinised epidermal cells. Short round, oval or spindle-shaped resin bodies in the mesophyll.

*Remarks:* The status of the type-species of *Nehvizdya*, *Nehvizdya obtusa* Hlušík, was recently discussed by Kvaček (1999) who included this genus and *Euryspatha* Prinada within the genus *Eretmophyllum* Thomas emend. Harris et al. (1974). We disagree with this synonymisation since *Nehvizdya* lacks free and well-defined papillae, which is a character found in *Eretmophyllum*. Although the latter observation is not considered in the usual diagnosis of *Eretmophyllum*, all authors who studied Jurassic–Lowermost Cretaceous species of this latter genus pointed out the constancy of papillate stomata. In order to clear this difference between the leaves of *Nehvizdya* and *Eretmophyllum*, we discuss the status of *Eretmophyllum* and emend the diagnosis given by Harris et al. (1974).

*Nehvizdya penalveri* Gomez, sp. nov. (Plate I, 1–9; Plate II, 1–8; Plate III, 1–8; Fig. 4)

*Synonymy:* 1999, *Nehvizdya* sp. — Gomez et al. (1999, Fig. 15).

*Material and repository:* Light microscope slide numbers. MPZ 99/144–MPZ 99/149. Scanning electron microscope stub numbers MPZ 99/150 and MPZ 99/151 deposited in the Museo Paleontológico de Zaragoza (Zaragoza, Spain).

*Holotype:* Light microscope slide: No. MPZ 99/144.

*Paratypes:* Scanning electron microscope stubs: No. MPZ 99/150–MPZ 99/151.

*Type locality:* Arroyo de la Pascueta, Rubielos de Mora, Teruel, Eastern Iberian Ranges, Spain (Fig. 1).

*Stratigraphic horizon:* Organic clays of the Escucha Formation (Lower to Middle Albian) arrowed in Fig. 3.

*Derivation of name:* The name refers to Mr. Enrique Peñalver (University of València) who discovered the layer bearing the plant cuticles in Rubielos de Mora.

**Diagnosis:** Narrowly oblanceolate to lanceolate leaves of *Nehvizdya*, straight to slightly bent; total length exceeding 4.5 cm and about 1 cm in width. Venation commonly from two parallel veins in the petiole and usually from six to ten in the wider part of the lamina. Amphistomatic leaves with stomata dispersed in the adaxial cuticle and between the veins in the abaxial cuticle; greater stomatal density in the abaxial cuticle; stoma surrounded by four to seven subsidiary cells and bearing inner folds inside the stomatal pits without free and well-defined papillae; epidermal cells, rather more rectangular and arranged in longitudinal rows above the veins in the abaxial cuticle, polygonal or more or less isodiametric; anticlinal walls straight or slightly curved with blunt corners and without thickenings. Trichomes absent.

**Description:** The leaf shape is narrowly oblanceolate to lanceolate, nearly straight or slightly bent (S-shaped). The maximum length measures >47 mm. The width is generally between 8 and 12 mm but can reach up to 19 mm. The base is progressively tapered to form a narrow-ended petiole (Plates I, 4,6; II, 1). This petiolar tapering

base is quite long compared to the total leaf length. The apices are retuse, rounded or mucronate to appendiculate (Plates I, 1,2; II, 1, Fig. 4). The wide range of shapes is not the result of fungal or animal damage and subsequent healing, but due solely to ontogenetic variations in leaf growth. The leaf outlines are entire but have asymmetrically waved edges forming very flat lobes.

The venation is visible in the naturally translucent leaf cuticles even before hydrogen peroxide ( $H_2O_2$ ) extraction or Schulze's solution action but is clearer after treatment. One or two parallel veins arise from the petiole and initially branch dichotomously into four veins (Plate I, 4–6). There are from two to five orders of dichotomy and most occur in the lower two thirds of the blade (Plate I, 3). The dichotomies form narrow angles. Subsequently, the branching continues more or less symmetrically to the tip of the lamina (Plate I, 2). The veins are most abundant near the maximal width of the blade, their number being proportionally related to the width of the lamina (usually six to ten). The maximal vein number observed is 19 in the widest (19 mm) lamina. The width of the

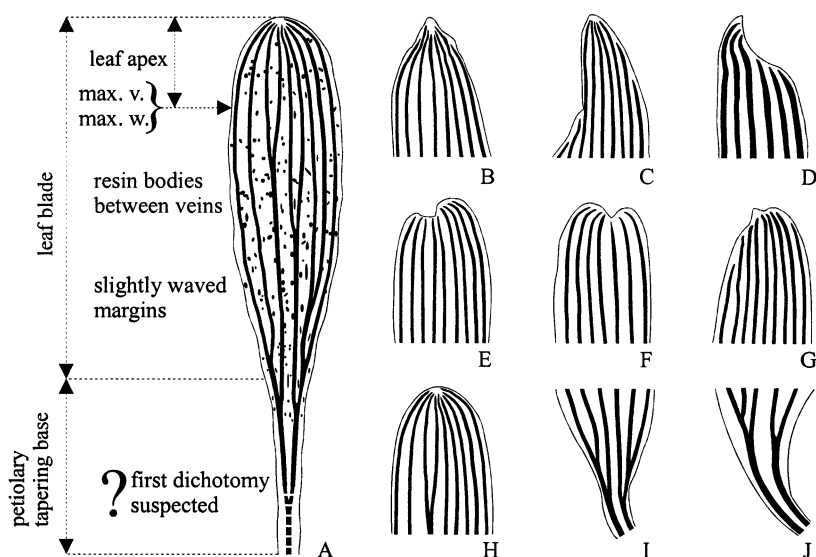
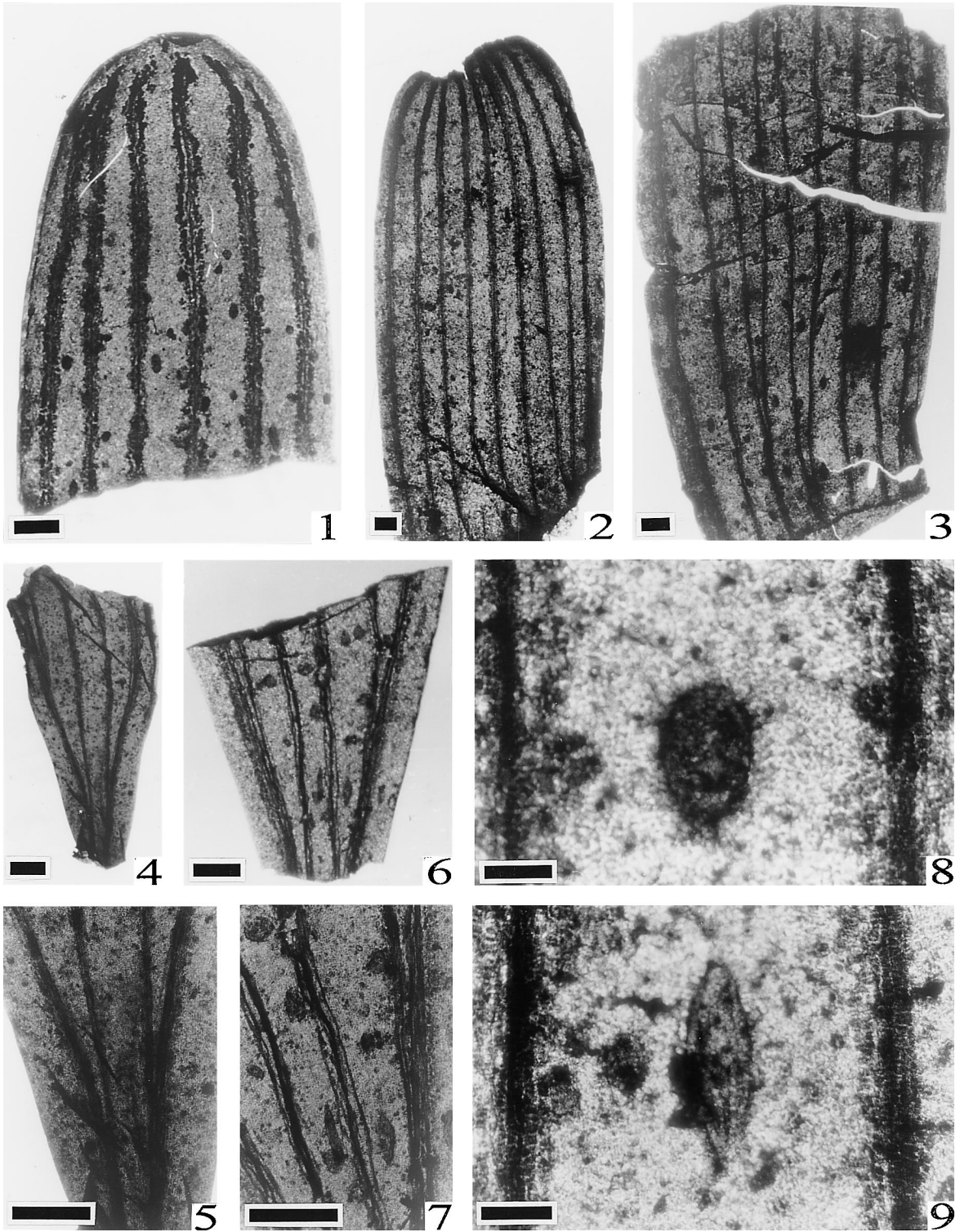


Fig. 4. (A) Reconstruction of the lamina of *Nehvizdya penalveri* sp. nov. showing its main morphological features, pattern of narrowly dichotomising veins and resin bodies (based on all the material): max. v., maximal number of veins; max. w., maximal width of the blade. Variability of shapes and venation in the apices. (B–G, cases more rarely observed; H, average case observed) and in the petiolar tapering bases (I and J). Magnification: ca.  $\times 1.8$  (A–H); ca.  $\times 2.7$  (I and J).

PLATE I





veins ranges from 0.1 to 0.3 mm and they are regularly spaced, from 0.10 to 0.15 mm apart, forming longitudinal parallel venation along most of the length of the lamina. The venation is prominent upon the lower side of the lamina. There is no evidence of secondary venation. The veins are largely parallel in the upper part of the leaf and all curve inwards to the centre of the leaf and symmetrically converge to the centre of the normally rounded tip (Plate I, 1,2). When the apex is retuse, the veins tend to follow the leaf margins and curve inwards to the neck between the two lobes. In divided leaves, where the lobes are well marked, the veins end at regular intervals in the lobe margins. In one particular specimen with an appendiculate apex, the three left veins extended to the claw-shaped or hook-shaped tips, as in the latter case. Nevertheless, the veins always terminate just before the apical margins.

A reconstruction of the shape and the venation of *Nehvizdya penalveri* sp. nov. is shown in Fig. 4.

The leaf epidermis is heavily cutinised and the epidermal cells are polygonal, in the main isodiametric, and two to three times longer than they are wide (Plate II, 5,6). Above the veins, the abaxial epidermal cells are arranged in rows usually elongated in the longitudinal direction (Plate III, 1). The length of these cells varies from 25 to 60  $\mu\text{m}$  and the width from 20 to 30  $\mu\text{m}$ . Elsewhere, between the stomata in areas between

the veins or in the adaxial epidermis, the cells are arranged in a pavement pattern without preferential direction of the elongation (discontinuous longitudinal wedge-shaped rows). The cell size varies from 20 to 70  $\mu\text{m}$ . The anticlinal walls are straight or slightly curved with blunt corners and show no thickening. The thickness of the anticlinal walls varies from 2 to 6  $\mu\text{m}$  on both abaxial and adaxial cuticles.

The leaves are amphistomatic and the stomata are scattered in areas between the veins of the abaxial side and in the whole cuticle of the adaxial side (Plate II, 5,6). The stomatal density of the abaxial cuticle is higher than the adaxial, 17–20 and 7–9  $\text{mm}^{-2}$ , respectively (stomatal index: 2.5–2.9 versus 1.0–1.3). The stomata are haplocheilic in type and are monocyclic or incompletely dicyclic (Plate II, 7,8). The stomatal pits have a round or slightly oval shape (Plate III, 3,4,7,8) and measure 15–27  $\mu\text{m}$  long and 11–19  $\mu\text{m}$  wide. The stoma is surrounded by four to seven subsidiary cells (Plates II, 7,8; III, 5,6) and the diameter of the stomatal apparatus varies from 50 to 85  $\mu\text{m}$ . The subsidiary cells are strongly cutinised and show inner folds of outer periclinal walls which partly overhang the guard cells (Plate III, 3,4,7,8). The subsidiary cells are also prominent outward, forming an asymmetrically elevated rim around the stomatal pits and slightly above the cuticle surface but lack free and well-defined papillae (Plate III, 3). The size and

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#### PLATE I

Morphological features, venation, resin bodies of *Nehvizdya penalveri* sp. nov.

- 1 Rounded leaf apex showing six veins curved inwards to the centre. Some resin bodies are present in the mesophyll between the veins. LM No. MPZ 99/147. Scale bar = 1 mm.
- 2 Asymmetrical retuse apex showing nine veins curved inwards following the lobes. The venation is strictly parallel in the mid-blade. LM No. MPZ 99/148. Scale bar = 1 mm.
- 3 Mid-lamina part with veins dichotomising at different levels. Some resin bodies are also visible in the mesophyll. LM No. MPZ 99/146. Scale bar = 1 mm.
- 4 Petiolarly tapering base where two parallel veins arise and initially branch dichotomously into four veins at the same level. The vein further to the left shows a second dichotomy. LM No. MPZ 99/145. Scale bar = 1 mm.
- 5 First dichotomy in the petiolarly tapering base (detail of Fig. 4). LM No. MPZ 99/145. Scale bar = 1 mm.
- 6 Petiolarly tapering base presenting a dichotomy of the most external veins only, with six veins at the top of the fragmented leaf. Round, oval and spindle-shaped resin bodies can also be discerned. LM No. MPZ 99/145. Scale bar = 1 mm.
- 7 Round, oval and spindle-shaped resin bodies located between the veins in the mesophyll (detail of Fig. 6). LM No. MPZ 99/145. Scale bar = 1 mm.
- 8 Oval-shaped resin body positioned parallel to the veins. LM No. MPZ 99/145. Scale bar = 200  $\mu\text{m}$ .
- 9 Spindle-shaped resin body positioned parallel to the veins (detail of Fig. 7). LM No. MPZ 99/145. Scale bar = 200  $\mu\text{m}$ .

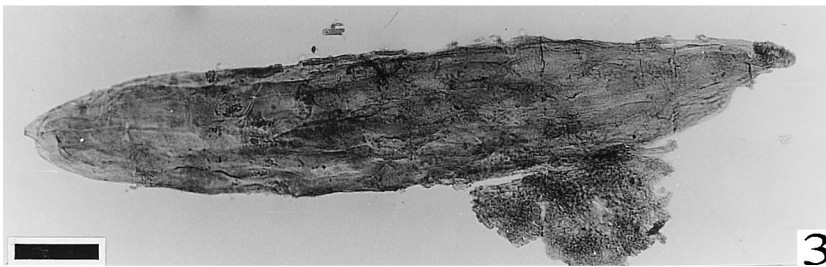
PLATE II



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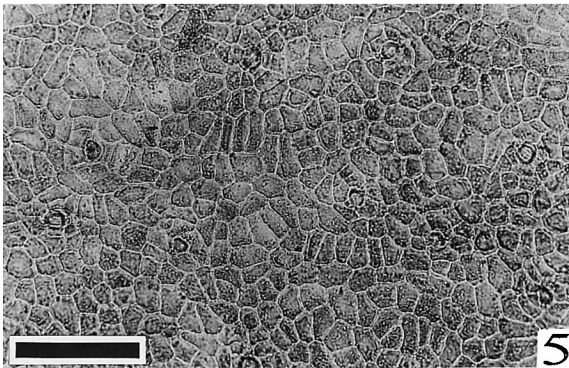
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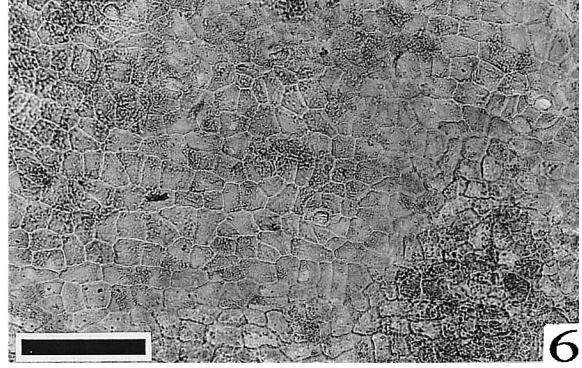
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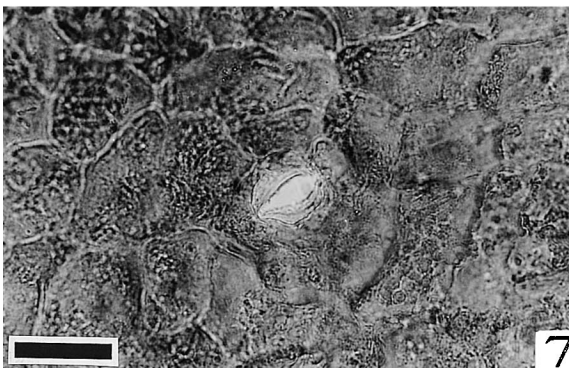
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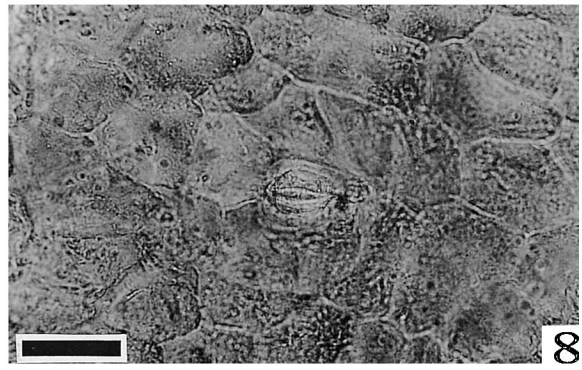
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7



8

the shape of the subsidiary cells are similar to those of the ordinary epidermal cells. The slightly cutinised guard cells are symmetrically arranged and are sunken in the stomatal pits. The guard cells are elongated and the tips have small, horn-like projections (Plate III, 5,6). The length of each guard cell varies from 20 to 50  $\mu\text{m}$  and their width from 8 to 15  $\mu\text{m}$ . The stomatal aperture is irregularly oriented (Plate II, 5,6) and is 16–24  $\mu\text{m}$  long and 4–9  $\mu\text{m}$  wide.

No trichomes were observed. Small, flattened, globular to spindle-shaped resin bodies were seen in the mesophyll (Plates I, 1,3,6–9; II, 2–4). They were resistant to the hydrogen peroxide and Schulze's macerations and were most probably composed of a cutin-like matrix. The round and oval-shaped resin bodies vary from 50 to 300  $\mu\text{m}$  long and from 50 to 200  $\mu\text{m}$  wide. The length of the spindle-shaped resin bodies measures up to 900  $\mu\text{m}$ . Resin bodies have no direct connection with stomatal openings.

*Comparison with related fossil taxa:* Hluštík (1977, 1980, 1986) considered the genus *Nehvizdya* to be a distinct taxon of the extinct Ginkgoales. The new material from Spain sharing the same stomatal structure as *Nehvizdya*, with inner folds and without papillae, unlike *Eretmophyllum*, reinforces Hluštík's position that *Nehvizdya* represents an useful morphological type or even natural genus. The megasporangiophores (cupulae), arising from very short petiole-like projections and bearing globular, slightly pointed ovules (seeds),

were analogous to those of *Ginkgo* and proved to be related to the type species leaves of *Nehvizdya obtusa* (Velenovský) Hluštík. Hluštík included *Nehvizdya* within the Glossophyllaceae [Division 3 after Tralau (1968)] near the species *Glossophyllum florinii* Kräusel and different species of the genus *Eretmophyllum* Thomas. The classification proposed by Tralau (1968) was based, however, entirely on leaf genera. So far, no reproductive organs have been found in connection with the *Eretmophyllum*- and *Glossophyllum*-type leaves. A recent parsimonious cladogram was proposed on the basis of the best preserved taxa, including eight well-defined female reproductive organs as well as vegetative organs (Zhou, 1991, 1997, Fig. 1 and Table 2). This analysis resulted in the distinction of six families of Ginkgoales. The non-homogeneous leaves of the *Eretmophyllum*-type (Zhou, 1997, Table 1) were associated with *Sphenobaiera*- and *Ginkgoites*-types and altogether attributed to the family Karkeniaceae Krassilov. According to Zhou and Zhang (1989) this family became extinct during Late Mesozoic. The *Karkenia* lineage appears to represent a distinct lineage and is much nearer to the Palaeozoic representative *Trichopitys* than all other Mesozoic ginkgoaleans (Zhou, 1997), whereas the phylogenetic relationships of *Glossophyllum* are poorly known (Dobruskina, 1980). The general trend towards planation, webbing and fusion of telomes and mesomes observed in Ginkgoales (Zhou, 1991) may have led to the tongue-shaped leaves of *Eretmophyllum* and

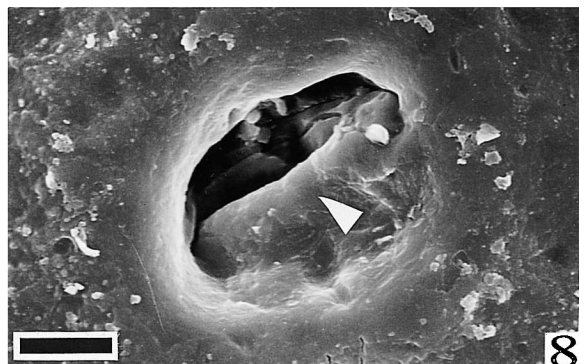
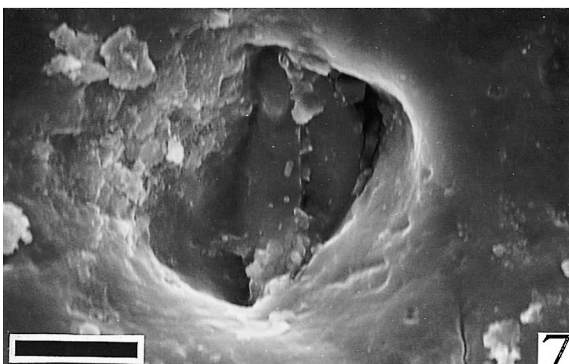
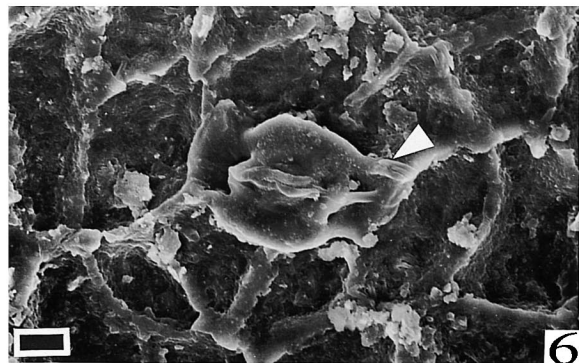
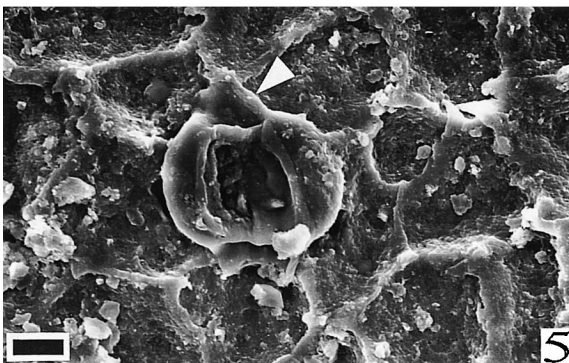
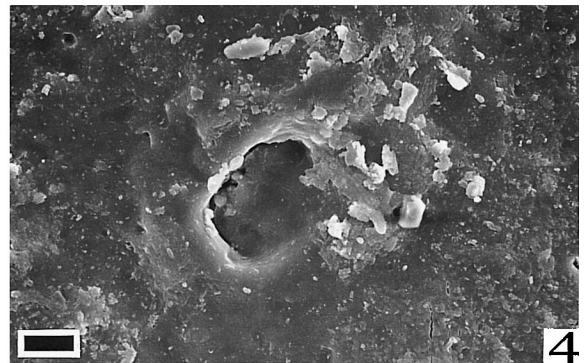
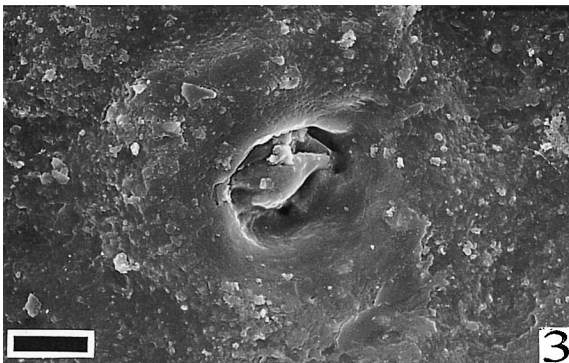
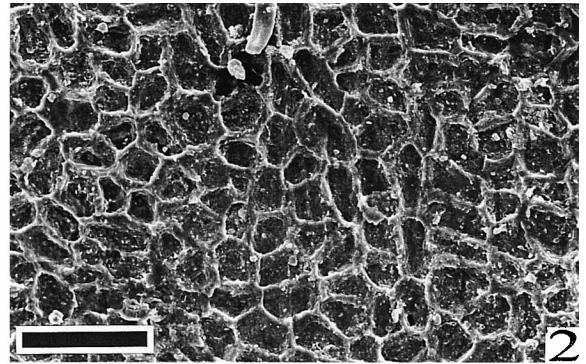
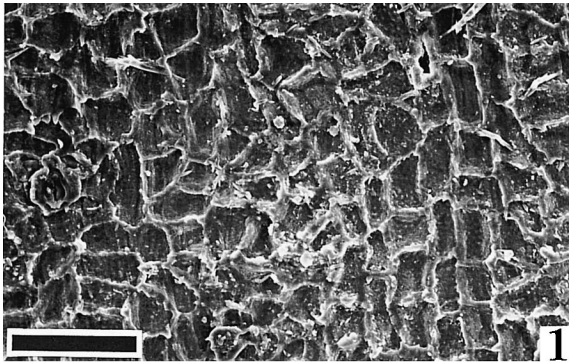
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## PLATE II

Light microscopy: epidermal features and resin bodies of *Nehvizdya penalveri* sp. nov.

- 1 Two entire leaves showing petiolarly cunate bases and oblanceolate or obovate blades. Holotype is the leaf in the lower part. LM No. MPZ 99/144. Scale bar = 5 mm.
- 2 Oval-shaped resin body. LM No. MPZ 99/149. Scale bar = 100  $\mu\text{m}$ .
- 3 Spindle-shaped resin body. LM No. MPZ 99/149. Scale bar = 100  $\mu\text{m}$ .
- 4 Round-shaped resin body. LM No. MPZ 99/149. Scale bar = 50  $\mu\text{m}$ .
- 5 General view of the abaxial cuticle showing the pavement arrangement of the epidermal cells, stomata dispersed with randomly oriented stomatal apertures, and higher stomatal density than that of the adaxial cuticle. LM No. MPZ 99/149. Scale bar = 500  $\mu\text{m}$ .
- 6 General view of the adaxial cuticle showing the pavement arrangement of the epidermal cells, stomata dispersed with randomly oriented stomatal apertures, and lower stomatal density than that of the abaxial cuticle. LM No. MPZ 99/149. Scale bar = 500  $\mu\text{m}$ .
- 7 Close stoma surrounded by six subsidiary cells from the abaxial cuticle. LM No. MPZ 99/149. Scale bar = 100  $\mu\text{m}$ .
- 8 Open stoma surrounded by five subsidiary cells from the adaxial cuticle (detail of Fig. 6). LM No. MPZ 99/149. Scale bar = 100  $\mu\text{m}$ .

PLATE III



*Nehvizdya*. Further collection and studies are needed to elucidate the nature of reproductive organs of *Nehvizdya*. However, a number of characters point towards ginkgoalian affinity. Thus, veins ending separately in the distal margin of segments, lysigenous resin bodies between veins throughout the length of the lamina, general shape and cuticular structures are characters shared by other Ginkgoales.

A number of the characters of *Nehvizdya*, such as its separated coriaceous leaves with oblanceolate shape, entire margin, petiolar base, round apex and venation longitudinally parallel, dichotomously branched and convergent in the apex, have been described in several Mesozoic genera.

The described species resembles isolated lobes of *Ginkgoites dilatata* (Heer) Teixeira from the Jurassic of Portugal (Heer, 1881; Teixeira, 1948). These, though, are only segments of deeply lobed leaf blades. The leaves also differ from *Ginkgodium* in that the latter has interstitial veins (Hlušík, 1977).

The genera *Torellia* Heer and *Pseudotorellia* (Florin) emend. Bose & Manum have certain features in common with the species studied, such as the oblanceolate leaves and venation pattern. Differences between the former genera and the new species include wavy walls of epidermal cells, delicate cutinisation and stomatal distribution.

*Torellia* bears leaves attached to deciduous leafy shoots (Heer, 1870). These differ from those of *Pseudotorellia* which are found separated in the sediments (Florin, 1936) like those of *Nehvizdya*. Epidermal features of *Torellia* include hypostomy, epidermal cells with highly papillous periclinal walls, stomatal apparatus with papillous subsidiary cells and low cutinised guard cells, whereas *Pseudotorellia* has strict hypostomy with stomatal strips between narrower, non-stomatal longitudinal rows (Lundblad, 1957). Also, the stomatal apertures of *Pseudotorellia* are always oriented regularly and longitudinally and some species have resin canals (Watson and Harrison, 1998). In contrast to these genera, the material of Rubielos de Mora has amphistomatic leaves with stomata distributed evenly in both abaxial and adaxial cuticles, irregularly oriented stomatal apertures and resin bodies.

The new species may be easily distinguished from *Culgoweria* Florin and *Windwardia* Florin by the arrangement of stomata on the leaf cuticle. Whereas these genera show stomatal rows or strips on both cuticles, *Nehvizdya*'s stomata are scattered throughout the entire leaf epidermis.

*Glossophyllum florinii* Kräusel from the Upper Triassic Lunzer Beds (Keuper) in Austria was distinguished from other representatives of Ginkgoales, such as the Ginkgoaceae and the

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### PLATE III

Scanning electron micrographs of *Nehvizdya penalveri* sp. nov.

- 1 Inner view of the abaxial cuticle with dispersed stomata and with polygonal or largely isodiametric epidermal cells, sometimes arranged in longitudinal rows. Stub No. MPZ 99/151. Scale bar = 100  $\mu\text{m}$ .
- 2 Inner view of the adaxial cuticle with rare stomata and with polygonal or largely isodiametric epidermal cells. Stub No. MPZ 99/150. Scale bar = 100  $\mu\text{m}$ .
- 3 Outer view of the abaxial cuticle with a stoma showing rim elevation around the closed stomatal pit. Stub No. MPZ 99/150. Scale bar = 10  $\mu\text{m}$ .
- 4 Outer view of the adaxial cuticle with a stoma showing rim elevation around the stomatal pit. Stub No. MPZ 99/150. Scale bar = 10  $\mu\text{m}$ .
- 5 Inner view of the abaxial cuticle with an open stoma with 6 subsidiary cells and elongated guard cells symmetrically arranged with one of the small, horn-like projection ends arrowed. Stub No. MPZ 99/151. Scale bar = 10  $\mu\text{m}$ .
- 6 Inner view of the adaxial cuticle with a closed stoma with six subsidiary cells and elongated guard cells symmetrically arranged with one of the small, horn-like projection ends arrowed. Stub No. MPZ 99/151. Scale bar = 10  $\mu\text{m}$ .
- 7 Outer view of the abaxial cuticle with a closed stoma with slightly marked folds inside the stomatal pit. Stub No. MPZ 99/151. Scale bar = 10  $\mu\text{m}$ .
- 8 Outer view of the adaxial cuticle with a opened stoma with prominent fold arrowed inside the stomatal pit. Stub No. MPZ 99/150. Scale bar = 10  $\mu\text{m}$ .

Sphenobaieraceae, and assigned to the family Glossophyllaceae by Tralau (1968) and Dobruskina (1998), whereas Meyen (1984) included this latter family in the order Peltaspermales (pteridosperms). The Triassic species resembles *Nehvizdya penalveri* nov. sp. especially in leaf-shape (petiolar base, dichotomous venation), cuticle structure (amphistomatic character) and occurrence of resin bodies. Nevertheless, the former species differs from our material by having longer falcate leaves, stomata in rows with massive papillae distinctly overhanging the guard cells (Kräusel, 1943), higher stomatal density on both cuticles, epidermal cells on both cuticles with well-developed papillae, and elongated epidermal cells on the abaxial cuticle which are often arranged in longitudinal rows parallel to veins (Dobruskina, 1998).

*Eretmoglossa lacasae* Barale (1981) from Berriasian–Valanginian of El Montsec (Pyrenees, Spain) is similarly characterised by entire, tongue-shaped leaves with symmetrical or slightly falcate and rounded apices. These leaves, however, are widest near the top, whereas *Nehvizdya penalveri* sp. nov. does have a maximum width at variable levels of the lamina. There are probably two veins in the proximal part of the *Eretmoglossa* leaf, dichotomising and ending separately at the apical margin. The Montsec's ginkgoalian leafy shoots also contain oval or round resin bodies, which in this species, are more abundant towards the base of the leaves and present in the leaf cushion. Although both Spanish leaf species are amphistomatic, *Eretmoglossa lacasae* differs from *N. penalveri* sp. nov. by alternating stomatal and non-stomatal strips on both sides of the cuticle, stomata with small papillae, and papillate epidermal cells (Barale, 1991, 1995).

Amphistomy also characterises the ginkgoalean leaf *Eretmophyllum* (Thomas) emend. Harris et al., though Gomolitzky (1987) included the strictly hypostomatic leaf, *Eretmophyllum harrisii* from the Jurassic of Middle Asia, as a member of the genus. The genus *Eretmophyllum* is considered to have been predominantly a Jurassic–Lowermost Cretaceous type of Mesozoic Ginkgoales. Both the species of *Eretmophyllum* and *Nehvizdya penalveri*

sp. nov. have similar epidermal cell forms (built without undulate walls) and similar stomatal structure (radially arranged subsidiary cells around the stomatal pits). The cuticles of the species of *Eretmophyllum*, however, are not as thick, do not always have inner folds inside the stomatal pits and bear clearly free and well-defined papillae (e.g. Harris et al., 1974; Gomolitzky, 1987; Thévenard, 1992).

The resin bodies of *Nehvizdya* resemble secretory tracts as they are known in *Eretmophyllum* and in the extant *Ginkgo biloba* L. The spindle-shaped bodies have a similar shape to *G. biloba* being embedded within the mesophyll and oriented parallel to the blade venation.

*Discussion:* (a) Status of the type-species of *Nehvizdya*

Kvaček (1999) discussed the validity of the genus *Nehvizdya* Hluštík and synonymised *Nehvizdya* with *Eretmophyllum* Thomas emend. Harris et al. (1974) on the basis of overall stomatal similarity. In our opinion such a procedure is not justified since *Nehvizdya obtusa*, the type species of genus *Nehvizdya*, as well as *Eretmophyllum andegavense* and *Nehvizdya penalveri* lack free and well-defined papillae inside the stomatal pits, unlike other species of genus *Eretmophyllum*. As a matter of fact all Jurassic–Lowermost Cretaceous species of *Eretmophyllum* bear such papillae. Although this character is not indicated in the diagnosis of the genus it may be noticed in the descriptions and plates supplied by a number of authors such as Harris et al. (1974), Gomolitzky (1987) or Thévenard (1992). On the other hand, the absence of papillae is observed in the information available from *E. andegavense* and *N. obtusa* by Hluštík (1977, 1986), Pons et al. (1976), Pons and Vozenin-Serra (1992) and Kvaček (1999, Plate 10 and p. 20). In consequence it seems necessary to keep the distinction between *Nehvizdya* and *Eretmophyllum* on the basis of the presence or absence of papillae in stomatal pits.

Female reproductive organs are the basis of recent plant systematics. This kind of systematic assessment is difficult to achieve in the fossil record which only exceptionally bears reproductive female organs. Therefore, rather than being based on

reproductive characters, the classifications of Mesozoic gymnosperms are based on vegetative features (e.g. Stewart and Rothwell, 1993, p. 413). Such features are the cuticle characters, the stomatal arrangement or the presence/absence and density of papillae. On the other hand in modern plants the presence of papillae is known to be extremely variable and such a variation has been also demonstrated in fossil material (e.g. Watson, 1977). Evidence indicates that the presence or absence of papillae is a strong diagnostic character to separate *Nehvizdya* from *Eretmophyllum*. Free and well-defined papillae are constant in all species of *Eretmophyllum* and even in the two Lowermost Cretaceous representatives of the genus (Table 1). Although the size of papillae shows intraspecific and interspecific variation in *Eretmophyllum*, these variations never lead to the complete absence of papillae in the stomata of the blade. In the same way, the amphistomatic taxa of *Eretmophyllum* do not show preferential absence of papillae on one side of the blade and the length of the papillae on the two faces is similar. All these observations indicate that the character ‘presence of papillae’ in genus *Eretmophyllum* is not ecophenotypically determined and represents rather a specific character. *Nehvizdya* was in contrast with *Eretmophyllum* because Czech, French and Spanish specimens lack free and well-defined papillae when observed under the light microscope and scanning electron microscope. In order to allow a clear distinction of the Jurassic–Lowermost Cretaceous genus *Eretmophyllum* from the Albian–Cenomanian (‘Middle’ Cretaceous) genus *Nehvizdya* clearer, we propose a slight emendation of genus.

Form-genus: *Eretmophyllum* Harris et al., 1974

Type species: *Eretmophyllum pubescens* Thomas, 1913

*Original diagnosis* of *Eretmophyllum* Harris et al., 1974: Leaf shed individually by abscission at base of petiole. Leaf entire, oblanceolate to almost linear, symmetrical or slightly falcate. Apex wavy, or retuse, or obtuse or rounded, sometimes asymmetrical. Lamina gradually narrowing below and merging with petiole. Margins of lamina at leaf

base often thickened. Veins distant, dichotomising in basal portion of lamina, parallel above but converging slightly near apex. Veins ending separately at apical margin. Round to spindle-shaped resin bodies often present.

Cuticle amphistomatic or with stomata mostly confined to lower side. Epidermal cells quadrate or polygonal, with straight or wavy anticlinal walls, surface walls flat or with median thickening or papilla. Unicellular trichomes sometimes present. Lower cuticle showing stomatal and non-stomatal strips. Stomata in stomatal strips scattered or arranged in longitudinal rows. Guard cells thinly cutinised, surrounded by ring of regularly arranged haplocheilic subsidiary cells.

*Emended diagnosis* of *Eretmophyllum* Harris et al., 1974 emend. Gomez: Leaf shed individually by abscission at base of petiole. Leaf entire, oblanceolate to almost linear, symmetrical or slightly falcate. Apex wavy, or retuse, or obtuse or rounded, sometimes asymmetrical. Lamina gradually narrowing below and merging with petiole. Margins of lamina at leaf base often thickened. Veins distant, dichotomising in basal portion of lamina, parallel above but converging slightly near apex. Veins ending separately at apical margin. Round to spindle-shaped resin bodies often present.

Cuticle amphistomatic to hypostomatic. Epidermal cells quadrate or polygonal, with straight or wavy anticlinal walls, surface walls flat or with median thickening or papilla. Unicellular trichomes sometimes present. Lower cuticle showing stomatal and non-stomatal strips. Papillate stomata in stomatal strips scattered or arranged in longitudinal rows. Guard cells thinly cutinised, surrounded by ring of regularly arranged haplocheilic subsidiary cells.

(b) Taxonomic relationships of *Nehvizdya penalveri* sp. nov. and *Nehvizdya obtusa* Hluštík

A number of characters of *Nehvizdya penalveri* nov. sp. correspond to those described for genus *Nehvizdya* Hluštík. These characters include a thick cuticle, the shape and distribution of epidermal cells, the stomatal distribution, stomata of the haplocheilic type, guard cells in deep stomatal pits forming irregularly oriented stomatal apertures and inner folds of periclinal walls of subsidiary

Table 1  
Comparison of species of the genera *Eretmophyllum* and *Nehvizdya* showing that the stratigraphic distribution and the papillate stomata stage are clearly distinct in both taxa (modified after Kvaček, 1999)

Species and location	Stratigraphy	Stomatal distribution	Trichome bases	Papillae around pits	Resin bodies
<i>Eretmophyllum baikonuricum</i> Orlovskaya (1962, p. 166). Baikonur, Kazakhstan	Middle Jurassic	?	Absent	Present	Present
<i>Eretmophyllum boroldaicum</i> Orlovskaya in Doludenko and Orlovskaya (1976, p. 70). Karatau, South Kazakhstan	Middle Jurassic	Amphistomatic	?	Present	Absent
<i>Eretmophyllum caussenense</i> Thévenard (1992, p. 95). Causses, Lozère, France	Lower Jurassic (Hettangian)	Amphistomatic	Present	Present	Present
<i>Eretmophyllum glandulosum</i> (Samylina) Krassilov (1972, p. 50). Aldan River, Bureia Basin, Siberia	Lower Cretaceous	Amphistomatic	Present	Present	Present
<i>Eretmophyllum harrisi</i> Gomolitzky (1987, p. 127). Gissat Mts., Uzbekistan	Middle Jurassic (Bajocian–Bathonian)	Hypostomatic	Present	Present	Present
<i>Eretmophyllum ketoviae</i> Gomolitzky (1965, p. 129). Gissar Mountains, Uzbekistan	Middle Jurassic (Aalenian–Bajocian)	Amphistomatic	Absent	Present	? Absent
<i>Eretmophyllum lovisatoi</i> Edwards (1929, p. 388). Laconie, Sardinia	Middle Jurassic	Amphistomatic	Absent	Present	Present
<i>Eretmophyllum magnum</i> Doludenko in Doludenko and Orlovskaya (1976, p. 113). Karatau, South Kazakhstan and Gissar Mts., Uzbekistan	Middle Jurassic (Bajocien–Bathonien)–Upper Jurassic	?	Present	Present	?
<i>Eretmophyllum ovatum</i> Teslenko (1970, p. 166). Kuzbas, South-western Siberia	Upper Jurassic	?	?	?	?
<i>Eretmophyllum pubescens</i> Thomas (1913, p. 256). Yorkshire, England	Lower Jurassic (Bathonian)	Amphistomatic	Rarely present	Present	Present
<i>Eretmophyllum pulchellus</i> (Heer, 1876) Nathorst, 1919; Spitzbergen (Norway)	Upper Jurassic	?	?	?	?
<i>Eretmophyllum (?) rigens</i> Savizkaya, Sixtel et al. (1971, p. 97). Shurab, South Fergana, Uzbekistan	Trias (Rhetian)	?	?	?	?
<i>Eretmophyllum saighanense</i> (Seward) Seward (1919, p. 60). Afghanistan, Mts. Ural, Korea	Middle Jurassic	?	?	?	?
<i>Eretmophyllum tetoriense</i> Kimura and Sekido (1965, p. 1). Hokaido, Japan	Lowermost Cretaceous (Early Neocomian)	?	?	?	?
<i>Eretmophyllum thomasii</i> Doludenko and Svanidze (1969, p. 71). Georgia (Middle Asia)	Lower Jurassic	Amphistomatic	Present	Present	Absent
<i>Eretmophyllum whitbense</i> Thomas (1913, p. 259). Yorkshire, England	Middle Jurassic (Bajocian)	Amphistomatic	Absent	Present	Present
<i>Eretmophyllum</i> sp. Kovalchuk (1961, p. 75). Kazakhstan	?	?	?	?	?
<i>Eretmophyllum</i> sp. Orlovskaya (1962, p. 1444). Kazakhstan	Middle Jurassic	?	?	?	?
<i>Eretmophyllum</i> sp. Sixtel et al. (1971, p. 97). Uzbekistan	Lower Jurassic	?	?	?	?
<i>Eretmophyllum</i> sp. Srebrodolskaya (1964, p. 58). Primorie	Upper Trias	?	?	?	?
<i>Nehvizdya andegavense</i> (Pons et al.) comb. nov. Anjou, France	Upper Cretaceous (Cenomanian)	Amphistomatic	Absent	Absent	Present
<i>Nehvizdya obtusa</i> (Velenovský) Hlušítk (1986, p. 99). Bohemia, Czech Republic	Upper Cretaceous (Cenomanian)	Hypostomatic	Absent	Absent	Present
<i>Nehvizdya penalveri</i> sp. nov., Teruel, Spain	Lower Cretaceous (Albian)	Amphistomatic	Absent	Absent	Present



cells which often partly overhang the guard cells. Until now, *Nehvizdya obtusa* (Velenovský) Hlušík was the only species attributed to the genus (Hlušík, 1977, 1980). It is known in several places of the Central Bohemian Peruc Formation (Velenovský, 1885; Hlušík, 1977; Uličný et al., 1997). This Czech leaf has been linked to defoliated shoots clothed in decurrent leaf bases with spirally arranged foliage leaf scars (Hlušík, 1986). Velenovský and Viniklár (1926, 1927) also noted the possible connection of these leaves to fragmentary twigs with spirally arranged rhombic leaf scars, indicating spiral phyllotaxy, though this has not been proved (Hlušík, 1977). In addition, Hlušík (1986) inferred the association of the leaves of *N. obtusa* with secretory elements and isolated, small rounded seeds with an inner stony layer, possibly held in a cup-like structure and, considered both structures as evidence of ginkgoalean affinities. Although *N. obtusa* shows strict hypostomy and the Spanish species has a marked amphistomy, the above epidermal features suggest the leaf compressions of Rubielos de Mora are a new species of *Nehvizdya*. Since hypostomy does not appear as a diagnostic character in Hlušík's diagnosis for the genus, we propose *N. penalveri* sp. nov. as a specific binomial for the new material from Rubielos de Mora.

(c) Taxonomic relationships of *Nehvizdya penalveri* sp. nov. and *Eretmophyllum andegavense* Pons et al.

*Eretmophyllum andegavense* Pons et al. (1976) is a leaf found in Le Brouillard and Le Gué de Moré sites of the Middle Cenomanian Clays of Beaugeois Member of Jumelles and Brissac Formation, 8 km north of Angers in France (Nguyen Tu et al., 1999). This species shows clear similarities with the new species in stomatal orientation, distribution and structure. Pons (1979), Hlušík (1980) and Pons (in Alvarez-Ramis et al., 1981) raised certain doubts as to its appropriate generic attribution, although *E. andegavense* Pons et al. (1976) certainly shared similar features with *Nehvizdya* Hlušík (1977). Previously, Pons et al. (1976) stressed the lack of anastomosed interstitial venation and the lack of papillae in epidermal cells and stomatal pits in the French Cenomanian

leaves. These characters are unlike those in other eretmophyllous species. Hlušík (1986) presented the very slight differences in the morphology and epidermal features between *E. andegavense* and *Nehvizdya obtusa* to represent intraspecific subdivision and chose the names *N. obtusa* (Velenovský) Hlušík ssp. *andegavensis* (Pons et al.) stat. nov. and *N. obtusa* (Velenovský) Hlušík ssp. *obtusa* respectively. Further studies on the scope of the French species, Pons and Vozenin-Serra (1992) and Nguyen Tu et al. (1999), did not mention or discuss the new status of *E. andegavense* and continued to use the latter name. Leaves of *Nehvizdya penalveri* sp. nov. from Rubielos de Mora, with clear amphistomy and the particular stomatal structure without papillae in the stomatal pits, also suggested that it would be more appropriate to assign, definitively, *E. andegavense* to the genus *Nehvizdya* Hlušík. In our opinion, the differences between the Czech, French and Spanish specimens appear to be sufficiently significant to raise these three taxa to a specific rank, rather than merely subspecific as Hlušík suggested. Therefore we propose the following new combination.

*Nehvizdya andegavense* (Pons et al.), Gomez comb. nov.

*Basionym:* *Eretmophyllum andegavense* Pons et al. (1976, pp. 358–369, Plates I–III, Figs. 1–4).

*Synonymy:*

1979, *Eretmophyllum andegavense* Pons et al. — Pons (1979, p. 210), suggested as belonging to *Nehvizdya* Hlušík.

1980, *Eretmophyllum andegavense* Pons et al. — Pons et al. [1980, pp. 151–153, 157, Plate I(1–8)].

1980, *Eretmophyllum andegavense* Pons et al. — Hlušík (1980, p. 26), suggested as belonging to *Nehvizdya* Hlušík.

1981, *Eretmophyllum andegavense* Pons et al. — Pons in Alvarez-Ramis et al. (1981, p. 350), suggested as belonging to *Nehvizdya* Hlušík.

1986, *Nehvizdya obtusa* (Velenovský) Hlušík ssp. *andegavensis* (Pons et al.) stat. nov. — Hlušík (1986, pp. 106–110, Tables 3 and 4).

1992, *Eretmophyllum andegavense* Pons et al. — Pons and Vozenin-Serra (1992, pp. 199–201, Plate 1), slightly completed description, (suppos-

edly associated woods: *Ginkgoxylon gruetii* sp. nov.).

1999, *Eretmophyllum andegavense* Pons et al. — Nguyen Tu et al. (1999, pp. 79–93), palaeoecology distribution.

1999, *Eretmophyllum andegavense* Pons et al. — Kvaček (1999, pp. 19–21), revision of generic status.

Pons and Vozenin-Serra (1992) assumed links between small permineralised fragments of *Ginkgoxylon gruetii* and the leaves of *Nehvizdya andegavense* comb. nov. with scattered secretory cells on both cuticles (Pons et al., 1976), both found in the same bedding plane, but never in connection. Pons and Vozenin-Serra (1992) also described small round or spindle-shaped resin bodies between the venation in the mesophyll of *N. andegavense* comb. nov. Such resin bodies have been observed inside the lamina of *Nehvizdya penalveri* sp. nov.

(d) Comparison of stomatal density between the three taxa

Stomatal density of adaxial surface distinguishes *Nehvizdya andegavense* comb. nov. from *Nehvizdya penalveri* sp. nov., though both leaves show amphistomy. According to Pons et al. (1976), *N. andegavense* comb. nov. has an abaxial stomatal density of 56 stomata mm<sup>-2</sup> and adaxial s.d. variable from 2.5 stomata mm<sup>-2</sup> near the outlines to 0.5 on mid-lamina. Whereas, in *N. penalveri* sp. nov. the abaxial stomatal density is 17–20 stomata mm<sup>-2</sup> and adaxial s.d. 7–9 stomata mm<sup>-2</sup>. *Nehvizdya obtusa* remains clearly distinct from the French and Spanish species with hypostomatic leaves showing stomatal densities of 38–65 (average 50) in areas between veins of the abaxial cuticles (Hlušík, 1986).

*Nehvizdya penalveri* sp. nov. from Rubielos de Mora locality appears to be stratigraphically the earliest appearance of this genus. Now *Nehvizdya* has a Lower–Middle Albian to Cenomanian stratigraphic distribution and includes three species from Czech, French and Spanish localities. Consequently, the stratigraphic occurrence of *Eretmophyllum* appears to be limited to rocks of Upper Triassic–Lowermost Cretaceous and mainly Jurassic age as given in the general sum-

mary of Pons et al. (1976) and later detailed for the middle Asian species by Gomolitzky (1987).

## 5. Taphonomy and palaeoecology

Leaves of *Nehvizdya penalveri* sp. nov. were found dispersed in the sediment, unassociated with any leaf-shoots which might have borne them. This may indicate that sorting of leaves and shoots, with subsequent selection of leaves, occurred before deposition. These processes may be produced during leaf-abscission or during transport.

The leaf cuticles studied are frequently broken longitudinally and/or transversally. Transversal breakage, which cuts a number of veins, is more frequent than longitudinal tearing. Even longitudinal tears often cut transversally a few adjacent veins rather than following a single vein. In all cases, broken margins are neat and do not present evidence of wound healing, which indicates that breakage occurred after leaf abscission. *Nehvizdya penalveri* sp. nov. are relatively small, elongated and coriaceous leaves which were probably capable of withstanding significant transport in streams or water without apparent damage. As a general rule, fresh leaves tend to tear following venation after being stretched during transport in water streams (Ferguson, 1985). This process may be responsible for longitudinal tears in our samples. From our observations in extant, coriaceous leaves with parallel venation (e.g. *Zamia*, *Podocarpus*, *Agathis*), transversal breakage through stretching is not either with fresh or dried leaves. Even after being folded and stretched, coriaceous leaves with parallel venation are difficult to break transversally. In consequence with these data we do suggest that transversal breakage occurred during the fossil-diagenetical stage of fossilisation, rather than during the biostratigraphical stage. Most probably, transversal breakage was produced when leaves were already preserved as a cuticle compression.

In the sedimentary context where the cuticle bed was deposited, transport in water streams carried the leaves towards ponds or interdistributary bays in the lower delta plain, where they were deposited. Accumulation of large quantities of

leaves forming a leaf-bed in such a quiet environment indicates that leaves were transported there massively, perhaps during a single event of translocation of the whole leaf litter horizon during overbank flooding, and that they still conserved some buoyancy before deposition. After deposition in fine sediment (clays), a rapid burial and the oxygen-poor conditions of the water-sediment interphase meant a smaller diagenetic alteration and excellent preservation of highly cutinised compressions.

The taphonomical analysis carried out shows that the leaf assemblage of the Arroyo de la Pascueta cuticle bed underwent massive transport from the leaf litter horizon to the deposition site. As a result, the association of *Nehvizdya penalveri* sp. nov. with other taxa in the same layer probably reflects some original association of these taxa. In that sense a characteristic association appears to occur between *Nehvizdya penalveri* sp. nov. leaves and shoots of *Frenelopsis alata* (K. Feistmantel) Knobloch. Such an association is not unique to the Albian of the Iberian Ranges, but has also been described, in a similar sedimentary context, in the Cenomanian of Czech Republic (Kvaček, 1995) and France (Pons and Boureau, 1977).

In recent years there has been considerable interest in elucidating the autecology of *Nehvizdya* and *Frenelopsis*. Thus, Uličný et al. (1997) found that *Nehvizdya obtusa* and *Frenelopsis alata* were shrubby halophytes growing in the muddy supratidal marsh area, on the tidal creek margins and on the surface of the salt marsh of the Peruc–Korycany Formation (Czech Republic). Evidence from sedimentology and palynology suggest that the shrubby habit of these Czech Cenomanian plants was a response to brackish or marine water influences rather than the consequence of aridity. Also, Nguyen Tu et al. (1999) analysed the  $^{13}\text{C}/^{12}\text{C}$  ratios in leaves of *Nehvizdya andegavense* comb. nov. and/or *F. alata*, from the Cenomanian Baugeois Clays (France), which is thought to indicate soil-palaeosalinity. According to these authors, *N. andegavense* grew in a number of habitats with a wide range of ground-water salinities, whereas *F. alata* resisted salt stress and grew around coastal lagoons. Evidence from sedimentology and palynology found in the Albian of

Rubielos de Mora show that both *Nehvizdya penalveri* and *F. alata* lived in the lower delta plain, around ponds and interdistributary bays which recorded marine and freshwater water inputs. Marine influences resulted in high edaphic salinity, which probably conditioned the xeromorphy of *N. penalveri* leaves.

## 6. Conclusions

The description of a *Nehvizdya penalveri* nov. sp. in the Lower to Middle Albian of Spain sheds new light on the diagnostic characters of this formerly monotypic ginkgoalian genus. The emended diagnosis of the genus proposed includes three European species, *Nehvizdya obtusa* Hlušík, *Nehvizdya andegavense* (Pons et al.) comb. nov. and *N. penalveri* sp. nov. ranging from the Albian to the Cenomanian. Evidence from leaf anatomy, sedimentology and taphonomy suggests that these species grew in coastal biotopes with high saline edaphic conditions surrounding the ancient Tethys. Unfortunately, no fertile parts were collected to confirm the systematic position of the genus *Nehvizdya*.

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