NEOGENE SPECIES OF THE GENUS *FAGUS* L. FROM LA CERDAÑA (LÉRIDA, SPAIN). TAXONOMIC CONCLUSIONS AND PHYLOGENETIC CONSIDERATIONS

by

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Resumen

BARRÓN, E. & C. DIÉGUEZ (1994). Especies del género Fagus L. del Neógeno de La Cerdaña (Lérida, España). Conclusiones taxonómicas y consideraciones filogenéticas. *Anales Jard. Bot. Madrid* 52(1): 21-32 (en inglés).

Se realiza un estudio taxonómico de los restos fósiles asignables al género *Fagus* L. que se han colectado en los yacimientos de la cuenca lacustre del Mioceno superior de La Cerdaña (Lérida, España), tras el cual se reagrupan a éstos en dos especies: *F. pristina* Saporta y *F. gussonii* Massalongo, invalidándose un conjunto de cinco paratáxones. Se enuncian, asimismo, conclusiones de tipo filogenético.

Palabras clave: *Fagus*, Mioceno Superior, La Cerdaña, Taxonomía, Filogenia.

Abstract

BARRÓN, E. & C. DIÉGUEZ (1994). Neogene species of the genus Fagus L. from La Cerdaña (Lérida, Spain). Taxonomic conclusions and phylogenetic considerations. *Anales Jard. Bot. Madrid* 52(1): 21-32.

Fossil remains assigned to genus *Fagus* L. were collected in La Cerdaña (Lérida, Spain) outcrops and studied taxonomically. On the basis of this study, fossil remains were regrouped into two species: *F. pristina* Saporta and *F. gussonii* Massalongo. A group of five parataxa is invalidated and some phylogenetic considerations discussed.

Key words: *Fagus*, Upper Miocene, La Cerdaña, Taxonomy, Phylogeny.

INTRODUCTION

La Cerdaña is an old lacustrine basin of tectonic origin (CABRERA & *al.*, 1988) dated as Vallesian-Turolian (fig. 1). Physical and chemical characteristics of its sediments permit an excellent preservation of plant remains.

From a paleobotanical point of view, the presence of both macroscopic and microscopic plant remains attributed to the genus *Fagus* in Upper Miocene lacustrine sediments of La Cerdaña are of great interest, since this genus, which has been detected in a large number of other Tertiary outcrops in Eurasia and North America, has not been well studied in the fossil condition. This has led to mistakes in its taxonomy and phylogeny.

The genus *Fagus* now includes about ten extant species and its distribution is restricted to the Northern Hemisphere: Europe, Asia Minor, Eastern China, Japan, Taiwan and Eastern North America. This distribution

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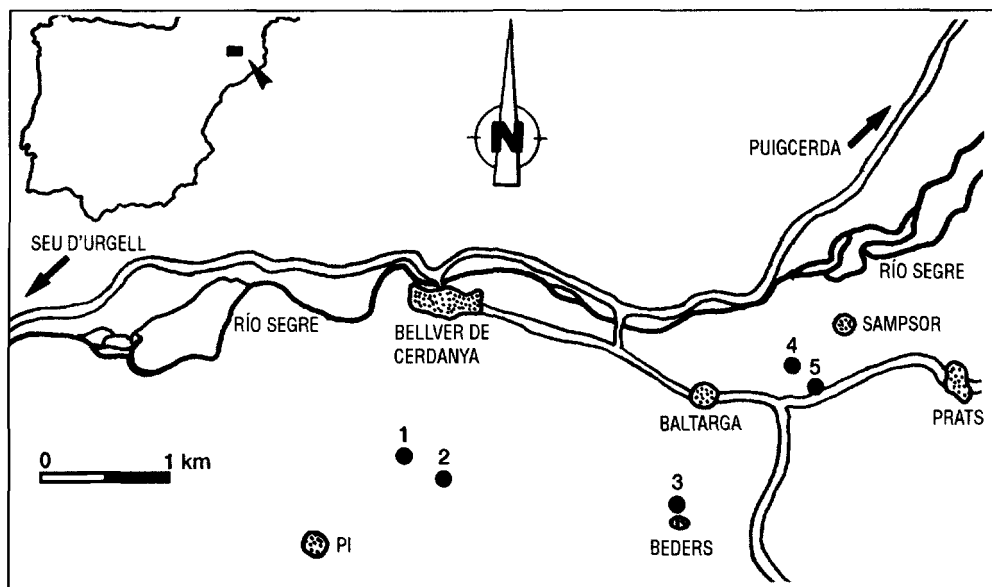** Museo Nacional de Ciencias Naturales. C/ José Gutiérrez Abascal, 2. E-28006 Madrid.

Fig. 1.– Geographical setting: 1, outcrop of Barranco de Salanca; 2, outcrop of Torrente de Vilella; 3, outcrop of Beders; 4, outcrop of Can Pilbre; 5, outcrop of Coll de Saig.

seems to be an effect of the Quaternary freezes and the formation of arid regions in Central Asia.

In order to facilitate the taxonomic study of fossil species of the genus *Fagus*, this genus had been analyzed with respect to leaf morphology (TRALAU, 1962; TANAI, 1974). JONES (1986) demonstrated that the diagnostic character for grouping extant as well as fossil species of genus *Fagus* is the stomatal structure. He revealed the existence of two groups with phylogenetic if not taxonomic value:

1) The first group has ciclocytic stomata, and is comprised of the extant species *F. orientalis* Lipsky, *F. sylvatica* L., *F. crenata* Bl. and *F. lucida* Redher.

2) The second group with anomocytic stomatas, is formed by *F. grandifolia* Ehr. and *F. longipetiolata* Seem.

KVAČEK & WALTHER (1991) put forward four groups based on characteristics of the epidermis and of the cupula but without formally refuting or invalidating Jones' proposals (1986).

Some controversy surrounds the first record of the genus *Fagus*, with references as old as the Late Cretaceous. TAKHTAJAN (1982 apud JONES, 1986) presented Eocene and some Upper Paleocene records. JONES (1986) accepted this conclusion and suggested that while *Fagus* evolved as early as the Upper Paleocene, it was undoubtedly represented in the Oligocene, flourished during the Miocene and, indeed, several Miocene species are still in existence today.

Some authors have suggested the ancestors of the genus *Fagus* originated during the Upper Cretaceous in North America (OLIVER, 1925), while others place its origin in Southeastern Asia (TAKHTAJAN, 1969; ROMERO, 1986). There is general consensus, however, on the Boreal Tertiary origin of the genus, with several of its species being clearly Turgayan (MEYEN, 1987).

ANTECEDENTS

The existence of macroremains attributable to the genus *Fagus* in the Miocene sediments of La Cerdaña has been noted by several authors. RÉROLLE (1884-1885) described the variety *ceretana* of the fossil species *F. pliocenica* Sap., on the basis of leaf remains and cupules. VILLALTA & CRUSAFONT (1945) added

F. castaneaefolia Ung., but identified it erroneously as "*F*. (*Castanea*?) cf. *castaneaefolia*". MENÉNDEZ AMOR (1955) described and represented graphically *F. pristina* Sap. Finally, ÁLVAREZ RAMIS & GOLPE-POSSE (1981) cited a new species of beech in open nomenclature, without specifying whether this finding was represented by leaves, cupules, woods or pollen.

Pollen which was assigned to the genus *Fagus* from various lignite outcrops at La Cerdaña (Sanavastre, Sampsor) has been mentioned but not described by JELSGERMA (1957) and BESSEDIK (1985). In these outcrops, macroscopic remains attributed to the genus *Fagus* have also appeared (SANZ DE SIRIA CATALÁN, 1980).

In relation to cupules, we do not know of any data from La Cerdaña's Miocene, with the exception of RÉROLLE's (1884) reference.

MATERIALS AND METHODS

Remains were collected from the outcrops of La Cerdaña corresponding to the Upper Miocene. These include leaves and cupules, and form part of the J. Menéndez Amor collection (Museo Nacional de Ciencias Naturales, CSIC), J. F. Villalta collection (Museu de Geologia de Barcelona), Museu del Seminari de Barcelona, Museo del Instituto Tecnológico Geominero de España, and private collections, as well as specimens collected by us.

Leaves and cupules always occur as impressions or compressions. On rare occasions foliar compressions keep their cuticles and these have been obtained by the maceration method proposed by BATHER (1908). The results, however, were not as satisfactory as we had desired since no stomata could be observed; the only possibility for study was the morphology of epidermal cells which were located over the leaf veins.

Leaf remains were analyzed morphologically according to the terminology proposed by HICKEY (1973).

The analysis of cupules was problematic since, as we have suggested, they appeared two dimensionally in the form of impressions

and compressions, thus only permitting us a relative idea of their volume. An additional problem was that the cupules which we encountered were not in organic connection with collected leaves.

Both cupules and leaves were compared with extant species from the Real Jardín Botánico de Madrid (CSIC), the Royal Botanic Gardens of Kew and the Jardin des Plantes de Paris herbaria. They were also compared with other fossil remains from the collections of the Museo Nacional de Ciencias Naturales (CSIC).

The PHIPPS & PLAYFORD (1984) method was applied to obtain pollen slides by removal of the sediments. In order to gather together the palynomorphs we used sieves of different mesh. We then studied these under a Leitz Laborlux D microscope with an incorporated Wild Photoautomac MPS 45 camera.

Finally, an exhaustive revision was undertaken, which showed the existence of species from other Neogene outcrops of the Northern Hemisphere which were similar to those collected, and indicated that several of the ceretana fossil species had been subjected to incorrect taxonomic and phylogenetic treatment.

PALAEONTOLOGICAL STUDY

The genus *Fagus* occurs in La Cerdaña Basin in the form of both macroscopic (leaf remains and cupules) and microscopic remains (pollen).

– *Leaf remains*. Fundamentally, two morphological types have been found.

i) Short petiolated leaves; lamina with 8-3.5 cm length and 3-1.5 cm width; lanceolate (fig. 2, 1; fig. 3, 1, 3) or narrow ovate form (fig. 2, 2); acute apex; acute to rounded base; serrate margin, sometimes slightly sinuous (fig. 3, 2), containing small teeth with acute apical angles; simple craspedodromous pinnate venation (fig. 2, 1, 2; fig. 4) or mixed craspedodromous pinnate when the most basal teeth of the margin are attenuate; secondary veins with straight course and moderate acute angle of divergence in a maximum number of 18 to 20 couples, sometimes recur-
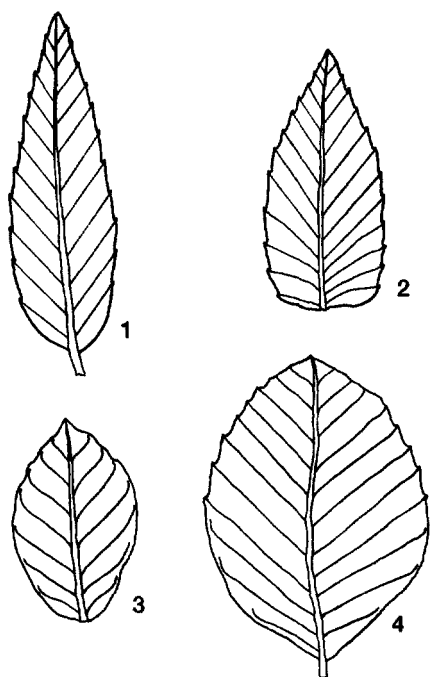
Fig. 2.–Schematic representation of *Fagus* species fossil leaves from La Cerdaña: 1, 2, *Fagus pristina* Saporta; 3, 4, *Fagus gussonii* Massalongo.

ved in the basal zone; percurrent tertiary veins with simple or sometimes forked course and arranged obliquely in relation to the midvein (fig. 4); higher order of venation forming a network with well-developed quadrangular areoles.

ii) Leaves with short but robust petiole of 8-4 mm length; lamina with 10-3 cm length and 6-2 cm width; usually elliptic (fig. 3, 5), though ovate (fig. 2, 4) and obovate (fig. 3, 4; fig. 2, 3) specimens exist; rounded, obtuse or acute base; always acute apex; entire, or more or less, undulate margin, sometimes serrate in their upper part (fig. 2, 4); pinnate venation adapted to the margin characteristics: if it is entire it will be eucamptodromous (fig. 5), while if it is serrate it will be mixed craspedodromous; between 10 and 12 pairs of secondary veins which in the smallest leaves could be reduced to 7; moderately acute angle of divergence; percurrent tertiary veins with simple or sometimes forked course and oblique in relation to the midvein; higher order of vena-

tion forming a network with well developed quadrangular areoles; epidermal rectangular or quadrangular cells well developed on the primary and secondary veins occasionally presenting thicker zones along their length (fig. 6, 1, 6); approximately with 4-5 μm width and 5-22.5 μm length; thickened cellular walls, about 1.28 μm; straight contours, never sinuous; longitudinal cells oriented from the route of the midvein which they overcover; lateral connection between cells always parallel to their longest axis.

– Pedunculate *cupules* with 2 cm length and 1.5 to 1.7 cm width; peduncle shorter than cupule's length, about 5-6 mm; two rounded or visible pods pointed apically, finishing with decurrent forms in the peduncle; scarce ornamentation, small and dispersed thorns (fig. 6, 2).

– Spheroidal or subprolate *pollen* (fig. 6, 3, 5), with a diameter of 35-45 μm; 3-zonocolporate; narrow colpi, with 1-2 μm width, which seem not to fuse at the poles; 4-5 μm of diameter lolongate ora with equatorial position; thin nexine of 0.6 μm; thick sexine, around 1 μm, unfolding cannot be observed with optical microscopy; the exine detaches from the intine forming a fringe on the ora; an internal enlargement of the exine around colpi may be seen in several specimens (fig. 6, 3); rough ectexine.

DISCUSSION

The type of *leaf remains* outlined under (i) above (fig. 3, 1, 3), can be assigned to the parataxonic fossil species *F. pristina*, described by SAPORTA (1867) based on a group of Lower Miocene specimens from Bois d'Asson. In Cantal Pliocene, the same author, referring to identical remains, described the species as *F. pliocenica* (SAPORTA, 1873). Due to the lack of significant differences between these two species, and according to the priority principle of the *International Code of Botanical Nomenclature*, *F. pliocenica* must be considered as synonymous with *F. pristina*.

In 1885 GOEPPERT described the species *F. attenuata* from Silesian material. While re-
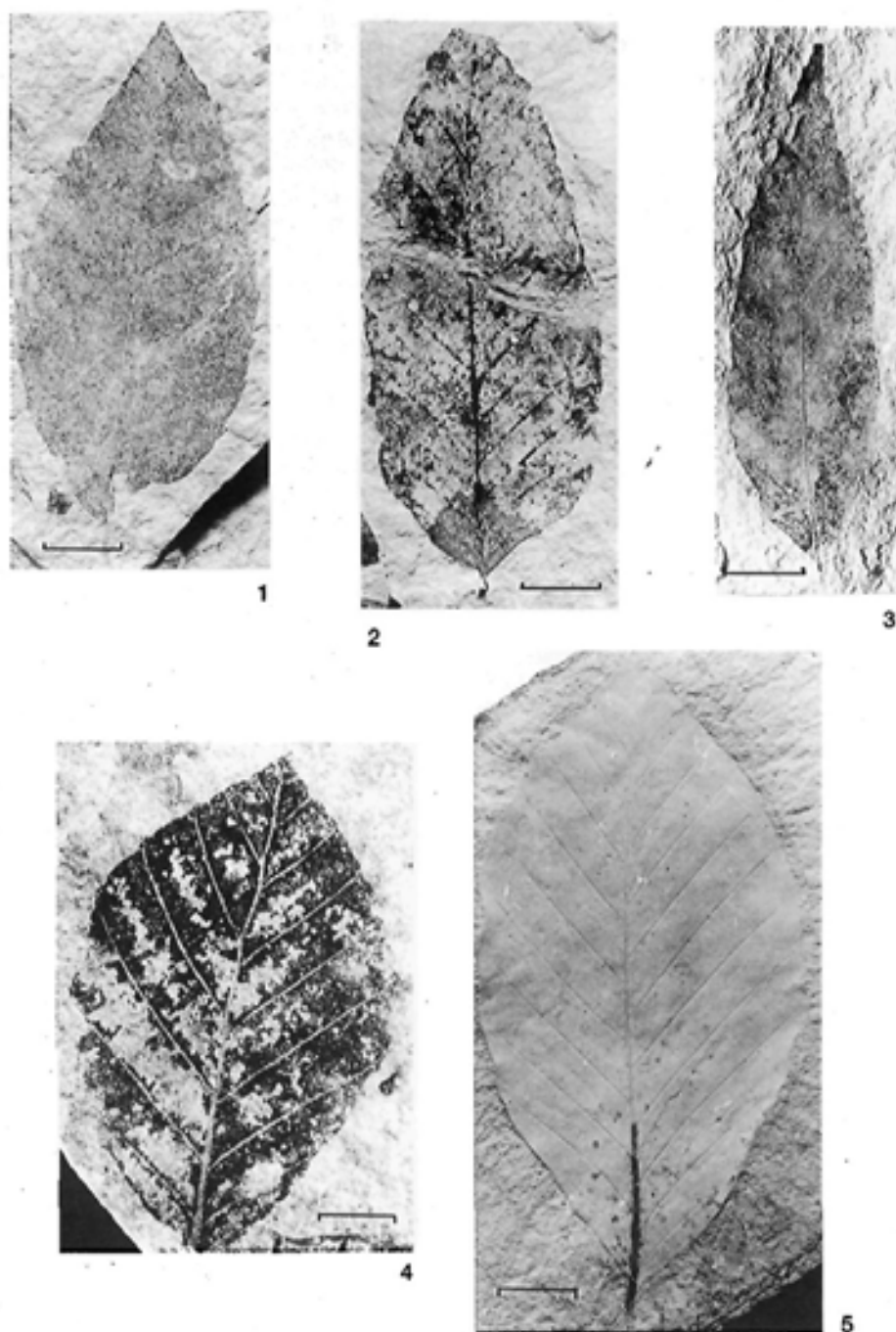
Fig. 3.–1, leaf of *Fagus pristina* Saporta, specimen MNCNV-4426 collected in Beders outcrop; 2, idem, specimen MNCNV-3556 collected in Beders outcrop; 3, idem, specimen MNCNV-4423 collected in Beders outcrop; 4, leaf of *Fagus gussonii* Massalongo, specimen MGBV-9845 collected in Barranco de Salanca outcrop; 5, idem, specimen MNCNV-3043 collected in Coll de Saig outcrop. (Graphic scale.1, 2, 3, 5: 1 cm; 4: 5 mm.)
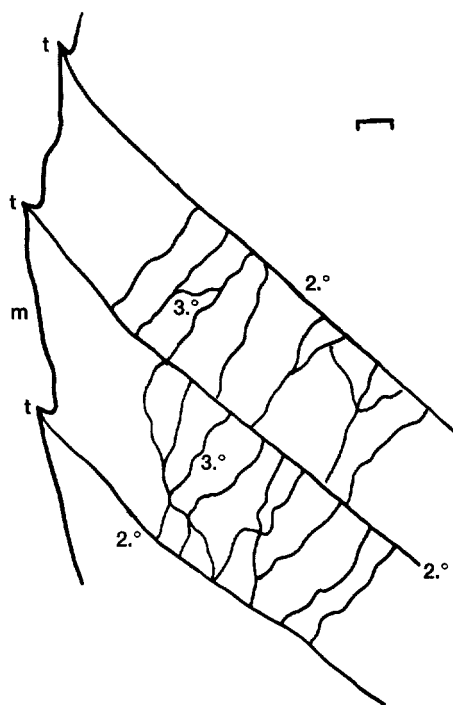
Fig. 4.–Venation detail of *Fagus pristina* Saporta, specimen MNCNV-4426 collected in Beders outcrops (graphic scale: 1 mm): m, margin; t, tooth; 2.°, secondary venation; 3.°, tertiary venation.

vising the material type, WALTHER & ZASTAWNIAK (1991) invalidate this species and verify it as corresponding to *Alnus julianaeformis* (Sternb.) Kvaček & Holý. Nevertheless, among the material from Sośnica and Malczyce (Silesia) outcrops, both authors found specimens attributable to the genus *Fagus*, and described the species *F. silesiaca* on the basis of foliar morphology and anatomy.

From a morphological point of view, *F. silesiaca* shows identical characteristics to *F. pristina*, which given the priority principle would invalidate *F. silesiaca*. However, since no cuticular study of *F. pristina* has been carried out, we cannot invalidate that species. For the time being we consider it appropriate to use *F. pristina* for material which is consistent in impressions with the described morphology, keeping in mind that this is not a wholly satisfactory solution.

The same case occurs with the species *F. saxonica* from the German Upper Oligoce-

ne and with *F. menzelii* from the Middle Miocene, described by KVAČEK & WALTHER (1991).

SAPORTA (1867) erroneously described a leaf remnant from the Bois d'Asson under the name *F. castaneaefolia* Ung., which, according to the same author (1891), should be attributed to *F. pristina*. Similarly, we can attribute to *F. pristina* the specimens described as *F. (Castanea?)* cf. *castaneaefolia* Ung. sensu VILLALTA & CRUSAFONT (1945) from the Ceretana Basin.

With respect to its morphology, *F. pristina* can be related with the fossil species of Clarkia's Miocene (North Idaho): *Pseudofagus idahoensis* Smiley & Huggins, and with the extant *F. grandifolia*.

While *P. idahoensis* shows actinocytic stomata surrounded by a ring of subsidiary cells (SMILEY & HUGGING, 1991), *F. grandifolia* has anomocytic stomata, and therefore must be included within the second group of beeches proposed by JONES (1986) and also in the fourth proposed by KVAČEK & WALTHER (1991).
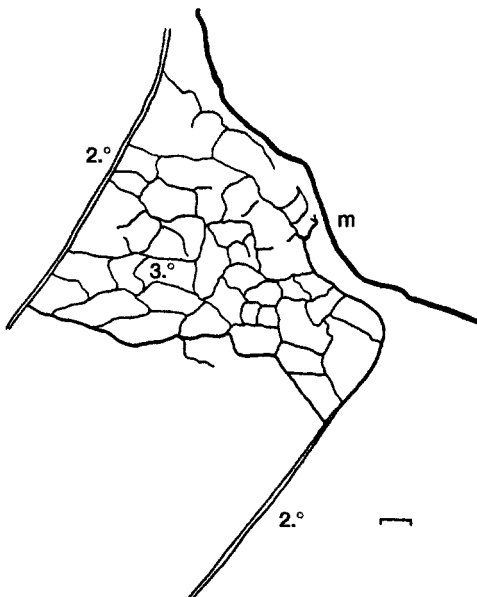

Fig. 5.–Venation detail of *Fagus gussonii* Massalongo, specimen MNCNV-320 collected in Pedró outcrops (graphic scale: 1 mm): m, margin; 2.°, secondary venation; 3.°, tertiary venation.
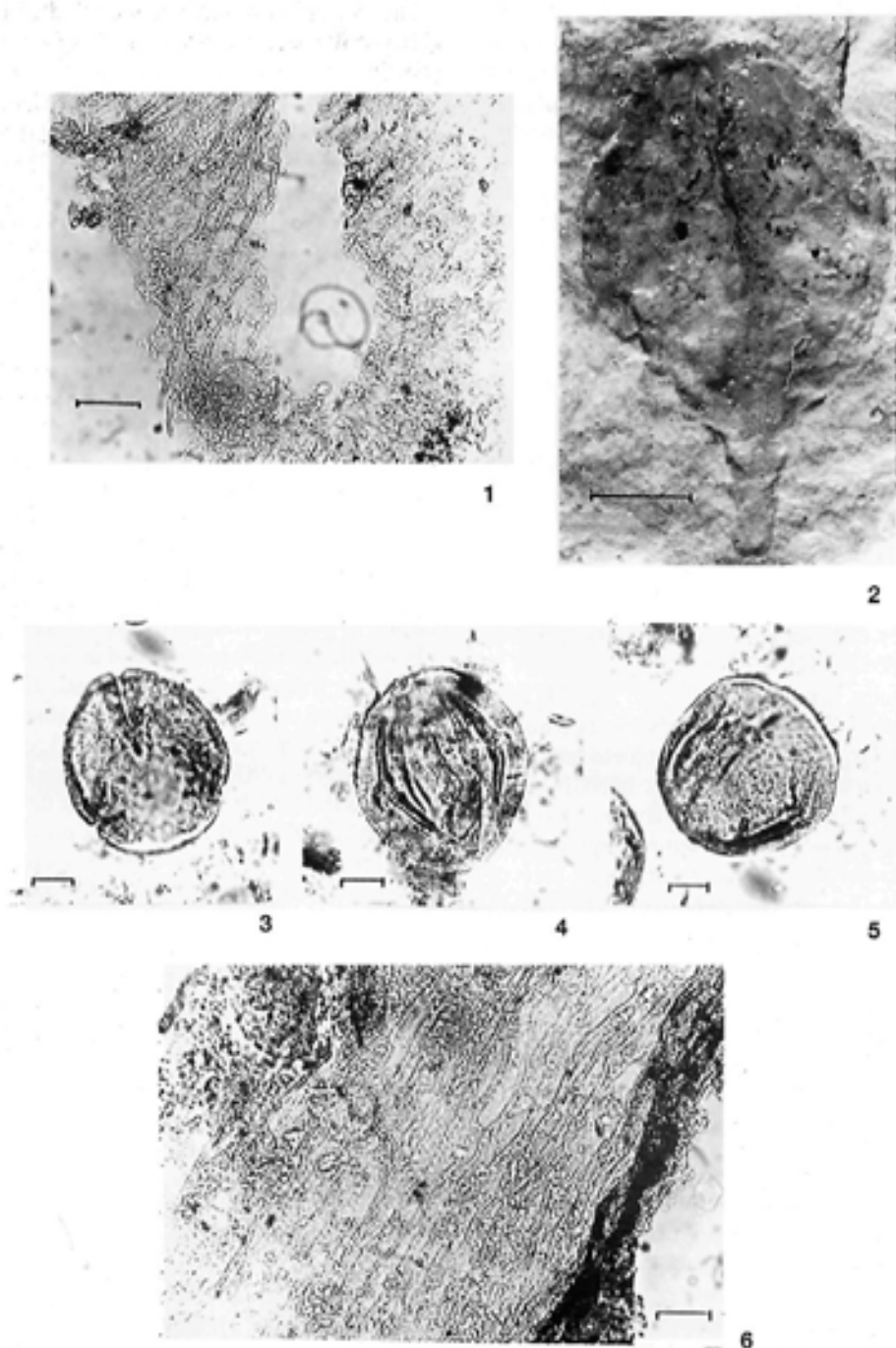
Fig. 6.–1, 6, fossil leaf cuticle of *Fagus gussonii* Massalongo from Beders outcrop; 2, cupule of *Fagus* sp., specimen MNCNV-140 collected in Coll de Saig outcrop; 3, 4, 5, fossil pollen of *Fagus* from sediments of Barranco de Salanca outcrops. (Graphic scale. 1, 6: 15 μm; 2: 5 mm; 3, 4, 5: 10 μm.)

The *leaf remains* of type (ii) (fig. 3, 4, 5) have been described by RÉROLLE (1884-1885) with reference to fossil materials from La Cerdaña, as the variety *ceretana* of *F. plioce-nica*. Previously, MASSALONGO & SCARABE-LLI (1859) had described *F. gussonii* based on Upper Miocene material from Senigaglia (Italy). This material was identical to the material described by RÉROLLE (1884-1885) from La Cerdaña. In light of the priority principle, the variety described by RÉROLLE (1884-1885) should be considered as synonymous with *F. gussonii*, while *F. ceretana* Sap. and the variety *ceretana* Zittel of *F. sylvatica* proposed by SAPORTA (1891) and ZITTEL (1891) should be considered as synonymous as well.

The morphological characteristics of parataxonic species *F. gussonii* are identical to those of the extant *F. orientalis*. We believe that closer affinities exist between these two species than supposed by KNOBLOCH & VE-LITZELOS (1987).

Finally, we must emphasize that MENÉN-DEZ AMOR (1955) erroneously cited *Castanea ungeri* Hr. based on an incomplete specimen of *F. gussonii* (specimens MNCNV320 (fig. 5) and MNCN721, part and counterpart).

Leaf remains with the same morphology as *F. gussonii* have been collected in all parts of Europe (fig. 7). However, it is necessary to point out that the most representative are the Miocene specimens from France, Poland, Czechoslovakia, Greece and Italy (DEPAPE, 1922; ŚRODOŃ, 1985; KNOBLOCH & VELITZE-LOS, 1986, 1987; TUREK & *al.*, 1989).

Cupules from sediments of La Cerdaña cannot be clearly attributed to any of the two previous species (fig. 6, 2). This is due primarily to the fact that, as already pointed out, they were not found attached; and secondly, because they appear as impressions and compressions, thus permitting observation of only two of the three or four valves that they usually have.

Possibly the latter is the reason for which MENÉNDEZ AMOR (1955) identified these cupules as floral buttons of *Punica granatum* L. var. *planchoi* Sap. (fig. 6, 2).

The ornamentation of cupules is scant, which could be due to:

i) the semaphoronts, to which they belong, had lesser ornamented cupules, or to

ii) a degradation of ornamentation after abcission or during the fossilization process.

Nevertheless, the collected cupules are very similar in size to those described by BIA-LOBRZESKA & TRUCHANOWICZÓWNA (1983) from the Western Carpathian Neogene. These authors attribute them to *F.* aff. *grandifolia*, in agreement with RÉROLLE (1884). According to KVAČEK & WALTHER (1989), cupules of this type have been found in the Oligocene and Neogene sediments of Central Europe, and were described as *F. deucalionis* Ung. from Bohemia and Styria (UNGER, 1847), and as *F. decurrens* Reid & Reid, from Poland (ŚRODOŃ, 1985). The description of *F. deuca-lionis* UNGER (1847) included leaf remains of intermediate characteristics between *F. sylva-tica* and *F. grandifolia*, and cupules and fruits, although the latter were not found in organical connection with these types of leaves. In accordance with this last point, it is possible that under the specific name *F. deucalionis*, other fossil remains of different beech species have been described. *Fagus decurrens* was descri-bed from cupules and fruits which probably could be related as much with La Cerdaña Miocene remains as with Western Carpathian specimens.

With regard to *pollen*, the existence of two types of grains could be predicted. One of them is clearly attributable to *Faguspollenites gemmatus* Nagy (fig. 6, 4, 5) and undoubtedly related to *F. orientalis* (NAGY, 1985). This corroborates the presence of this species in the Miocene of La Cerdaña, while raising the possibility that the parataxonic species *F. gusso-nii* is really attributable to *F. orientalis*. The other pollen type, morphologically differentiated by the internal thickness of the exine of the colpi, is related to several species of *Fagus* of Eastern Asia (PONS, 1964), such as *F. japo-nica* Maxim (fig. 6, 3). This fact supports the relationship between the Miocene flora of La Cerdaña and the extant flora from the temperate regions of Eastern China and Japan, evident in the presence in La Cerdaña outcrops of
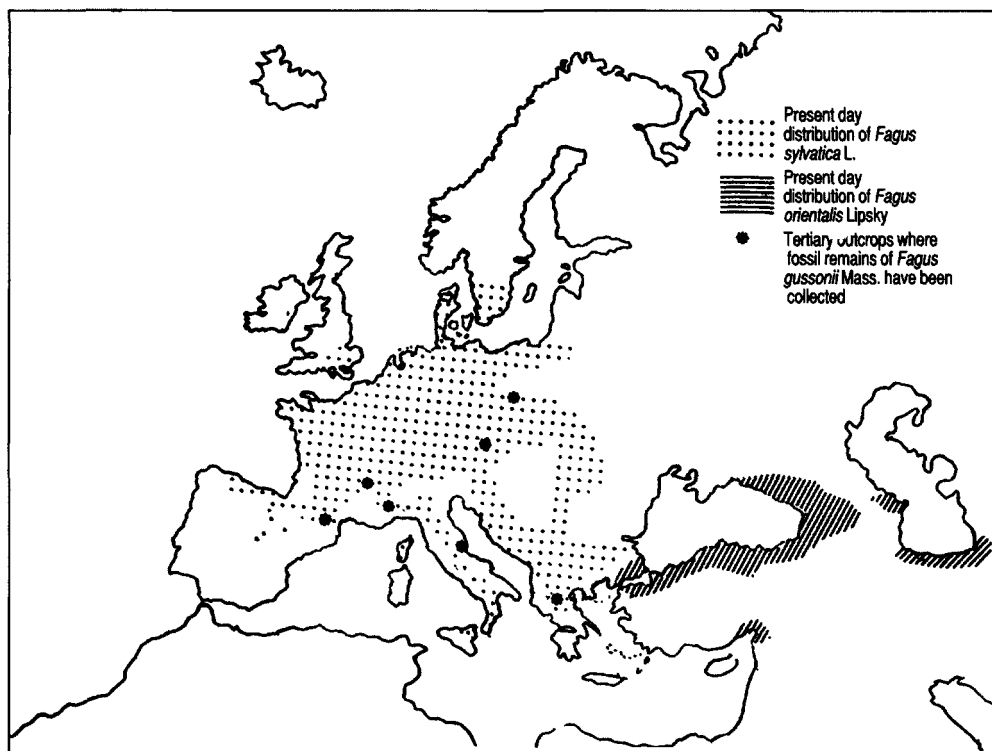
Fig. 7.– Geographical distribution of extant european *Fagus* species.

other taxa such as *Cryptomeria*, *Cinnamomum*, *Tsuga*, and certain species of Quercoideae such as *Quercus drymeja* Ung., related to the Asiatic oaks of the subgenus *Cyclobalanus*.

From a phylogenetic point of view, SAPORTA (1888) was the first author who tried to relate Tertiary Western European species of *Fagus* to extant ones. Taking only into account leaf morphology, he proposed the existence of two groups represented by *F. sylvatica* and *F. grandifolia*. This assertion was accepted as true until the second half of the twentieth century (TRALAU, 1962). Nevertheless, as we have already mentioned, in establishing a relationship between beech species, we must consider the epidermical characters of their leaves (JONES, 1986) or the union of the anatomical leaf characteristics and of the morphology of the cupule (KVAČEK & WALTHER, 1991).

The phylogenetic closeness of *F. orientalis* and *F. sylvatica* must be pointed out, since both present ciclocytic stomata (BANDULSKA, 1924); moreover, these two species are able to hybridize, giving rise to forms with leaves of mixed characteristics (*F. moesiaca* (K. May) Czecz., *F. taurica* Popl.). An interesting point which we have noted from the study of fossil specimens is the existence of leaf remains of *F. gussonii* that did not noticeably differ morphologically from *F. sylvatica*. This polymorphism not only occurs in fossils, but is also frequent in living plants of this group. Moreover, living specimens of *F. sylvatica* exist with leaves similar to those of *F. orientalis* (LAURENT & MARTY, 1939). We believe that *F. sylvatica* normally presents leaves of lesser surface area than those of *F. orientalis* due to its adaptation to zones of harsher climatic conditions.

If, as MAI (1989) explained, the palynological data support the idea of *F. sylvatica* as having a Quaternary postglacial origin, then this species must have evolved from a Tertiary ancestor by genetic isolation in several

zones of Southern Europe. We think that this ancestor could be *F. gussonii*, coinciding with KVAČEK & WALTHER (1991).

We agree with ROIRON (1981) in considering that *F. orientalis* and *F. sylvatica* could have evolved from a common ancestor. In our opinion this ancestor could have been *F. gussonii*, while Roiron proposes *F. pliocenica*, a species which from a taxonomical point of view lacks validity.

In support of the theory which we propose, we consider the existence of the circummediterranean beech forest of *F. sylvatica* as phenologically, genetically and floristically different from those of the rest of Western Europe (GAUSSEN, 1978; THIEBAUT, 1982), where beeches have wider leaves, sometimes with toothed margins like *F. orientalis*, and a later foliation in sunny areas as compared to shaded areas. Logically, this point is impossible to demonstrate paleontologically.

The Quaternary glaciations led, to the extinction and/or to the emigration of a high number of plant taxa within Europe. Amongst these taxa might be the genus *Fagus*, which could have migrated south. Thus, from palynological data, we know that beeches inhabited several places free of ice in the Lower Holocene, such as Calabria. Later, in the Preboreal period, the genus *Fagus* is found in some regions of the Balkans and Romanian Carpathians (HORVAT-MALROT, 1992), in places along the Cantabrian coasts, and in Northeastern Catalonia (MARTÍN ATIENZA & MORLA JUARISTI, 1992). During interglacial periods, these nuclei of resistence served as dispersal areas in recuperating territories lost during the ice ages. It is possible that population remains of *F. gussonii*, which occurred throughout Europe during the Upper Miocene, were trapped in the refuge areas mentioned, and adapted themselves to new climatic conditions, thereby originating *F. sylvatica*. This species is at the present moment dominant in Northwestern and Central Europe (fig. 7).

Further populations of *F. gussonii* possibly migrated southeast, establishing themselves in Asia Minor, where the environmental and ecological conditions were closer to those which were evident in Europe at the end of the Cenozoic, thus giving rise to *F. orientalis* which later recolonized parts of its ancestral territory in Southeastern Europe (fig. 7).

Another point to consider is that two fossil species, which in this paper we recognize from leaf remains, could also be phylogenetically related, since both, if we relate *F. gussonii* with *F. orientalis* and *F. sylvatica*, possess ciclocytic stomata (BANDULSKA, 1924; KVAČEK & WALTHER, 1991). It is possible that *F. pristina*, whose oldest fossil record is from the Upper Oligocene, is in the same manner related to *F. gussonii*, a more modern species which appeared in Upper Miocene. If this assertation is true, *F. gussonii* would have a genome derived in part from *F. pristina*. In that case, it would not be surprising that the two species could hybridize, which would be one possible explanation for the discovery of leaves with mixed characters among the two species in La Cerdaña.

CONCLUSIONS

In this work we have made a study of fossil remains belonging to the genus *Fagus*, collected in the Vallesian-Turolian (Upper Miocene) outcrops of La Cerdaña (Lérida, Spain). These consist of leaf remains, cupules and pollen.

From the taxonomic analysis carried out, we can conclude that in La Cerdaña there existed only two species of *Fagus* that correspond to the two types of leaf remains: *F. pristina* and *F. gussonii*. The latter species is first cited in the Upper Miocene of La Cerdaña, as well as throughout all of the Spanish Tertiary. The cuticle which covered the primary and secondary veins of *F. gussonii* has also been described for the first time.

In La Cerdaña, cupules corresponding to the genus *Fagus* which could not be attributed to any species in particular have been found. This is the only reference from the ceretanum Miocene after RÉROLLE (1884-1885).

A description of the palynomorphs attributed to the genus *Fagus* collected in La Cerdañas'outcrops is given for the first time. This confirms the existence of *F. orientalis* in La

Cerdaña Basin, and leads to a discovery of other types of beech corresponding to extant species which inhabit temperate regions of Eastern Asia.

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