Taxonomic revision of the J. Vicente collection dicotyledon leaves from the lower Maastrichtian of Isona (northeastern Iberia)

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Resumen

MARMI, J. Revisión taxonómica de las hojas de dicotiledóneas de la colección J. Vicente del Maastrichtiense inferior de Isona (noreste de Iberia). El yacimiento de mega-fósiles de plantas del Maastrichtiense inferior de Isona (Lleida, Catalunya, NE de España) fue descubierto en 1979 y su primer estudio detallado fue publicado por Joan Vicente i Castells en 2002. La colección, de aproximadamente 400 fósiles, se conserva en el Museu de Geologia – Museu de Ciències Naturals de Barcelona (MGB-MCNB). En un estudio reciente, la colección Vicente fue revisada parcialmente proporcionando hasta 15 morfotipos diferentes de hojas de dicotiledóneas, aunque sólo tres de ellos pudieron ser asignados a familias de angiospermas como son Lauraceae, Betulaceae y Celastraceae. En este nuevo trabajo, los morfotipos se comparan con "*cleared leaves*" de angiospermas actuales y se proponen hipótesis taxonómicas para la mayoría de ellos. Entre los 17 morfotipos de dicotiledóneas actualmente distinguibles en la colección de plantas fósiles de Isona, se han identificado posibles miembros de Laurales, Proteales, Eurósidas y Astéridas. Además, se describen tres nuevas especies de hojas de dicotiledónea lo que sugeriría que la flora fósil de Isona podría ser más singular de lo que se creía en estudios previos.

Palabras clave: colección Vicente, dicotiledóneas, hojas fósiles, Maastrichtiense, Isona, "*cleared leaves*".

Abstract

The lower Maastrichtian plant megafossil site of Isona (Lleida, Catalonia, NE Spain) was discovered in 1979 and its first detailed study was published by Joan Vicente i Castells in 2002. The collection, of around 400 fossils, kept in the Museu de Geologia – Museu de Ciències Naturals de Barcelona (MGB-MCNB). In a recent study, the Vicente collection was partially revised resulting in 15 different morphotypes of dicot leaves of which only three could be assigned to the angiosperm families Lauraceae, Betulaceae and Celastraceae. In the present study, morphotypes are compared with cleared leaves of extant angiosperms and taxonomical hypotheses are proposed for most of them. Among the 17 morphotypes of dicotyledons currently distinguished in the fossil plant collection of Isona, likely members of Laurales, Proteales, Eurosids and Asterids have been identified. In addition, three new species of dicot leaves are described suggesting that the fossil flora from Isona could be more singular than previously thought.

Key words: Vicente collection, dicotyledons, fossil leaves, Maastrichtian, Isona, cleared leaves.

INTRODUCTION

In the spring of 1979, the amateur geologist Enric Sunyer discovered a plant megafossil site at the edge of an unpaved trail being opened south of the Isona village (Lleida province, Catalonia, NE Spain). The discoverer communicated the finding to Mr. Joan Vicente i Castells and colleagues from the Institut d'Estudis de la Natura del Barcelonès Nord (Santa Coloma de Gramenet, Catalonia). During the following years, the team collected numerous plant megafossils in this site (the so called Isona-*sud*) and in up to five other outcrops (Isona-*nord-est*, Isona-*est*, Isona-Comiols, Isona-*oest* and Isona-*sud-oest*) near the village (Vicente, 2002). The *Isona-sud* site was firstly announced to science in the *IV^{ème} Conférence de l'Organisation Internationale de Paléobotanique* held in Paris, by Barrón & Diéguez (1992). These authors identified members of Taxodiaceae (now included within Cupressaceae), Lauraceae, Hamamelideae and Arecaceae among the specimens previously collected by Joan Vicente and colleagues. In addition, they suggested that the plant fossils from Isona were latest Cretaceous or earliest Paleocene in age.

Twenty years after the discovery, Joan Vicente published (Fig. 1) a monograph describing the plant megafossils from the Isona sites (Vicente, 2002). He assigned a late Maastrichtian age to the sites and across the 450 specimens, identified a total of 132 species belonging to fungi, algae and vascular plants. Dicot leaves were the most abundant and were attributed to 66 species, nine of which were described for the first time. Vicente compared the specimens from Isona with plant fossil remains quoted from the Upper Cretaceous-Paleogene of Europe (Heer, 1855-1859; Velenovský, 1882-1887; Krasser, 1896) and North America (Bullock, 1916; Berry, 1916, 1925, 1930; Knowlton, 1922; Hollick, 1930; Bell, 1957, 1963; Brown, 1962). However, as noticed by Marmi *et al.* (2014), diagnoses and descriptions provided by Vicente (2002) were mostly incomplete or ambiguous and many of his taxonomic assignments appeared to be incorrect. When Vicente performed his work, the potential application of leaf architecture to palaeobotany and plant systematics was not yet fully developed (Ellis *et al.*, 2009). Moreover,

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angiosperm phylogeny was not updated making difficult to understand the phylogenetic significance of leaf characters. Like palaeobotanists of the nineteenth and twentieth centuries, he based his classification on similarities on gross morphology (leaf shape, primary and secondary vein courses or marginal outline) and related most of fossil specimens to extant genera. Vicente was unable to access the modern techniques of morphotyping and ignored the possibility of convergence in leaf structures among unrelated lineages (Doyle, 2007; Little *et al.*, 2007).

When the plant fossil collection of Isona was revised by Marmi *et al.* (2014), conifers (taxodioids, cheirolepidiaceans), monocot angiosperms (palms and likely Pandanaceans) and at least 15 types of magnoliid and eudicot angiosperm leaves were identified. Dicot leaves were morphotyped following the methods of Ellis *et al.* (2009) and were also compared with plant fossils from the Upper Cretaceous of Europe and North America reported in publications like Lesquereux (1874, 1892), de Saporta (1890, 1894), Knowlton (1922), Berry (1925), Hollick (1930), Teixeira (1948-1950, 1952), Herman & Kvaček (2010) and Halamski (2013). Of the 15 dicot morphotypes distinguished, only three were able to be assigned to a taxon: Dicot type 1 was a possible member of Lauraceae; Dicot type 7 likely belonged to Betulaceae; and Dicot type 12 was a member of Celastraceae. The botanical affinities of remaining dicot types were uncertain.

The Isona-*sud* site was excavated again in the summer 2010 and 116 plant fossils as well as pollen samples were collected. This campaign provided relevant data for sedimentology and taphonomy, indicating that the plant fossil assemblage of Isona-*sud* was parautochthonous and allochthonous and deposited in a distal floodplain (Villalba-Breva *et al.*, 2015). Pollen samples were collected from the different plant beds within one meter thick series and showed a relative abundance of fern spores. Plant remains likely came from different source plant communities growing in fluvial settings. Taphonomical data suggested that some riparian communities could be composed of alder-like trees (Dicot type 7 in Marmi *et al.*, 2014; Eudicot form 2 in Villalba-Breva *et al.*, 2015) with a diversity of ferns growing in the understory. The age of the site was restricted to Early Maastrichtian based on chrono- and biostratigraphic data (Villalba-Breva *et al.*, 2015 and references therein).

Extant angiosperms are mostly identified and classified based on comparative analysis of reproductive characters. However, reproductive structures, such as flowers, are usually scarce in the plant fossil assemblages, which in many cases are exclusively composed of leaf fossils. Frequently, leaf fossils are the only source of data to know the diversity of angiosperms in the past. As mentioned above, structures in angiosperm leaves may be highly homoplasic. However, phylogenetic evidence can be detected if leaf architecture is accurately analysed, especially in angiosperms with net-venation (Ellis *et al.*, 2009 and references therein). One of the first attempts to elucidate phylogenetic signatures from the leaf characters of dicots were carried out by Hickey & Wolfe (1975). These authors listed a number of architectural features of great importance in assessing systematic affinities at the higher taxonomic levels: 1) Simple *vs* compound organisation, 2) entire *vs* toothed margins, 3) features of teeth, 4) major vein configuration and 5) features of intercostal venation. Recent research has confirmed or refined many of the patterns noted by these authors (Doyle, 2007; Wilf, 2008 and references therein). Hickey & Wolfe based their conclusions on the classification systems of Takhtajan (1966, 1969) and Cronquist (1968), which are now outdated. In fact, many of the patterns recognised by Hickey

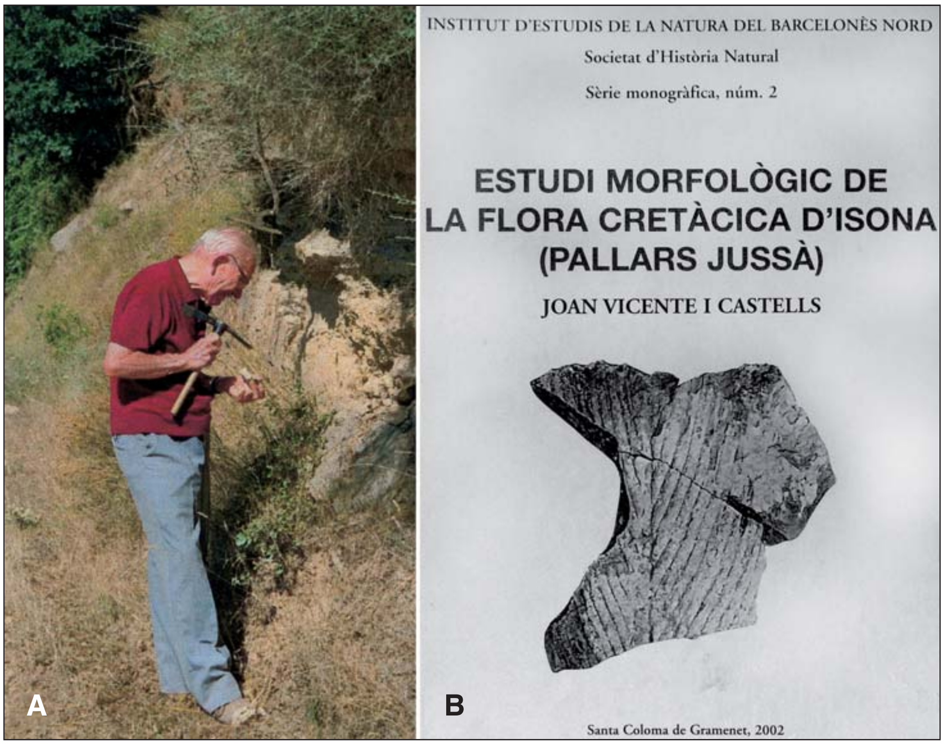


Fig. 1. A, Picture of Joan Vicente Castells taken at the Isona-*sud* site in 2003. B, Cover of the monograph on the Isona flora published by J. Vicente in 2002.
Fig. 1. A, Fotografía de Joan Vicente Castells tomada en el yacimiento Isona-*sud* en 2003. B, Portada de la monografía sobre la flora de Isona publicada por J. Vicente en 2002.

& Wolfe (1975) are even more consistent with modern molecular phylogenies than they were in the Takhtajan-Cronquist systems (Doyle, 2007). Besides generic or higher taxonomic levels, leaf characters may also be diagnostic among closely related taxa (e.g. Sajo & Rudall, 2002; Espinosa *et al.*, 2006; Doyle, 2007). Thus, it is well demonstrated that leaf architecture has a great potential to explore the taxonomic relationships of extinct flowering plants from which only the leaves are known.

Frequently, current palaeobotanists classify fossil leaves in morphotypes instead of assigning them to extant taxa. Leaf morphotypes derive from vouchered specimens and are subject to review by later researchers (Wilf, 2008). Although leaf morphotypes are not necessarily named entities, they comprise a parataxonomy for fossil floras and play a major role in many studies of regional biodiversity through time (e.g. extinction, recovery or response to climate change) (Wilf, 2008 and references therein). Morphotypes derived from specimens of the Vicente collection were coded as dicot types 1 to 15 by Marmi *et al.* (2014). In the same locality, morphotypes from newly collected specimens in the 2010 campaign were coded as eudicot forms 1 to 6 by Villalba-Breva *et al.* (2015). These coding systems may become tedious and difficult to interpret if they are repeatedly used. In the present study, dicot leaf morphotypes from the lower Maastrichtian of the Isona-*sud* site (Isona i Conca Dellà municipality, Lleida province, Catalonia, NE Spain) are compared with cleared leaves of extant angiosperms. This allows proposing hypotheses on the botanical affinities of morphotypes and suggests a binomial parataxonomy when possible.

GEOLOGICAL SETTING

All the specimens studied here come from the Isona-*sud* site. It is located in the *Pont del Molí* trail, which crosses road C-1412 just south of Isona (Lleida province, Catalonia) village. Plant bearing beds were found within one meter thick section dominated by dark grey lutites interbedded with thin, laminated silstone layers (Villalba-Breva *et al.*, 2015). It belongs to the Xullí unit, which corresponds to the uppermost portion of the Grey unit of the Tremp Formation (Mey *et al.*, 1968; Rosell *et al.*, 2001; Villalba-Breva *et al.*, 2015). The studied section was interpreted by these latter authors as deposition of overbank, suspension-load sediments in fluvio-deltaic floodplains. For further details, readers may look up to Vicente (2002), Marmi *et al.* (2014) and Villalba-Breva *et al.* (2015).

MATERIAL AND METHODS

The Vicente collection is currently housed at the Museu de Geologia - Museu de Ciències Naturals de Barcelona under the acronym MGB. One hundred eleven specimens from the Vicente collection were previously examined by Marmi *et al.* (2014) following the methods of Ellis *et al.* (2009), resulting in a total of 15 morphotypes. In the present paper, leaf features of these morphotypes are described with more detail and compared with cleared leaves of the National Cleared Leaf Collection-Wolfe (NCLC-W; http://clearedleavesdb.org/) (Das *et al.*, 2014). This database contains up to 18,126 cleared leaf images representing most of extant angiosperm families. In a first screening, pictures of the cleared leaf specimens most resembling a given morphotype from Isona were selected based on general shape, major venation and margin features. In the next step, fossil specimens belonging to each morphotype were compared in detail with selected cleared leaf images taking into account features related to secondary veins (spacing, angle), tertiary to quinternary vein framework, terminal veins and tooth shape and density when applicable. The inclusion of leaf morphotypes from Isona to suprageneric taxonomic categories (i.e. orders, families) or clades depended on the phylogenetic position of extant species whose cleared leaves were the most similar to such morphotypes. Finally, those morphotypes including the best preserved material were assigned to form-genera and species based on comparisons with leaf fossils from the Upper Cretaceous of Europe and North America.

SYSTEMATIC PALAEONTOLOGY

Clade MAGNOLIIDS
Order LAURALES
Family LAURACEAE

Genus *Daphnogene* Unger, 1845

Type species. *Daphnogene cinnamomeifolia* (Brongniart) Unger, 1845 by original designation (p. 227).

Daphnogene sp.

Fig. 2; Fig. 3

Synonymy

2002 *Benzoin attenuatum* (Heer); Vicente: 65–66, pl. XI, fig. 2
2002 *Dewalquea isonensis* Vicente: 71–72, pl. XIV, figs. 1–5
2002 *Ficus cannonii* (Knowlton); Vicente: 77, pl. XVIII, fig. 3
2002 *Carya heerii* (Ettingshausen); Vicente: 82–83, pl. XIX, fig. 9
2002 *Zizyphus ripleyensis* (Berry); Vicente: 111–112, pl. XXXI, fig. 1
2014 Dicot type 1 Marmi *et al.*: 48, 53, pl. III, fig. 1; pl. IV, fig. 1

Material. Specimens MGB 38220, MGB 38223, MGB 38225–27, MGB 38229, MGB 38235, MGB 38239, MGB 38269, MGB 38302, MGB 38337–38, MGB 38403.

Occurrence. Isona-*sud* site (see Villalba-Breva *et al.*, 2015 for details).

Description. Leaves are simple, petiolate and microphyllous. The petiole-lamina attachment is marginal (Fig. 2F). Laminae are incomplete, lanceolate to linear, symmetrical and entire-margined (Fig. 2). They are 20.0–119.8 mm long and 12.7–24.8 mm wide. Based on the most complete blades (e.g. Fig. 2F), the length/width ratio ranges from 7 to 8. Lamina bases are symmetrical, acute and cuneate (Fig. 2C–D, F; Fig. 3A, C–D, F). Apices are narrow, acute and straight (Fig. 2A, E–F; Fig. 3A, E–F). There are three basal veins (Fig. 2C–D; Fig. 3A–D, F). The midvein is straight and two to three times wider than the basal secondary veins. The latter arise from or near the base at very acute angles (11º-13º) and run parallel to the midvein at least up to the middle of the lamina. They may be eucamptodromous or attach to the following secondary vein. Distal secondary veins are brochidodromous and excurrently attached to the midvein (Fig. 2E; Fig. 3E). The secondary vein spacing abruptly increases towards the base. Tertiary veins are not preserved except for MGB 38220 that shows a few, blurred percurrent tertiaries.

Discussion. Vicente (2002) assigned the Isona specimens to *Daphnogene lanceolata* Unger, 1851, *Carya heerii* Ettingshausen, 1854, *Benzoin attenuatum* Heer, 1855–1859, *Ficus cannonii* Knowlton, 1922, *Zizyphus ripleyensis* Berry, 1925 and to the new species *Dewalquea isonensis*. The species *D. lanceolata* includes elongated leaves with two long, basal secondary veins very similar in size, shape and venation to the specimens housed in the Vicente collection (cf. figs. 18–20, 23, 26–27, 25 in Hably, 1989; cf. Hably, 1994: pl. II, figs. 5–6). *Carya heerii* has dentate margins and the basal secondary veins are not widely spaced from subsequent secondary veins, unlike the studied specimens (cf. Heer, 1855–1859: pl. CXXXI, figs. 8–17). In *B. attenuatum*, basal secondaries are closer to subsequent secondary veins than in the specimens from Isona (Heer, 1855–1859: pl. XC, fig. 10). *Ficus cannonii* is obovate to elliptic instead of lanceolate or linear (Knowlton, 1922: pl. VI, fig. 3; pl. X, fig. 1). *Zizyphus ripleyensis* has dentate margins in the apical half of the lamina, unlike the studied specimens (Berry, 1925: pl. XIII, figs. 5–9). The holotype of *D. isonensis* contains different leaves that Vicente (2002) included in a single species of a three or five pinnately compound leaf. However, features of at least two of these leaves match those of *D. lanceolata*.

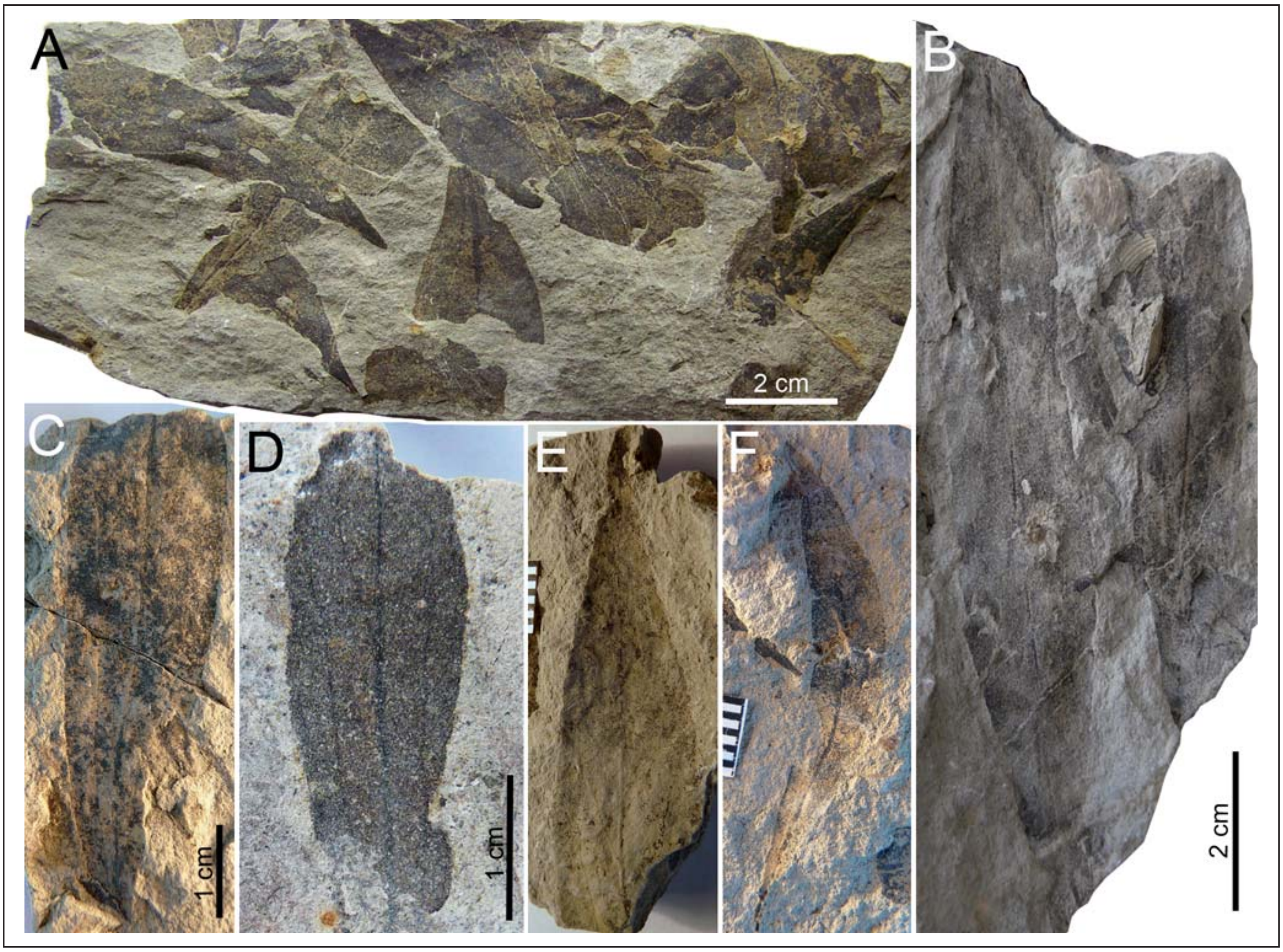


Fig. 2. *Daphnogene* sp. from Isona-*sud* site: A, MGB 38223, accumulation of several fragments of leaves; B, MGB 38227, two leaves lacking basal and apical ends; C, MGB 38229, leaf base showing a stout midvein and thin basal secondary veins. D, MGB 38337, leaf base showing basal secondary veins better preserved; E, MGB 38226, apical end showing thin, brochidodromous secondary veins. F, MGB 38235, complete leaf lamina. Scale in E and F, 1 cm.

Fig. 2. *Daphnogene* sp. del yacimiento Isona-*sud*: A, MGB 38223, acumulación de varios fragmentos de hojas; B, MGB 38227, dos hojas sin las partes basal y apical; C, MGB 38229, parte basal de una hoja mostrando el nervio principal grueso y nervios secundarios basales finos; D, MGB 38337, parte basal de una hoja mostrando nervios basales secundarios mejor preservados; E, MGB 38226, parte apical de una hoja mostrando nerviación secundaria fina y broquidódroma. F, MGB 38235, lámina completa. Escala en E y F, 1 cm.

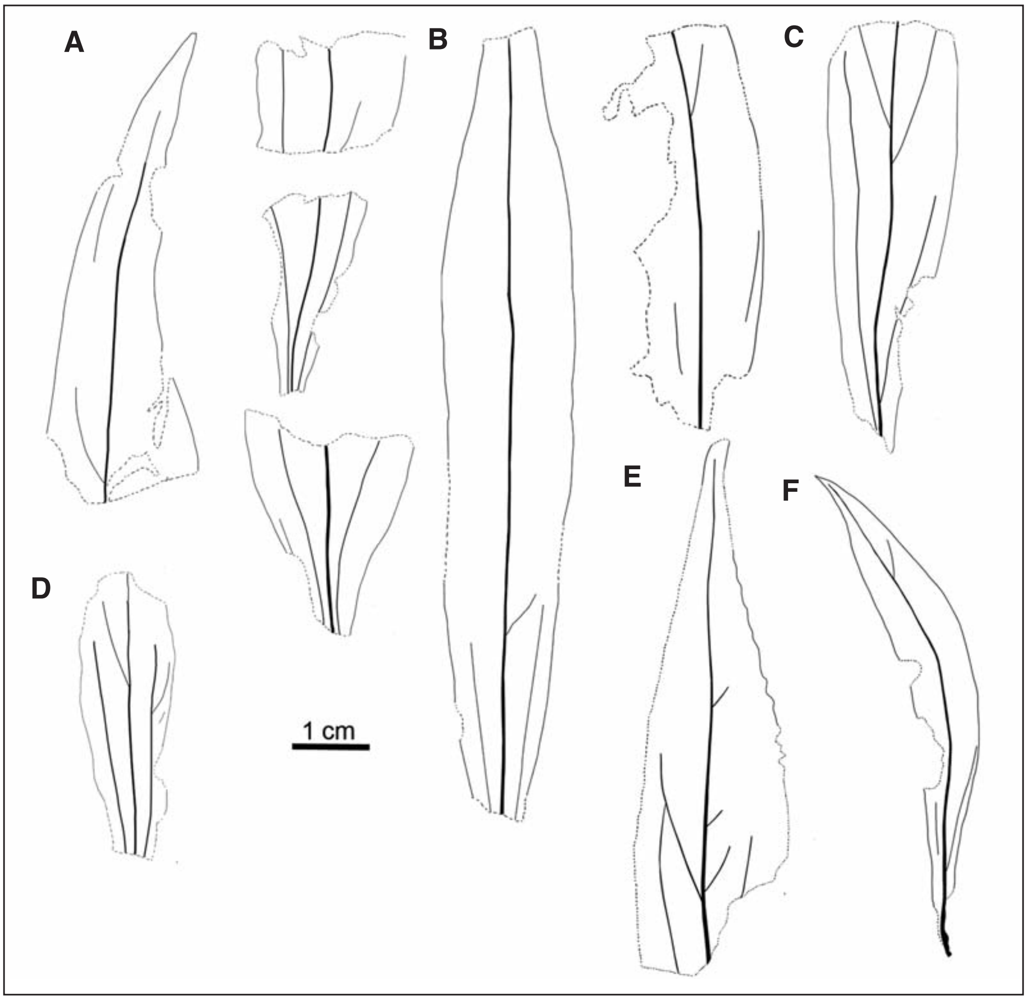


Fig. 3. *Daphnogene* sp. from Isona-*sud* site, interpretative drawings: A, MGB 38223; B, MGB 38227; C, MGB 38229; D, MGB 38337; E, MGB 38226; F, MGB 38235.
Fig. 3. Dibujos interpretativos de *Daphnogene* sp. del yacimiento Isona-*sud*: A, MGB 38223; B, MGB 38227; C, MGB 38229; D, MGB 38337; E, MGB 38226; F, MGB 38235.

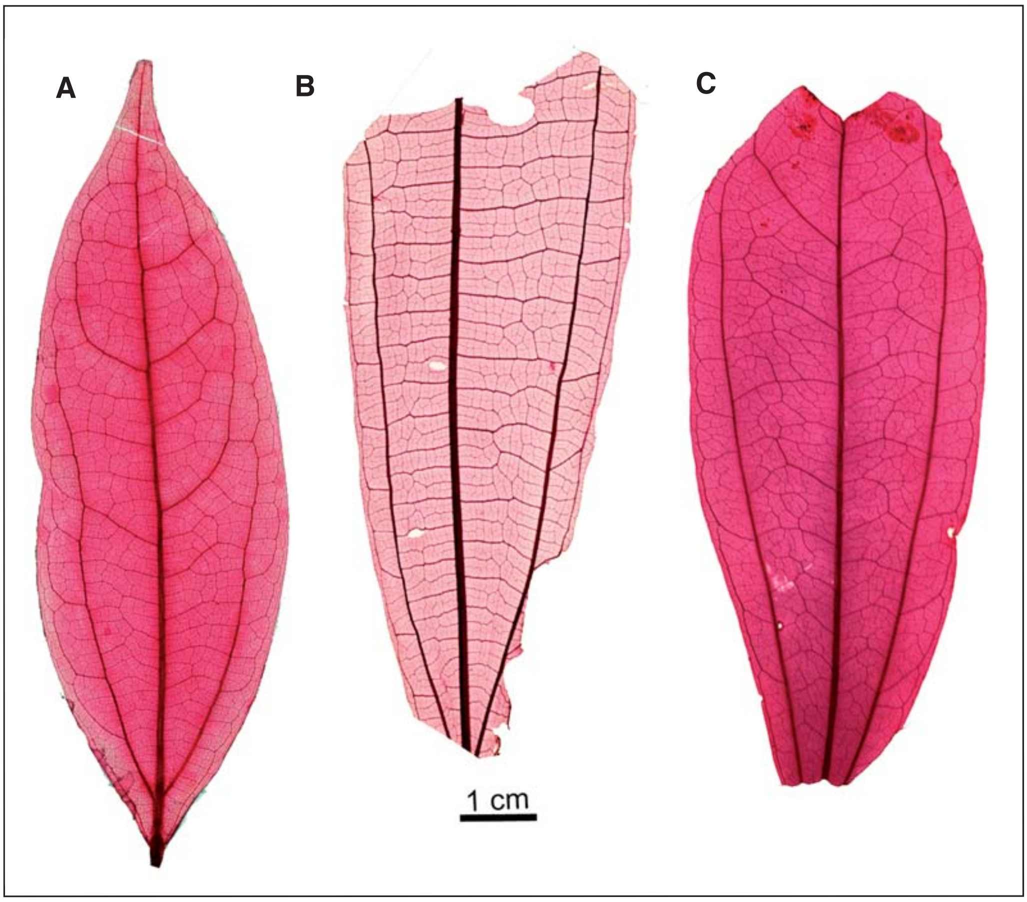


Fig. 4. Specimens of the National Cleared Leaf Collection-Wolfe (NCLC-W) compared to *Daphnogene* sp. from Isona-*sud*: A, Lauraceae, *Phoebe trinervis* Lund, DS652549; B, Malvaceae, *Quararibea sanblasensis* Robyns, UCH1389623: C, Oleaceae, *Myxopyrum smilacifolium* Blume, ID 90_14016.
Fig. 4. Ejemplares de la National Cleared Leaf Collection-Wolfe (NCLC-W) comparados con *Daphnogene* sp. de Isona-*sud*: A, Lauraceae, *Phoebe trinervis* Lund, DS652549; B, Malvaceae, *Quararibea sanblasensis* Robyns, UCH1389623; C, Oleaceae, *Myxopyrum smilacifolium* Blume, ID 90_14016.

Elongated fossil leaves, with entire margins and two long basal secondary veins are usually attributed to Lauraceae (e.g. Fig. 4A) (Hill, 1986; Conrad & Christophel, 1998; Doyle, 2007). Accordingly, Marmi *et al.* (2014) included specimens from Isona showing these characters in the Dicot type 1, which was a likely member of Lauraceae. These features, however, were also observed in members of some families of eudicots such as Malvaceae (e.g. *Quararibea sanblasensis* Robyns, Fig. 4B) and Oleaceae (e.g. *Myxopyrum smilacifolium* Blume, Fig. 4C). Nevertheless, based on the strong similarities, specimens from Isona may be assigned to *Daphnogene* sp. and are included within Lauraceae, as partially suggested Vicente (2002) and Marmi *et al.* (2014).

Family UNKNOWN

Genus *Cinnamomophyllum* Kräusel & Weyland, 1950

Type species. *Cinnamomophyllum (Cinnamomum) scheuchzeri* (Heer) Kräusel & Weyland, 1950 by original designation (p. 68, pl. 11, fig. 7; pl. 16, figs. 1-7; pl. 17, figs. 1, 4-6).

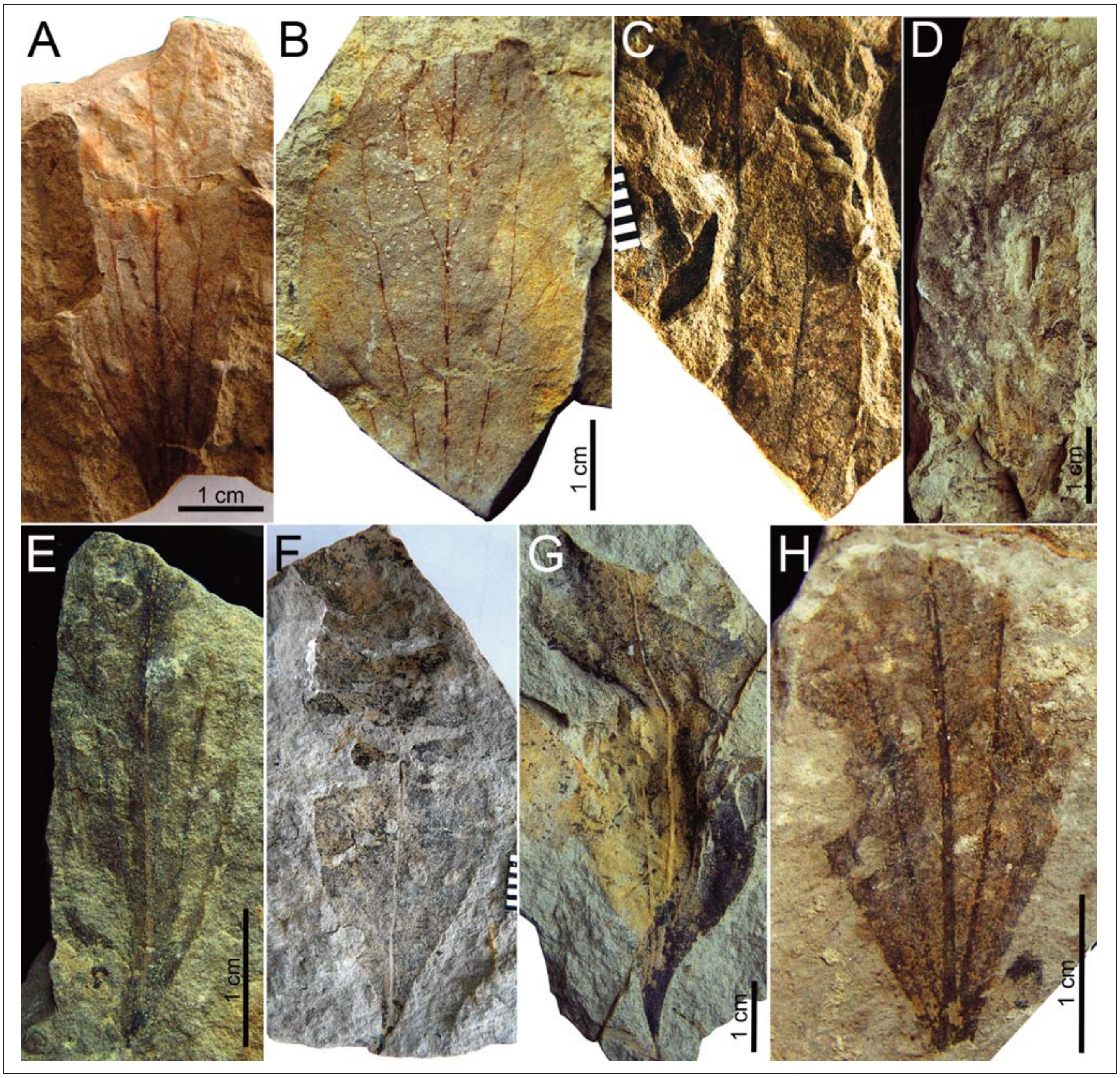


Fig. 5. *Cinnamomophyllum vicente-castellum* n. sp. from the Isona-*sud* site: A, holotype MGB 38257; B, paratype MGB 38256; C, paratype MGB 38233; D, MGB 38325, fragment of leaf lacking the base and the apex; E, MGB 38401, basal end of a leaf; F, MGB 38268, basal end of a leaf bearing a short petiole; G, MGB 38258, basal part of a leaf showing well preserved primary veins and a short petiole; H, MGB 38357, basal part of a leaf showing five primary veins.

Fig. 5. *Cinnamomophyllum vicente-castellum* n. sp. del yacimiento Isona-*sud*: A, holotipo MGB 38257; B, paratipo MGB 38256; C, paratipo MGB 38233; D, MGB 38325, fragmento de hoja sin las partes apical y basal; E, MGB 38401, parte basal de una hoja; F, MGB 38268, parte basal de una hoja con un corto peciolo unido; G, MGB 38258, parte basal de una hoja con las nervios primarios preservados y un peciolo corto; H, MGB 38357, parte basal de una hoja mostrando cinco nervios primarios.

Cinnamomophyllum vicente-castellum n. sp.
Figs. 5; Fig. 6

Synonymy
2002 *Malapoenna louisvillensis* (Knowlton); Vicente: 69, pl. XXVI, figs. 4–6; XLV, 1–2
2002 *Quercus turbulenta* (Hollick); Vicente: 84–85, pl. XX, fig. 3
2002 *Zizyphus ripleyensis* (Berry); Vicente: 111–112, pl. XXXI, fig. 1
2014 Dicot type 2 Marmi *et al.*: 53, pl. III, fig. 2; pl. IV, fig. 2

Holotype. Specimen MGB 38257.

Paratypes. Specimens MGB 38233 and MGB 38256.

Specific diagnosis. Leaf symmetrical, entire margined, microphyll to notophyll. Leaf base symmetrical, concave or decurrent. Five actinodromous primary veins diverging from the base. Interior secondary veins straight to arched. Exterior secondary veins brochidodromous. Epimedial and intercostal tertiary veins percurrent. Exterior tertiary veins looped.

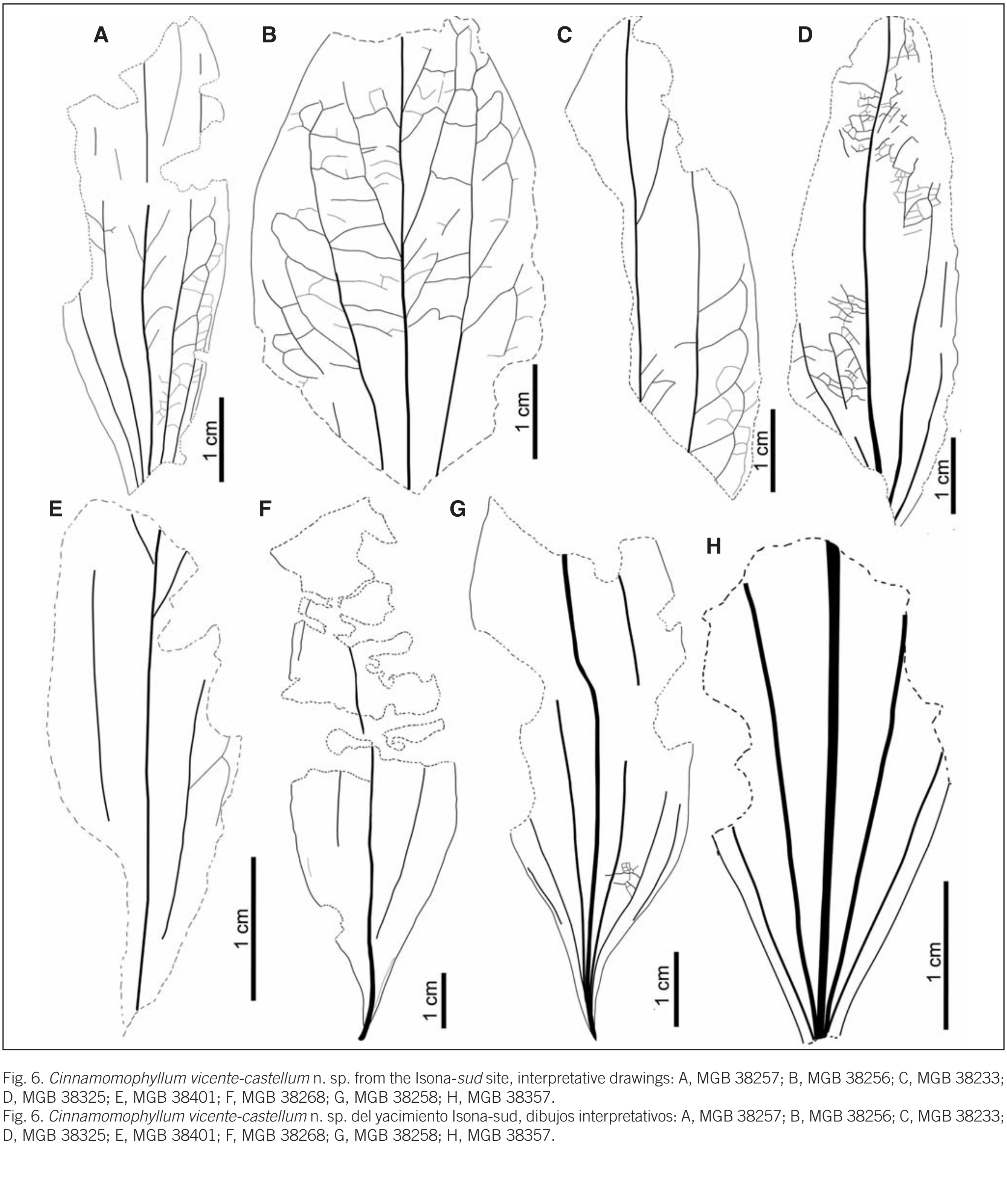


Fig. 6. *Cinnamomophyllum vicente-castellum* n. sp. from the Isona-*sud* site, interpretative drawings: A, MGB 38257; B, MGB 38256; C, MGB 38233; D, MGB 38325; E, MGB 38401; F, MGB 38268; G, MGB 38258; H, MGB 38357.
Fig. 6. *Cinnamomophyllum vicente-castellum* n. sp. del yacimiento Isona-sud, dibujos interpretativos: A, MGB 38257; B, MGB 38256; C, MGB 38233; D, MGB 38325; E, MGB 38401; F, MGB 38268; G, MGB 38258; H, MGB 38357.

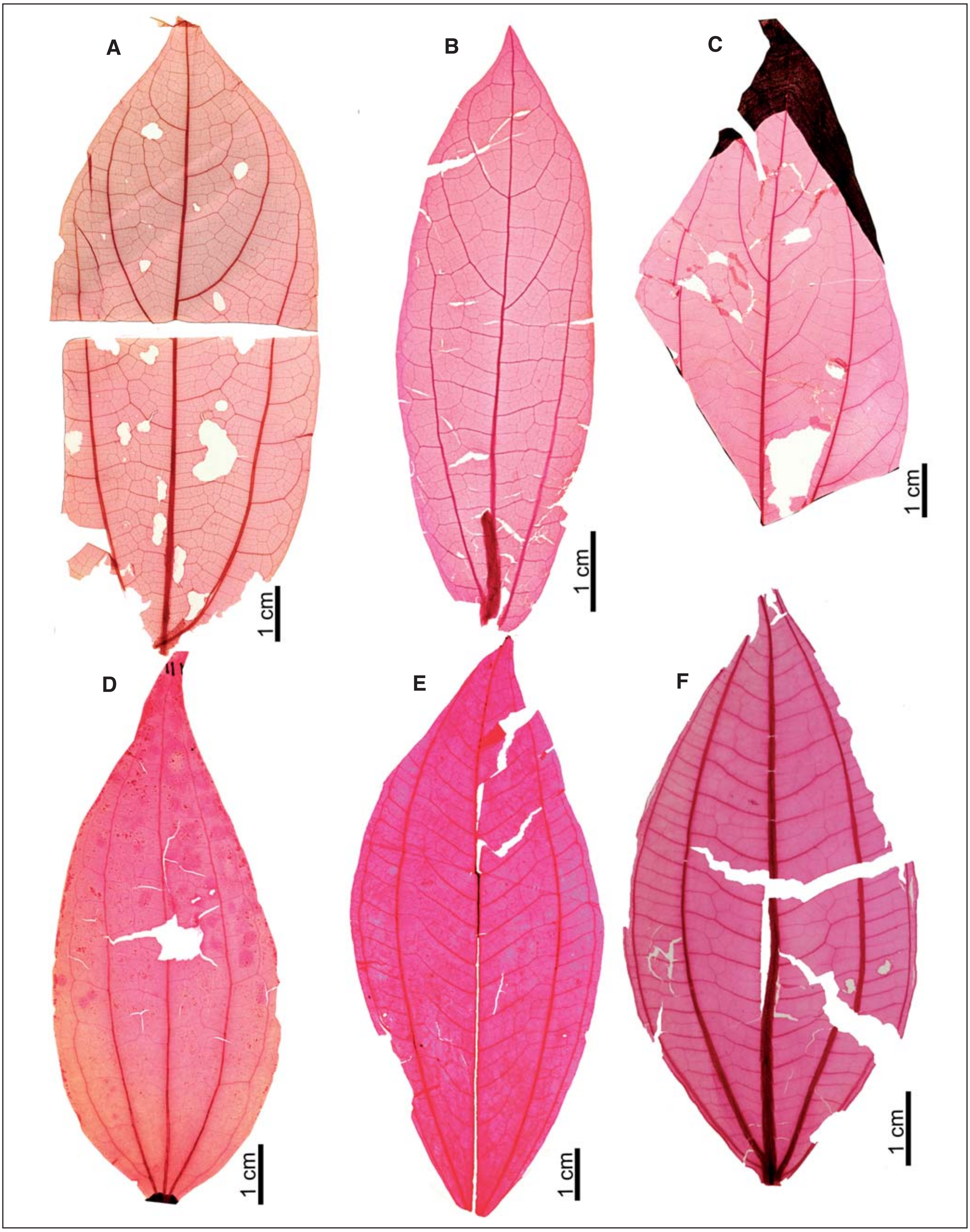


Fig. 7. Specimens of the National Cleared Leaf Collection-Wolfe (NCLC-W) compared to *Cinnamomophyllum vicente-castellum* n. sp. from the Isona-*sud* site: A, Lauraceae, *Caryodaphnopsis tonkinensis* (Lecomte) Airy Shaw, UCH316972; B, Hernandiaceae, *Sparattanthelium macusiorum* Smith, MO1163334; C, Bixaceae, *Bixa excelsa* Gleason and Krukoff, UCH605774; D, Loranthaceae, *Ginalloa cumingiana* Bentham and Hooker, UC449216; E, Melastomataceae, *Tristemma incompletum* Brown, UC1283772; F, Melastomataceae, *Barthea chinensis* Hooker, MO1275954.

Fig. 7. Ejemplares de la National Cleared Leaf Collection-Wolfe (NCLC-W) comparados con *Cinnamomophyllum vicente-castellum* n. sp. procedente de Isona-*sud*: A, Lauraceae, *Caryodaphnopsis tonkinensis* (Lecomte) Airy Shaw, UCH316972; B, Hernandiaceae, *Sparattanthelium macusiorum* Smith, MO1163334; C, Bixaceae, *Bixa excelsa* Gleason and Krukoff, UCH605774; D, Loranthaceae, *Ginalloa cumingiana* Bentham and Hooker, UC449216; E, Melastomataceae, *Tristemma incompletum* Brown, UC1283772; F, Melastomataceae, *Barthea chinensis* Hooker, MO1275954.

Etymology. In honour of Mr. Joan Vicente Castells, enthusiastic amateur palaeobotanist who carried out the first systematic study of the Isona flora.

Type locality. Isona-*sud* site, located along the *Pont del Molí* trail, 500 metres south of Isona village (Isona i Conca Dellà municipality, *comarca* (=county) Pallars Jussà, Lleida province, Catalonia, NE Spain).

Stratigraphic position. Marly beds belonging to the Xullí unit of the lower part of the Tremp Formation (see Villalba-Breva *et al*., 2015 for details).

Age. Early Maastrichtian as determined by stratigraphic correlation and biostratigraphy (see Villalba Breva *et al*., 2015 for details).

Material. Specimens MGB 38233, MGB 38256–57, MGB 38325, MGB 38401 and, most likely, MGB 38172, MGB 38258, MGB 38268, MGB 38356–57 and MGB 38400.

Description. Leaves are simple and the lamina attachment marginal. The petiole is short, 3.8 mm long and 1.1 mm wide (Fig. 5F–G). The leaf size ranges from microphyll to notophyll, being 29.7–91.8 mm long and 14.1–35.5 mm wide. The lamina is not completely preserved in any specimen. Nevertheless, it seems elliptic in outline and is symmetrical and entire-margined. The base is symmetrical, acute, and concave or decurrent (Fig. 5A, E–H). Apices are likely acute but their shapes are unknown because they are not well preserved (Fig. 5B–C). The venation is actinodromous with five primary veins diverging from the base (Fig. 5A, G–H; Fig. 6A, G–H). Admedial primary veins are thick, very long and connect with secondary veins emerging from midvein, in the apical third of the lamina (Fig. 5B; Fig. 6B). Exmedial primary veins are slender and connect with basalmost exterior secondary veins, in the basal third of the lamina (Fig. 5A; Fig. 6A). Exterior secondary veins are thin and brochidodromous (Fig. 5A–C; Fig. 6A–C). Interior secondary veins are straight to arched (Fig. 5A–C; Fig. 6A–C). Epimedial tertiary veins form a chevron or are opposite percurrent while intercostal tertiary veins are straight to sinuous opposite percurrent (Fig. 5B; Fig. 6B). The angles of percurrent tertiary veins are inconsistent. Exterior tertiary veins are looped (Fig. 5A, C; Fig. 6A, C). Quaternary veins are reticulate and weakly preserved in a few specimens (Fig. 5C–D; Fig. 6C–D).

Discussion. Vicente (2002) attributed the specimens from Isona to *Malapoenna louisvillensis* Knowlton, 1922, *Quercus turbulenta* Hollick, 1930 and *Zizyphus ripleyensis* Berry, 1925. In the original report of Knowlton, the description of *Malapoenna louisvillensis* was based on an apical half of a leaf in which it is difficult to ascertain the number of basal primary veins (Knowlton, 1922: pl. VII, fig. 5). Subsequently, this species was regarded as a synonym of *Ficus affinis* Brown, 1962. The latter is featured by having three, instead of five, primary veins (Brown, 1962: pl. 27, figs. 1–2, 5; pl. 43, figs. 7–8). *Quercus turbulenta* has pinnate venation unlike the specimens from Isona (Hollick, 1930: pl. 38, fig. 3). *Zizyphus ripleyensis* has up to five primary veins but dentate margins in the apical half of the lamina (Berry, 1925: pl. XIII, figs. 5–9). In addition, Marmi *et al.* (2014) compared these specimens with *Zizyphus hendersonii* Knowlton, 1922, *Z. coloradensis* Knowlton, 1922 and *Ficus impressa* Knowlton, 1922. *Zizyphus hendersonii* has five basal primary veins, but exterior secondary veins are eucamptodromous instead of brochidodromous (Knowlton, 1922: pl. XV, figs. 1–2). In addition the laminar base of *Z. hendersonii* is wide and rounded while in the specimens from Isona it is narrow and concave or decurrent. *Zizyphus coloradensis* has also five primary veins and resembles in shape the specimens from Isona, but the specimen figured by Knowlton (Knowlton, 1922: pl. XV, fig. 5) lacks details of secondary and tertiary venation. *Ficus impressa* has only three basal primary veins (Knowlton, 1922: pl. VII, figs. 1–3; pl. XVI, fig. 3). *Zizyphus* and *Ficus* are members of Rosales and belong to families Rhamnaceae and Moraceae, respectively. However, Marmi *et al.* (2014) attributed the specimens from Isona to Dicot type 2, of uncertain botanical affinity.

The new species from Isona is very similar in shape and venation to *Caryodaphnopsis tonkinensis* (Lecomte) Airy Shaw and *Sparattanthelium macusiorum* Smith, which are members of Lauraceae and Hernandiaceae, respectively, within Laurales (Fig. 7A–B). However, these species have three basal primary veins and exmedial thinner primary veins are completely replaced by brochidodromous secondary veins. The venation of specimen MGB 38256 strongly resembles *Bixa excelsa* Gleason & Krukoff, included within Malvales (Fig. 7C). However this species has wide and rounded leaf bases. *Ginalloa cumingiana* Bentham & Hooker, a member of Santalales, has five basal veins but, unlike the studied specimens, the admedial primary veins are acrodromous (Fig. 7D). Several species within family Melastomataceae have also five basal veins as well as acrodromous admedial primary veins (e.g. *Tristemma incompletum* Brown or *Barthea chinensis* Hooker) (Fig. 7E–F). Based on the following characters (entire margins, palmate venation, secondary veins brochidodromous) and strong similarities with the extant *Caryodaphnopsis tonkinensis* and *Sparattanthelium macusiorum*, the new species from Isona is attributed to Laurales and the form-genus *Cinnamomophyllum*. This form-genus is assigned to leaves showing pseudo-palmate venation with a pair of admedial veins departing nearly to the petiole, parallel to and thicker than secondary veins, and thinner marginal veins (cf. Hill, 1986).

Remarks. Marmi *et al.* (2014) included poorly preserved leaves with three to five basal actinodromous primary veins to Dicot type 2 (Fig. 5F–H). These specimens were previously assigned by Vicente (2002) to the following species: *Ginkgo adiantoides* Heer, 1878 (*in* Heer 1868-1880), *Ficus post-trinervis* Knowlton, 1922, *Macclintockia alaskana* Hollick, 1930, *Zizyphus hendersonii* Knowlton, 1922 and *Piper oblongifolia* Vicente, 2002.

Clade EUDICOTS
Clade ROSIDS
Clade EUROSIDS II
Order UNKNOWN
Family UNKNOWN

Genus *Myrtophyllum* Heer, 1869

Type species. *Myrtophyllum geinitzi* Heer, 1869 by original designation (p. 22, pl. 11, figs. 3-4).

cf. *Myrtophyllum* sp.

Fig. 8; Fig. 9

Synonymy

2002 *Laurophyllum ripleyensis* (Berry); Vicente: 68–69, pl. XI, fig. 5
2002 *Nectandra prolifica* (Berry); Vicente: 70, pl. XI, figs. 7–9
2002 *Juglans wadii* (Berry); Vicente: 82, pl. XX, fig. 6

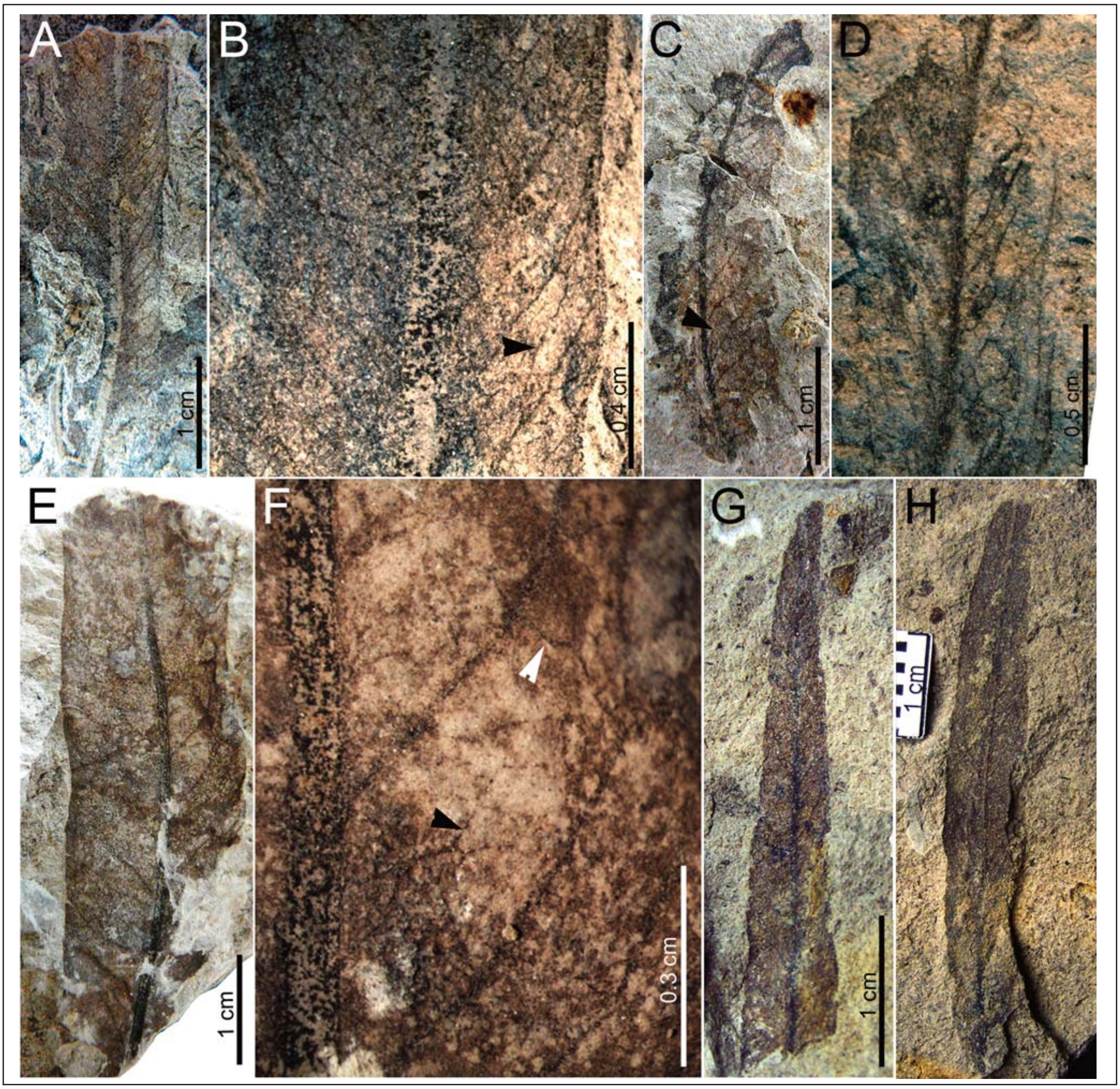


Fig. 8. cf. *Myrtophyllum* sp. from the Isona-*sud* site: A, MGB 38388, fragment of the middle of a lamina; B, detail of MGB 38388 venation showing thin secondary veins arising from the stout midvein and a composite admedial tertiary vein (arrowed); C, MGB 38386, fragment of leaf showing an intersecondary vein (arrowed); D, MGB 38383, fragment of leaf showing details of venation; E, MGB 38298, fragment of leaf; F, detail of MGB 38298 venation showing composite admedial (black arrow) and percurrent (white arrow) tertiary veins; G, MGB 38248, apical end of a leaf; H, MGB 38244, fragment of a leaf lacking the apical end.

Fig. 8. cf. *Myrtophyllum* sp. del yacimiento Isona-*sud*: A, MGB 38388, fragmento de la parte media de una lámina; B, detalle de MGB 38388 mostrando nervios secundarios finos que se separan de un nervio principal grueso y un nervio terciario admedial compuesto (flecha); C, MGB 38386, fragmento de hoja mostrando un nervio intersecundario (flecha); D, MGB 38383, fragmento de hoja mostrando detalles de la nervadura; E, MGB 38298, fragmento de hoja; F, detalle de MGB 38298 mostrando nervios admediales compuestos (flecha negra) y percurrentes (flecha blanca); G, MGB 38248, extremo apical de una hoja; H, MGB 38244, fragmento de hoja sin el extremo apical.

2002 *Carya heerii* (Ettingshausen); Vicente: 82–83, pl. XIX, fig. 4
2002 *Proteophyllum acus* (Velenovsky & Viniklar); Vicente: 104–105, pl. XIII, fig. 3
2002 *Eucaliptus angusta* (Velenovsky); Vicente: 106–107, pl. XXVIII, figs. 1–2
2002 *Eucaliptus geinitzii* (Heer); Vicente: 107–108, pl. XXVIII, figs. 4–5
2014 Dicot type 3 Marmi *et al.*: 53, pl. III, fig. 3; pl. IV, fig. 3
2015 Eudicot form 1 Villalba-Breva *et al.*: 39, figs. 3D, 4A–B

Material. Specimens MGB 38134, MGB 38232, MGB 38243, MGB 38245, MGB 38248, MGB 38289, MGB 38298, MGB 38358, MGB 38383, MGB 38386, MGB 38388 and MGB 38391–93.

Occurrence. Isona-*sud* site (see Villalba-Breva *et al.* 2015 for details).

Description. Leaves are petiolate, simple and microphyllous. All laminae are incomplete, 14.6–59.4 mm long and 4.6–14.8 mm wide. They are linear, symmetrical, with entire margins (Fig. 8). The apex is acute and straight, while the base is acute and decurrent (Fig. 8G–H). The midvein is stout and straight. The secondary veins are very thin and mostly eucamptodromous (Fig. 8B–D, F; Fig. 9). They are irregularly spaced and excurrently attached to the midvein. The secondary vein angles are inconsistent and range from 35.1° to 42.8°. A few intersecondary veins are present in some specimens (Fig. 8C). They run parallel to adjacent secondaries and are shorter than the 50% of the subjacent secondary vein. Tertiary veins are usually opposite percurrent but, in some cases, they seem composite admedial (Fig. 8B, F). Quaternary and quinternary veins are preserved in some specimens, showing well-developed areoles (Fig. 9).

Discussion. Vicente (2002) assigned these leaves to the following species: *Laurophyllum ripleyensis* Berry, 1925, *Nectandra prolifica* Berry, 1925, *Juglans wadii* Berry, 1925, *Carya heerii* Ettingshausen, 1854, *Eucaliptus angusta* Velenovsky, 1882–1887, *E. geinitzii* Heer, 1885 and *Proteophyllum acus* Velenovsky & Viniklar, 1926–1931. In *Laurophyllum ripleyensis,* leaves are elliptic instead of linear and the space between secondary veins is greater than in the specimens from Isona (Berry, 1925: pl. XVIII, figs. 4–8). *Nectandra prolifica, J. wadii* and *E. geinitzii* show brochidodromous venation (cf. fig. 1375 in Dana, 1896; Berry, 1925: pl. IV, figs. 1–3; pl. XVII, figs. 1–3; cf. Kvaček, 1992: pl. 1, fig. 5; pl. 2, fig. 2). *Carya heerii* has dentate margins unlike the studied specimens (cf. Heer, 1855–1859: pl. CXXXI, figs. 8–17). Based on the original drawings by J. Velenovsky, *E. angusta* has perimarginal veins (Velenovsky, 1882–1887: pl. XXX, figs. 2, 8, 10). Nevertheless, leaves with brochidodromous secondary veins were assigned to this species by Kvaček (1992: pl. 1, figs. 4–5; pl. 2, figs. 4–6). The specimen MGB 38383 was assigned to *Proteophyllum acus* by Vicente (2002). However, it closely resembles *Andromeda parlatorii* Heer, *in* Capellini & Heer, 1867 from the Upper Cretaceous of North America (cf. fig. 1372 in Dana, 1896). In the original publication, this species is repre-

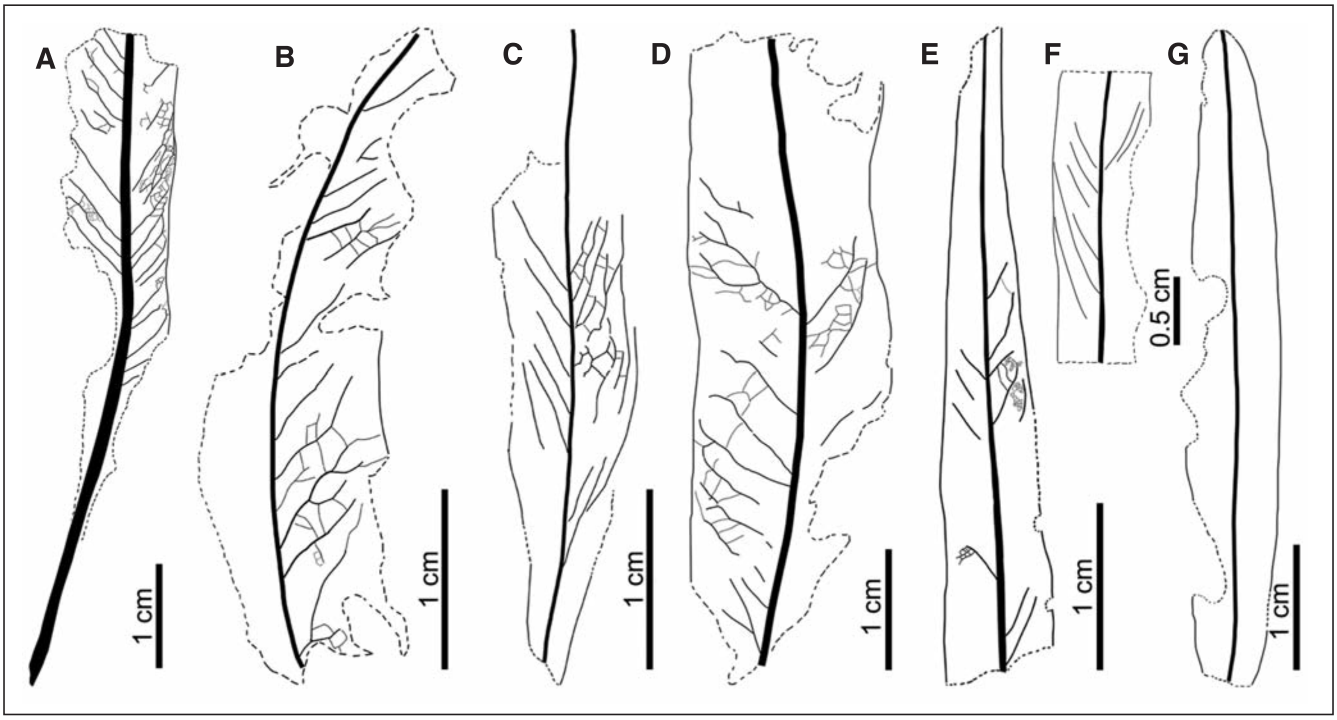


Fig. 9. cf. *Myrtophyllum* sp. from the Isona-sud site, interpretative drawings: A, MGB 38388; B, MGB 38386; C, MGB 38383; D, MGB 38298; E, MGB 38248; F, detail of MGB 38244 showing thin secondary veins; G, MGB 38244.
Fig. 9. cf. *Myrtophyllum* sp. del yacimiento Isona-*sud*, dibujos interpretativos: A, MGB 38388; B, MGB 38386; C, MGB 38383; D, MGB 38298; E, MGB 38248; F, detalle de MGB 38244 mostrando nervios secundarios; G, MGB 38244.

sented by a drawing of a partial leaf with pinnate camptodromous venation lacking more details (Capellini & Heer, 1867: pl. 1, fig. 5). A detailed description of *A. parlatorii* was provided by Berry (1914) with the following characters shared with the Isona specimens: cuneate or slightly decurrent base; midvein stout; secondaries, numerous, thin, subparallel, arising from the midvein at acute angles and camptodromous; tertiary veins mostly straight transverse. However, leaves belonging to *A. parlatorii* are longer (about 10–12 cm) and wider (3 cm). Extant species of *Andromeda* are included within Ericaceae. Marmi *et al.* (2014) assigned leaves from Isona to Dicot type 3 but did not resolve their botanical affinities. However, these authors found similarities among these specimens and *Salix assimilis* de Saporta, 1894 from the upper Albian from Nazareth (Portugal) (de Saporta, 1894: pl. XXXVI, fig. 8; pl. XXXVII, figs. 2–3, 6, 13). Nevertheless, in some specimens drawn in the work by G. de Saporta, secondary veins were brochidodromous unlike the specimens from Isona (e.g. de Saporta, 1894: pl. XXXVII, fig. 13). The leaf fossils from Isona-*sud* named as Eudicot form 1 by Villalba-Breva *et al.* (2015) are very similar to the leaves herein described and likely belong to the same taxon (fig. 3D, fig. 4A–B in Villalba-Breva *et al.*, 2015).

Several extant eudicot species show similar shape and venation like the leaf fossils from Isona assigned to Dicot type 3 by Marmi *et al.* (2014): *Astianthus viminalis* (Kunth) Baillon within Bignoniaceae (Fig. 10A), *Haplorhus peruviana* Engler within Anacardiaceae (Fig. 10B), *Heterodendron oleaefolium* Desfontaines within Sapindaceae

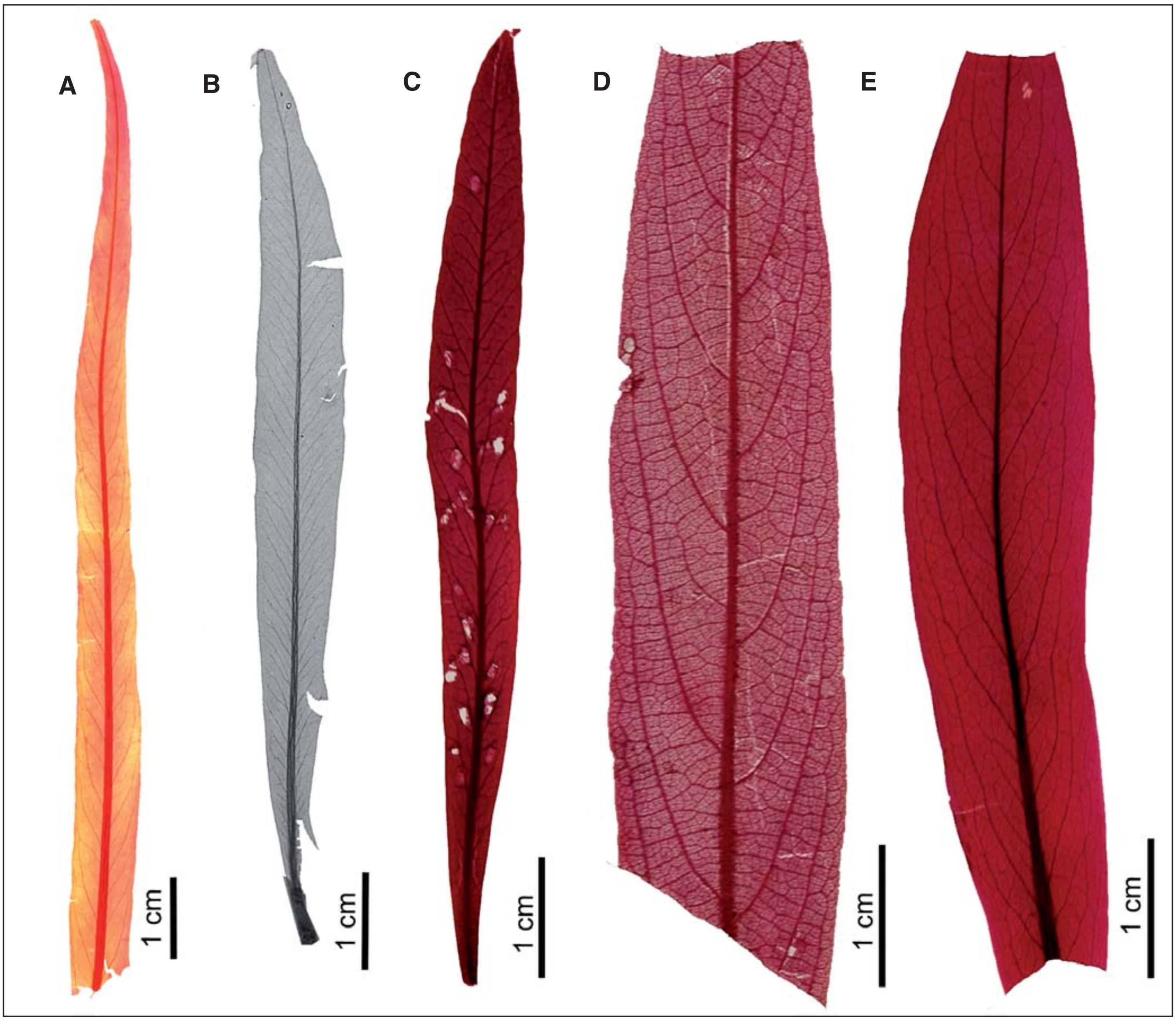


Fig. 10. Specimens of the National Cleared Leaf Collection-Wolfe (NCLC-W) compared to cf. *Myrtophyllum* sp. from the Isona-*sud* site: A, Bignoniaceae, *Astianthus viminalis* (Kunth) Baillon, DS631975; B, Anacardiaceae, *Haplorhus peruviana* Engler, UCH565038; C, Sapindaceae, *Heterodendron oleaefolium* Desfontaines, UC870357; D, Sterculiaceae, *Helicteres angustifolia* Linnaeus, UCH343661; E, Thymelaeaceae, *Lasiosiphon eriocephalus* Decaisne, UCH262245.

Fig. 10. Ejemplares de la National Cleared Leaf Collection-Wolfe (NCLC-W) comparados con cf. *Myrtophyllum* sp. del yacimiento Isona-*sud*: A, Bignoniaceae, *Astianthus viminalis* (Kunth) Baillon, DS631975; B, Anacardiaceae, *Haplorhus peruviana* Engler, UCH565038; C, Sapindaceae, *Heterodendron oleaefolium* Desfontaines, UC870357; D, Sterculiaceae, *Helicteres angustifolia* Linnaeus, UCH343661; E, Thymelaeaceae, *Lasiosiphon eriocephalus* Decaisne, UCH262245.

(Fig. 10C), *Helicteres angustifolia* Linnaeus within Sterculiaceae (Fig. 10D) and *Lasiosiphon eriocephalus* Decaisne within Thymelaeaceae (Fig. 10E). All these families, except Bignoniaceae, are members of the clade Eurosids II according to APG (2009). The genus *Myrtophyllum* includes linear, entire-margined leaves with pinnate venation, secondary veins joined into an intramarginal vein, intersecondary veins, tertiary veins ranging from reticulate to percurrent and reticulate quaternary veins (Kvaček, 1983, 1992). Even though the studied specimens lack intramarginal veins, they are tentatively assigned to the genus *Myrtophyllum* based on the remaining features and because the extant Myrtales belong to Eurosids II.

Clade EUROSIDS I
Order MALPIGHIALES?
Family SALICACEAE?

Genus *Saliciphyllum* Fontaine, 1889

Type species. *Saliciphyllum longifolium* Fontaine, 1889 by original designation (p. 302, pl. 150, figs. 17-19).

Saliciphyllum serratum n. sp.
Fig. 11; Fig. 12

Holotype. The specimen MGB 38307.
Paratypes. Specimens MGB 38306 and MGB 38310.

Synonymy

2002 *Myrica wadii* (Berry) Vicente i Castells: 83–84, pl. XX, fig. 1–2
2002 *Dewalquea isonensis* Vicente i Castells: 71–72, pl. XIV, figs. 1–5
2014 Dicot type 4 Marmi *et al.*: 53, pl. III, fig. 4; pl. IV, fig. 4

Specific diagnosis. Leaves microphyllous, lanceolate to linear. Apex acuminate. Margins slightly serrate. Teeth small, simple, triangular or hook-like shaped and regularly spaced. Teeth density is 3–4 teeth/cm. Sinuses shallow, broad and rounded. Venation pinnate, brochidodromous. Secondary veins regularly spaced. Angles between secondary veins and the midvein slightly decreasing toward the apex, ranging from 45º to 26º.

Etymology. From the Latin *serratum* and regarding the toothed margins of laminae.

Type locality. Isona-*sud* site, located along the *Pont del Molí* trail, 500 metres south of Isona village (Isona i Conca Dellà municipality, comarca Pallars Jussà, Lleida province, Catalonia, NE Spain).

Stratigraphic position. Marly beds belonging to the Xullí unit of the lower part of the Tremp Formation (see Villalba-Breva *et al.*, 2015 for details).

Age. Early Maastrichtian as determined by stratigraphic correlation and biostratigraphy (see Villalba Breva *et al.*, 2015 for details).

Material. MGB 38273, MGB 38306–07, MGB 38310, MGB 38313.

Description. Leaves are simple, microphyllous and lanceolate to linear (Fig. 11A). The apex is acuminate (Fig. 11D). Blades are partially preserved and, in some specimens, they are slightly curved (Fig. 11A). Laminae are medially symmetrical, 21.9–59.5 mm long and 6.4–15.1 mm wide. Margins are slightly serrate, bearing small, simple, triangular or hook-like teeth (Fig. 11A–C; Fig. 12) 0.3–0.4 mm long and regularly spaced. There are three to four teeth per cm, separated by shallow, broad and rounded sinuses (Fig. 11B–C; Fig. 12). The venation is pinnate and mostly brochidodromous (Fig. 11A–C; Fig. 12A–B). The midvein is prominent and secondary veins are very thin. The secondary veins are regularly spaced and are excurrently attached to the midvein (Fig. 11A–B; Fig. 12A). The angles between secondary veins and the midvein slightly decrease towards the apex, ranging from 45º to 26º (Fig. 11A; Fig. 12A). A single intersecondary vein is present between some pairs of secondary veins (Fig. 11B). These veins run parallel to the major secondary veins and are at least half as long as the subjacent secondary vein. Details of higher order venation are not preserved in any of the specimens.

Discussion. The holotype (MGB 38307) and paratypes (MGB 38306 and MGB 38310) were assigned to *Myrica wadii* Berry, 1925 by Vicente (2002). The secondary veins in *M. wadii* are semicraspedodromous and more widely spaced than in the specimens from Isona (Berry, 1925: pl. IV, figs. 4–8). Marmi *et al.* (2014) assigned these specimens to Dicot type 4 and compared them with *Dicotylophyllum* sp. 1 from the lower Campanian of Grünbach (Austria) (Herman & Kvaček, 2010) and *Eucalyptus geinitzii* Heer, 1885. The former has also secondary veins mostly craspedodromous (fig. 47 in Herman & Kvaček, 2010) and the latter is entire-margined instead of serrated (cf. fig. 1375 in Dana, 1896; Berry, 1919: pl. XXVIII, fig. 8).

Small, elongate leaves with serrated margins and teeth similar to the studied leaves from Isona are found in different species within the genus *Salix*: *S. alba* Linnaeus (Fig. 13A), *S. hindsiana* Bentham (Fig. 13B), *S. interior* Rowke (Fig. 13C), *S. melanopsis* Nuttal (Fig. 13D) and *S. purpurea* Linnaeus (Fig. 13E). The secondary vein framework in these species is variable, including brochidodromous, semicraspedodromous and camptodromous secondary veins (Fig. 13). Based on these features, the new species from Isona is tentatively assigned to Salicaceae. In the upper Maastrichtian locality of *Molí del Baró*-1, the new *Salix*-like species *Saliciphyllum gaetei* Marmi *et al.*, 2015, was described. It consisted of linear leaves with pinnate eucamptodromous to brochidodromous venation but having the margins entire instead of serrate (figs. 5 and 6 in Marmi *et al.*, 2015). Accordingly, the specimens from Isona are attributed to a different species within the genus *Saliciphyllum*.

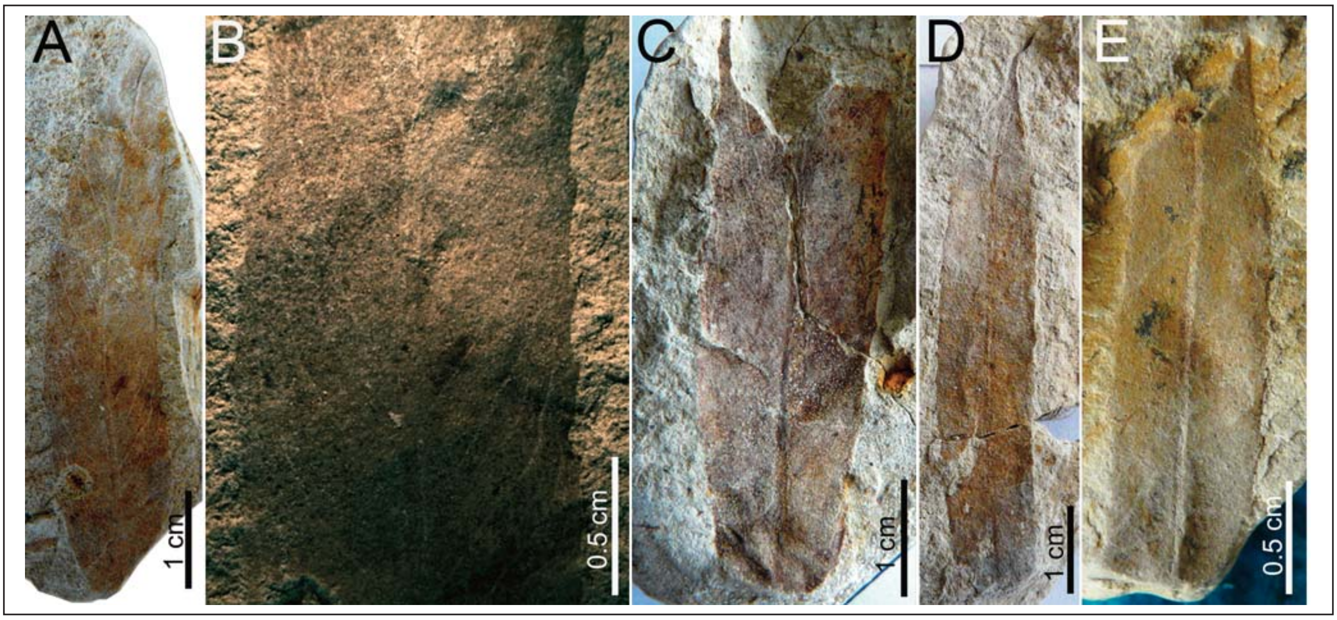


Fig. 11. *Saliciphyllum serratum* n. sp. from the Isona-*sud* site: A, holotype MGB 38307; B, detail of venation and serrate margins of this last; C, paratype MGB 38306, showing also details of venation and teeth; D, paratype MGB 38310, showing the apex acuminate and some teeth; E, MGB 38313, fragment of lamina with some teeth preserved.

Fig. 11. *Saliciphyllum serratum* n. sp. del yacimiento Isona-*sud*: A, holotipo MGB 38307; B, detalle de los nervios y los márgenes aserrados de este último; C, paratipo MGB 38306, mostrando detalles de la nervadura y los dientes; D, paratipo MGB 38310, mostrando el ápice acuminado y algunos dientes; E, MGB 38313, fragmento de lámina con algunos dientes preservados.

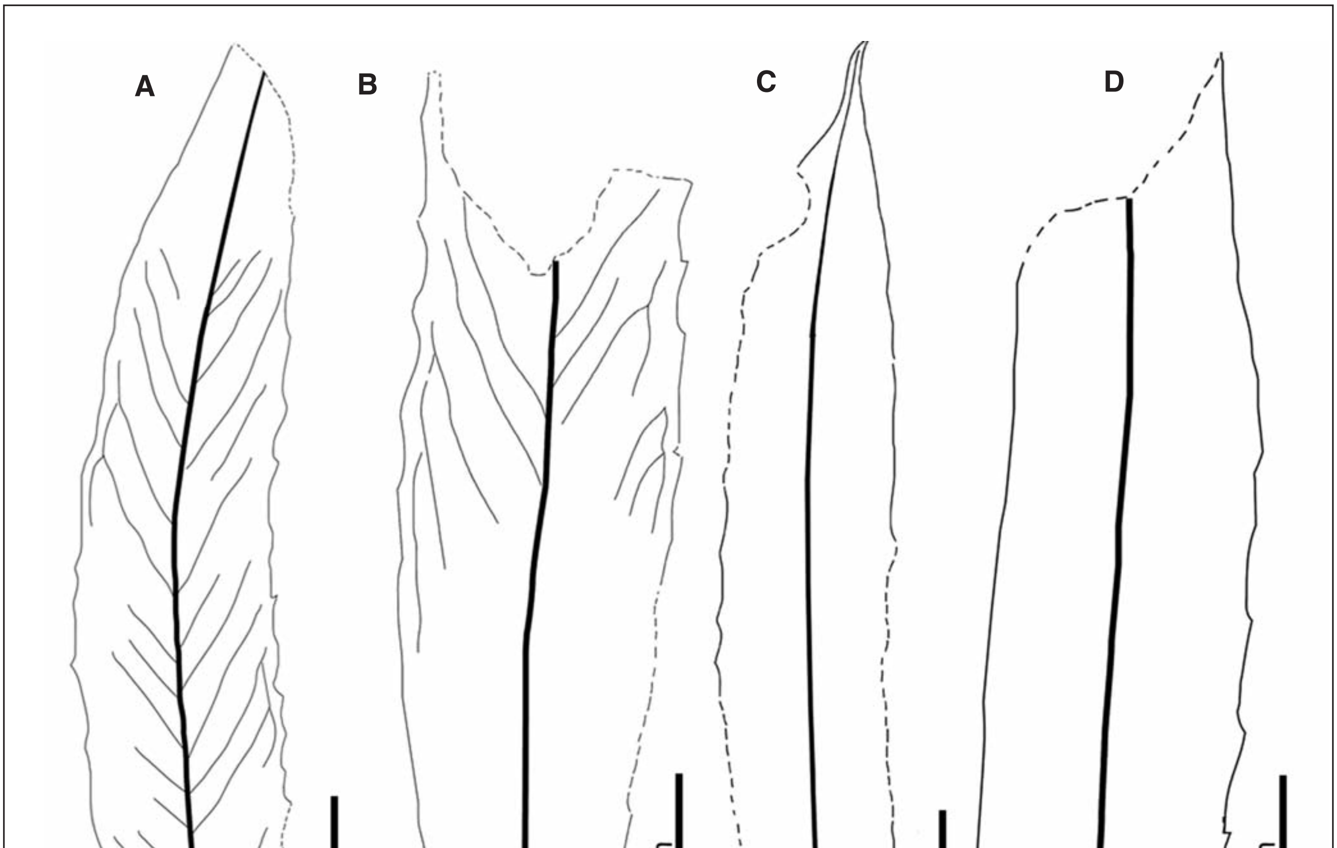


Fig. 12. *Saliciphyllum serratum* n. sp. from the Isona-*sud* site, interpretative drawings: A, MGB 38307; B, MGB 38306; C, MGB 38310; E, MGB 38313.

Fig. 12. *Saliciphyllum serratum* n. sp. del yacimiento Isona-*sud*, dibujos interpretativos: A, MGB 38307; B, MGB 38306; C, MGB 38310; E, MGB 38313.

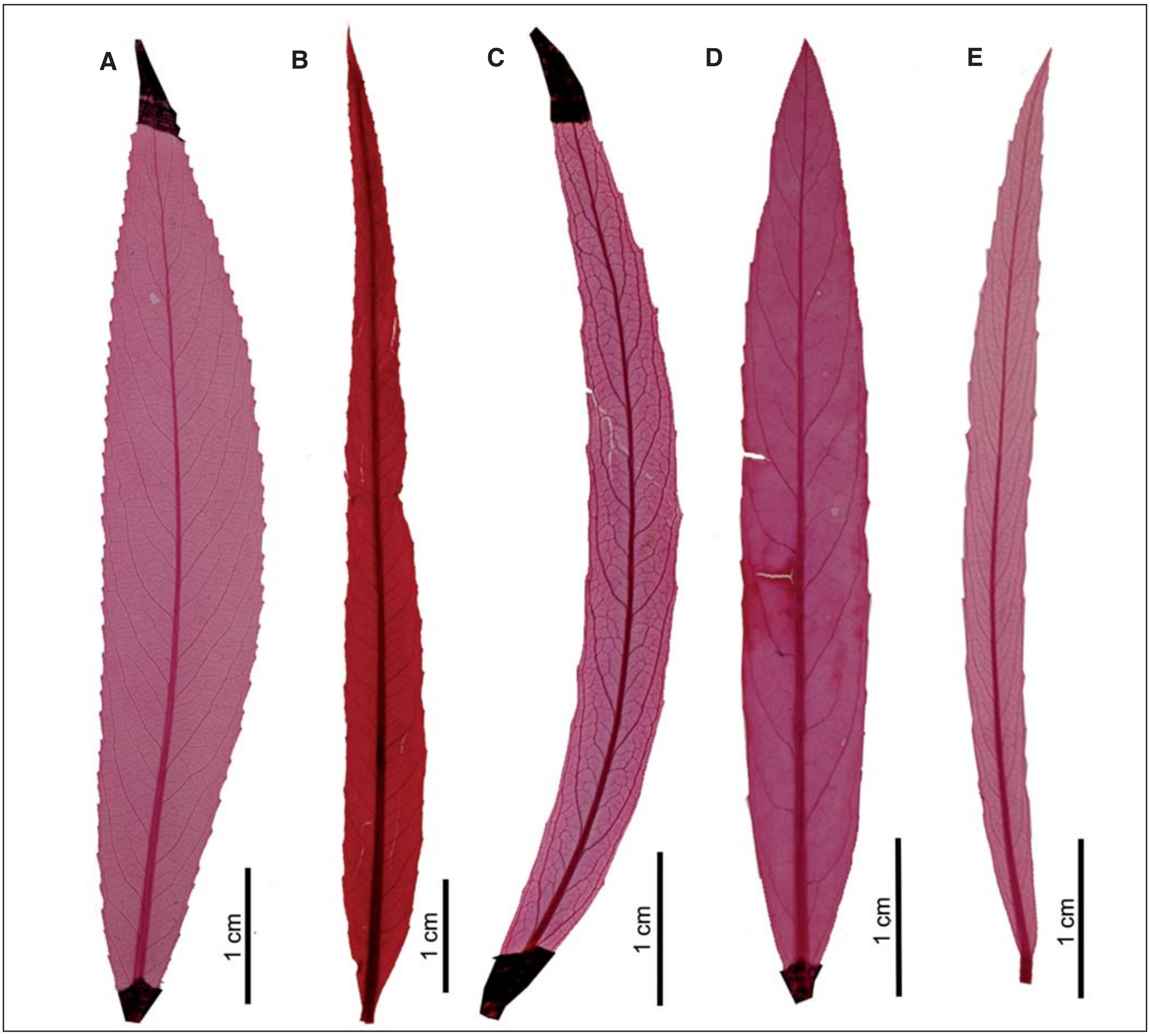


Fig. 13. Specimens of the National Cleared Leaf Collection-Wolfe (NCLC-W) compared to *Saliciphyllum serratum* n. sp. from the Isona-*sud* site: A, *Salix alba* Linnaeus, UC490957; B, *S. hindsiana* Bentham, CAS463858; C, *S. interior* Rowke, UCH486177; D, *S. melanopsis* Nuttal, UC482040; E, *S. purpurea* Linnaeus, UC266698.

Fig. 13. Ejemplares de la National Cleared Leaf Collection-Wolfe (NCLC-W) comparados con *Saliciphyllum serratum* n. sp. del yacimiento Isona-*sud*: A, *Salix alba* Linnaeus, UC490957; B, *S. hindsiana* Bentham, CAS463858; C, *S. interior* Rowke, UCH486177; D, *S. melanopsis* Nuttal, UC482040; E, *S. purpurea* Linnaeus, UC266698.

Clade ASTERIDS?
Order UNKNOWN
Family UNKNOWN

Genus *Cornophyllum* Newberry, 1895

Type species. *Cornophyllum vetustum* Newberry, 1895 by original designation (p. 119, pl. 9, fig. 10).

Cornophyllum herendeenensis Hollick 1930 n. comb.
Fig. 14; Fig. 15

Synonymy

1930 *Rhamnus herendeenensis* Hollick: 102, pl. LXXVIII, figs. 8–10

2002 *Rhamnus herendeensis* (Hollick); Vicente: 109, pl. XXIX, fig. 4–6

2002 *Acer (Rulac) quercifolium* (Hollick); Vicente: 118–119, pl. XXX, fig. 3

2014 Dicot type 5 Marmi *et al.*: 53–54, pl. III, fig. 5; pl. IV, fig. 5

Material. MGB38134, MGB 38269, MGB 38362–63, MGB 38366–67 and MGB 38411.

Occurrence. Isona-*sud* site (see Villalba-Breva *et al.*, 2015, for details).

Description. Leaves are simple, petiolate and microphyllous. The petiole is long (21.5–23.6 mm long and 1.8–2.0 mm wide), straight and marginally attached to the lamina (Fig. 14A–C). Laminae are incomplete, medially symmetrical and likely oblong (Fig. 14C; Fig. 15C), 20.9–58.1 mm long and 15.7–25.8 mm wide. Margins are entire. Bases are acute, convex and asymmetrical in width and insertion (Fig. 14A; Fig. 15A). Leaf apex is lacking in all specimens. Venation is pinnate eucamptodromous (Fig. 14B–C, H; Fig. 15B–C, F). In general, the midvein is straight and stout (Fig. 14B, F, H). However, in some cases, the primary vein axis may be deflected at each branch point, giving a sympodial branching of primary vein (Fig. 14C; Fig. 15C). The secondary veins are usually alternate, excurrently attached to the midvein and curved toward the apex (Fig. 14A–C, F, H; Fig. 15A–C, E, F). The spacing between secondary veins decreases toward the base (Fig. 14C, F, H; Fig. 15C, E, F). Intercostal and epimedial tertiary veins are dense and opposite percurrent (Fig. 14E, G; Fig. 15A, D–E). Epimedial tertiary veins are proximally acute and distally basiflexed (Fig. 14E; Fig. 15A, D). Quaternary and quinternary veins are reticulate, with well-developed areoles (Fig. 14E, G; Fig. 15A, D–F).

Discussion. Most of the studied specimens were assigned to *Rhamnus herendeensis* [*sic*] Hollick 1930 by Vicente (2002), but MGB 38411 was classified as *Acer (Rulac) quercifolium* (Hollick) Vicente (2002) n. comb. by the same author. Both species were described by A. Hollick from the Upper Cretaceous of Alaska, USA. *Rhamnus herendeenensis* strongly resembles the specimens from Isona in general shape and venation (Hollick, 1930: pl. 78, figs. 8–10). On the contrary, *Acer (Rulac) quercifolium* has deeply crenate margins instead of entire margins (Hollick, 1930: pl. 77, figs. 1–10). Marmi *et al.* (2014) assigned these specimens to Dicot type 5 and compared them to *Cornus* sp. from the Upper Cretaceous of Vale de Madeira, Portugal. However, leaves of *Cornus* sp. seem more elongate than the leaves from Isona (Teixeira, 1950: pl. IV, figs. 8–8a). Like in the specimens from Isona, secondary veins of *Cornus* sp. are strongly bent toward the

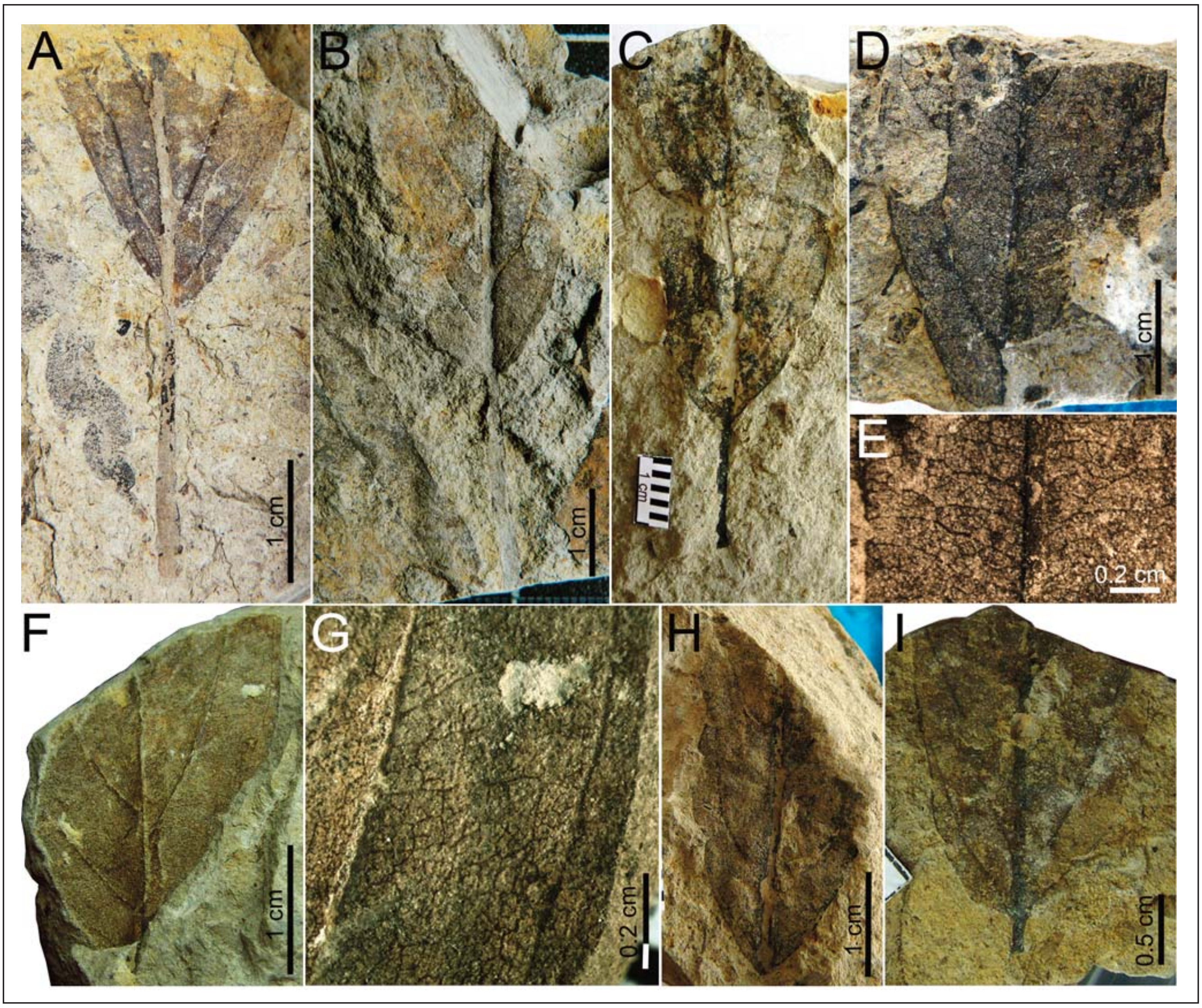


Fig. 14. *Cornophyllum herendeenensis* (Hollick, 1930) n. comb. specimens from the Isona-*sud* site: A, MGB 38134; B, MGB 38269; C, MGB 38363; D, MGB 38362; E, MGB 38362 detail of primary vein, admedial tertiary, quaternary and quinternary veins; F, MGB 38366; G, MGB 38366 detail of intercostal tertiary veins, quaternary and quinternary venation; H, MGB 38411, partial lamina; I, MGB 38367, partial lamina.

Fig. 14. Ejemplares de *Cornophyllum herendeenensis* (Hollick, 1930) n. comb. del yacimiento Isona-*sud*: A, MGB 38134; B, MGB 38269; C, MGB 38363; D, MGB 38362; E, MGB 38362, detalle del nervio primario y de los nervios terciarios admediales, cuaternarios y quinternarios; F, MGB 38366; G, MGB 38366 detalle de los nervios terciarios intercostales, cuaternarios y quinternarios; H, MGB 38411, fragmento de lámina; I, MGB 38367, fragmento de lámina.

apex. However in the middle of the lamina, up to four secondary veins run parallel to the midvein (Teixeira, 1950: pl. IV, fig. 8), a feature not observed in the studied leaves.

Similar leaf architecture features have been observed in extant members of Lauraceae and core eudicots. *Cryptocarya kurzii* (Hooker) Kostermans belongs to Lauraceae and resembles specimens from Isona in shape as well as in primary and secondary vein framework (Fig. 16A). However, in *C. kurzii*, tertiary veins are mixed percurrent and their spacing is wider. On the contrary, *Couepia calophlebia* Standley, within Chrysobalanaceae, has densely packed percurrent tertiary veins but secondary veins are more numerous and straight instead of curved towards the apex (Fig. 16B). The leaves of *Scorodocarpus borneensis* (Baillon) Beccari (Olacaceae) (Fig. 16C), *Aulacocalyx jasminiflora* Hooker (Rubiaceae) (Fig. 16D), *Huodendron biaristatum* (Smith) Rehder (Styracaceae) (Fig. 16E), *Actinidia latifolia* (Gardner & Champion) Merrill (Actinidiaceae) (Fig. 16F) and *Afrocrania volkensii* (Harms) Hutchinson (Cornaceae) (Fig. 16G), are elliptical or oblong, entire-margined and their venation is almost identical to that of the studied specimens. All these taxa are members of the Asterids or of their sister taxa (e.g. Santalales). Because of the similarities with *Rhamnus herendeenensis* as well as *Cornus* sp. from the Upper Cretaceous of Alaska and Portugal and taking into account that genus *Cornus* belongs to Asterids, the new combination *Cornophyllum herendeenensis* is proposed for the Isona leaf fossils.

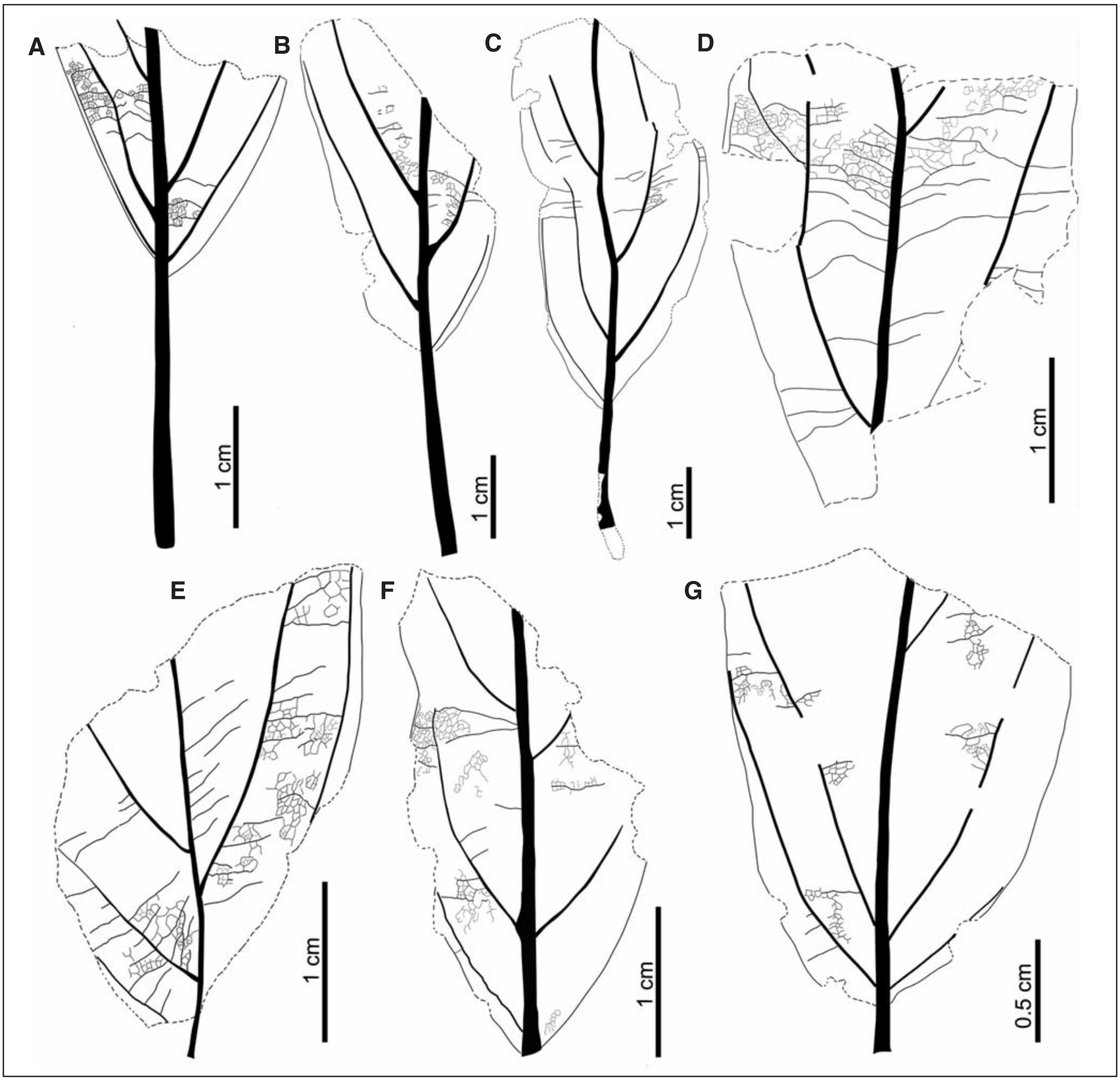


Fig. 15. *Cornophyllum herendeenensis* (Hollick, 1930) n. comb. from the Isona-*sud* site, interpretative drawings: A, MGB 38134; B, MGB 38269; C, MGB 38363; D, MGB 38362; E, MGB 38366; F, MGB 38411; G, MGB 38367.

Fig. 15. *Cornophyllum herendeenensis* (Hollick, 1930) n. comb. del yacimiento Isona-*sud*, dibujos interpretativos: A, MGB 38134; B, MGB 38269; C, MGB 38363; D, MGB 38362; E, MGB 38366; F, MGB 38411; G, MGB 38367.

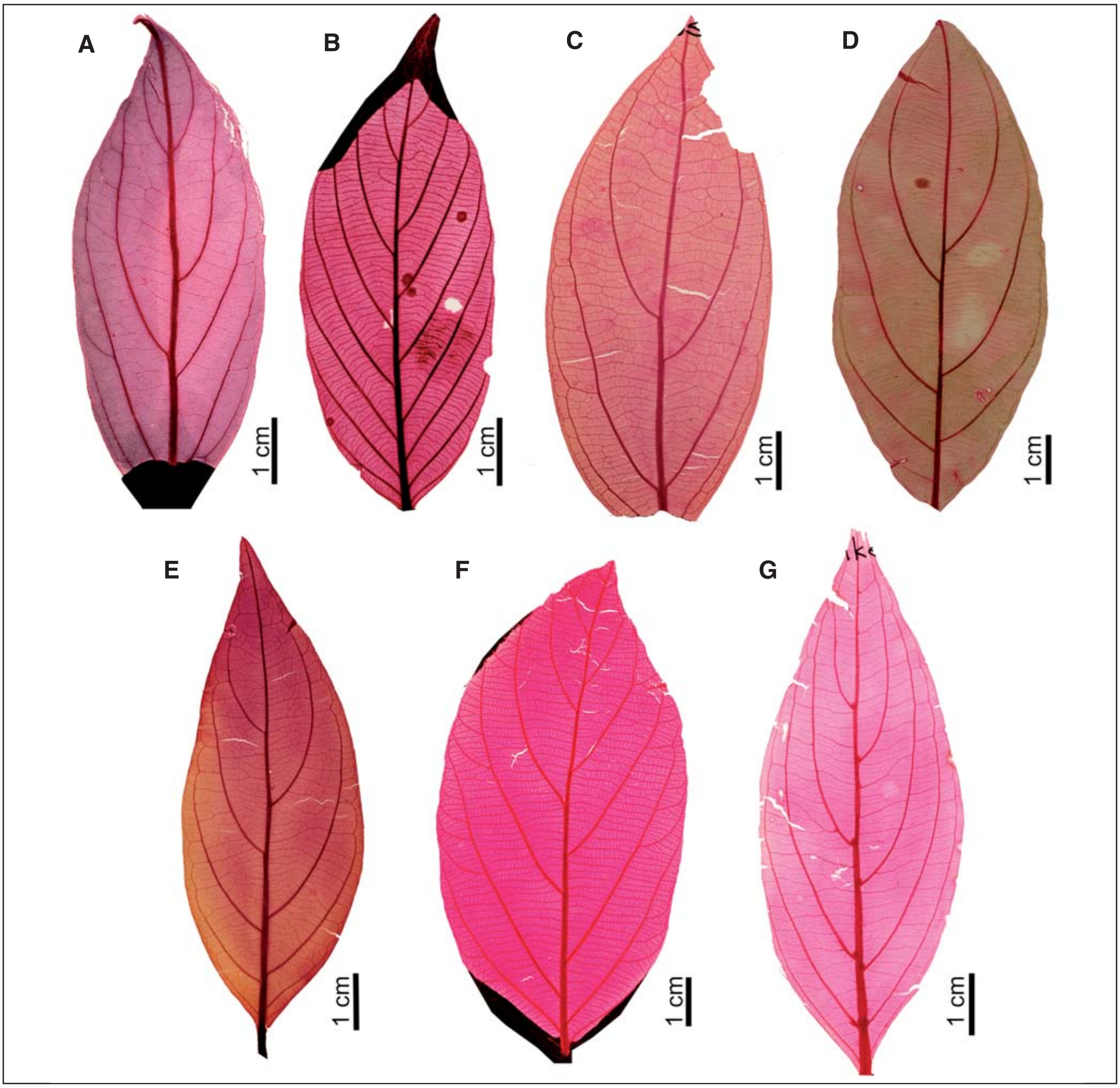


Fig. 16. Specimens of the National Cleared Leaf Collection-Wolfe (NCLC-W) compared to *Cornophyllum herendeenensis* (Hollick, 1930) n. comb. from the Isona-*sud* site: A, Lauraceae, *Cryptocarya kurzii* (Hooker) Kostermans, UCH541652; B, Chrysobalanaceae, *Couepia calophlebia* Standley, UCH606198; C, Olacaceae, *Scorodocarpus borneensis* (Baillon) Beccari, UC345877; D, Rubiaceae, *Aulacocalyx jasminiflora* Hooker, uncoded; E, Styracaceae, *Huodendron biaristatum* (Smith) Rehder, uncoded; F, Actinidiaceae, *Actinidia latifolia* Gardner & Champion) Merrill, uncoded; G, Cornaceae, *Afrocrania volkensii* (Harms) Hutchinson, uncoded.

Fig. 16. Ejemplares de la National Cleared Leaf Collection-Wolfe (NCLC-W) comparados con *Cornophyllum herendeenensis* (Hollick, 1930) n. comb. del yacimiento Isona-*sud*: A, Lauraceae, *Cryptocarya kurzii* (Kostermans), UCH541652; B, Chrysobalanaceae, *Couepia calophlebia* Standley, UCH606198; C, Olacaceae, *Scorodocarpus borneensis* (Baillon) Beccari, UC345877; D, Rubiaceae, *Aulacocalyx jasminiflora* Hooker, no codificado; E, Styracaceae, *Huodendron biaristatum* (Smith) Rehder, no codificado; F, Actinidiaceae, *Actinidia latifolia* (Gardner & Champion) Merrill, uncoded; G, Cornaceae, *Afrocrania volkensii* (Harms) Hutchinson, no codificado.

Clade EUDICOTS
Order UNKNOWN
Family UNKNOWN

Genus *Menispermophyllum* Velenovský, *in* Fric & Bayer, 1901

Type species. *Menispermophyllum celakovskii* Velenovský, *in* Fric & Bayer, 1901 by original designation (p. 128, fig. 90).

Menispermophyllum isonensis n. sp.
Fig. 17; Fig. 18

Holotype. Specimen MGB 38300.

Paratypes. Specimens MGB 38291, MGB 38297, MGB 38301 and MGB 38390.

Synonymy

2002 *Cinnamomum affine* (Lesquereux); Vicente: 66–67, pl. XI, fig. 4

2002 *Carya heerii* (Ettingshausen); Vicente: 82–83, pl. XIX, fig. figs. 5–9
2002 *Eucalyptus geinitzii* (Heer); Vicente: 107–108, pl. XXVIII, fig. 3
2014 Dicot type 6 Marmi *et al.*: 54, pl. III, fig. 6; pl. IV, fig. 6
2015 Eudicot form 5 Villalba-Breva *et al.*: 41, figs. 3I, 4F
2015 cf. *Cocculiphyllum* sp.; Marmi *et al.*: 519–520, figs. 7A, 8A

Specific diagnosis. Leaves simple, microphyllous, linear and entire-margined. Venation imperfect, suprabasal acrodromous. Intercostal tertiary veins mixed percurrent and epimedial tertiary veins percurrent. Exterior tertiary veins terminating at the margins. Quaternary and quinternary veins reticulate. Well-developed areoles including once branched freely ending veinlets. Marginal ultimate venation looped.

Etymology. From the village of Isona, head of the municipality in which the fossils were found.

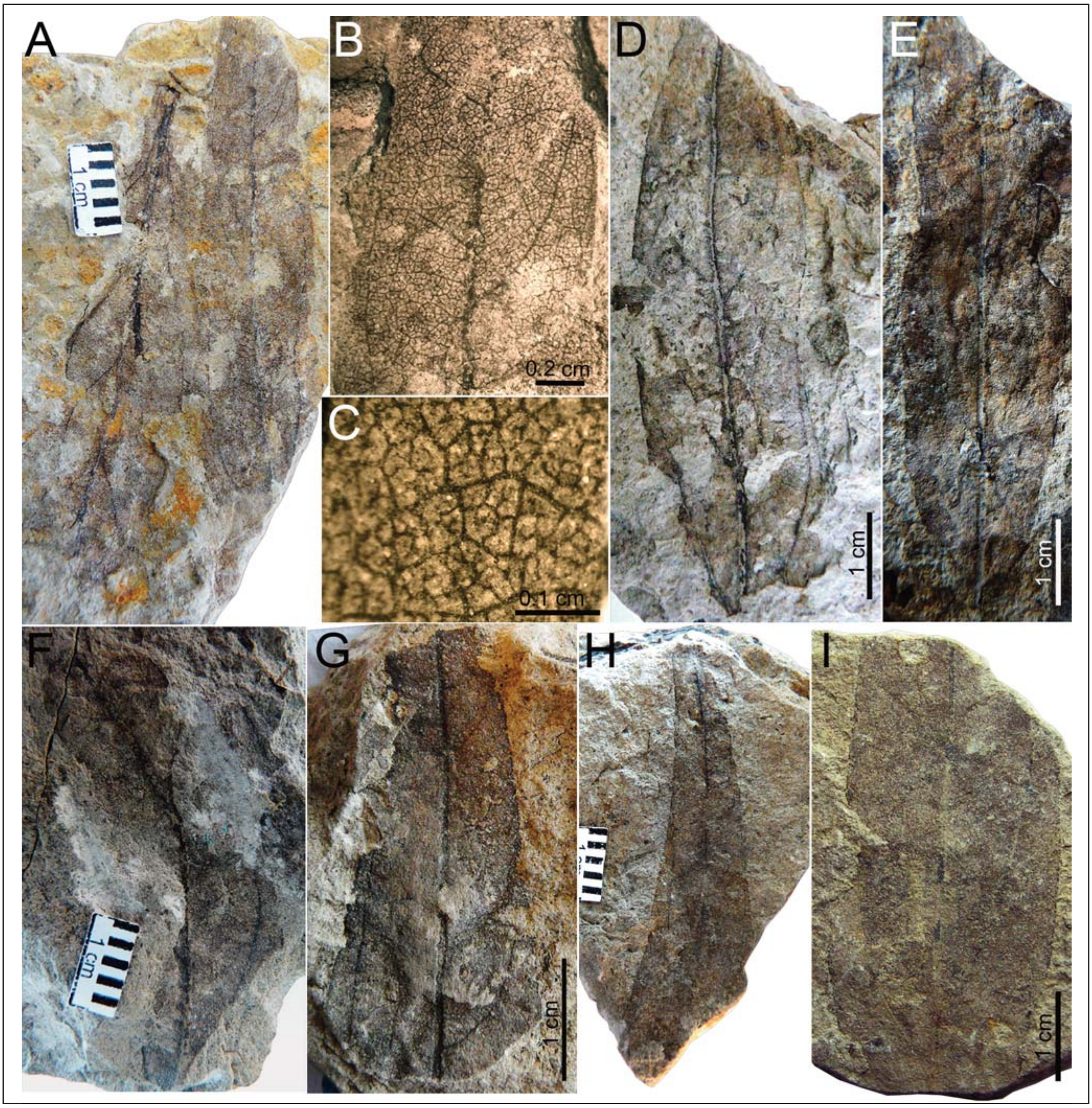


Fig. 17. *Menispermophyllum isonensis* n. sp. from the Isona-*sud* site: A, holotype MGB 38300; B, partial apical half of the holotype showing details of secondary and higher order venation; C, detail of areoles formed by tertiary, quaternary and quinternary veins as well as freely ending veinlets of the same; D, paratype MGB 38291; E, paratype MGB 38301; F, paratype MGB 38390; G, MGB 38294, partial apical end of a leaf; H, paratype MGB 38297; I, MGB 38222, partial lamina.

Fig. 17. *Menispermophyllum isonensis* n. sp. del yacimiento Isona-*sud*: A, holotipo MGB 38300; B, fragmento de la mitad apical del holotipo mostrando detalles de los nervios secundarios y de órdenes superiores; C, Detalle de las areolas formadas por nervios terciarios, cuaternarios y quinternarios, así como de los nervios terminales del mismo ejemplar; D, paratipo MGB 38291; E, paratipo MGB 38301; F, paratipo MGB 38390; G, MGB 38294, fragmento apical de una hoja; H, paratipo MGB38297; I, MGB 38222, fragmento de lámina.

Type locality. Isona-*sud* site, located along the *Pont del Molí* trail, 500 metres south of Isona (Isona i Conca Dellà municipality, *comarca* Pallars Jussà, Lleida province, Catalonia, NE Spain).

Stratigraphic position. Marly beds belonging to the Xullí unit of the lower part of the Tremp Formation (see Villalba-Breva *et al*., 2015 for details).

Age. Early Maastrichtian as determined by stratigraphic correlation and biostratigraphy (see Villalba Breva *et al*., 2015 for details).

Material. MGB38222, MGB 38291, MGB 38293–94, MGB 38297, MGB 38300–01 and MGB 38390.

Description. Leaves are simple, microphyllous, linear and entire-margined (Fig. 17A, D–E; Fig. 18A–C). The peti-

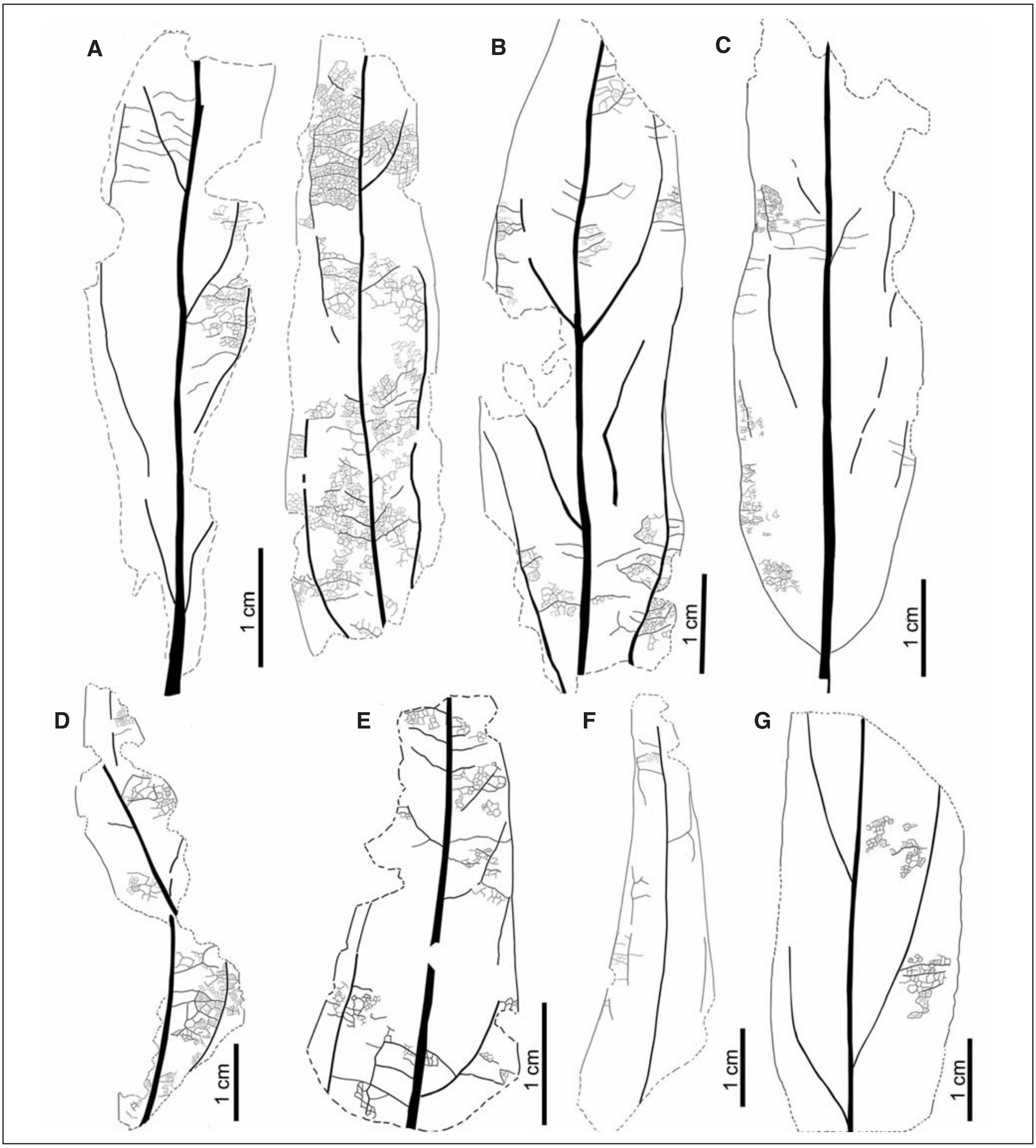


Fig. 18. *Menispermophyllum isonensis* n. sp. from the Isona-*sud* site, interpretative drawings: A, MGB 38300; B, MGB 38291; C, MGB 38301; D, MGB 38390; E, MGB 38294; F, MGB 38297; G, MGB 38222.
Fig. 18. *Menispermophyllum isonensis* n. sp. del yacimiento Isona-*sud*, dibujos interpretativos: A, MGB 38300; B, MGB 38291; C, MGB 38301; D, MGB 38390; E, MGB 38294; F, MGB 38297; G, MGB 38222.

ole is not well preserved in any of the specimens but was likely marginal (Fig. 17E; Fig. 18C). Laminae are incomplete, medially symmetrical, 35.6–88.8 mm long and 12.8–19.7 mm wide. Apices are acute and the bases symmetrical and rounded (Fig. 17E, H; Fig. 18C, F). Venation is imperfect, suprabasal acrodromous (Fig. 17A, D, F; Fig. 18A–D). The midvein is straight and stout. Two exmedial primary veins radiate from a point slightly distal to the petiolar insertion and run parallel to the midvein until at least the middle of the lamina (Fig. 17A, D; Fig. 18A–B). The secondary veins are alternate, eucamptodromous and excurrently attached to the midvein (Fig. 17A–B, D; Fig. 18). Intercostal tertiary veins are opposite to mixed percurrent; epimedial tertiary veins are percurrent, with their proximal course acute to midvein and their distal course basiflexed (Fig. 17B; Fig. 18). Exterior tertiary veins

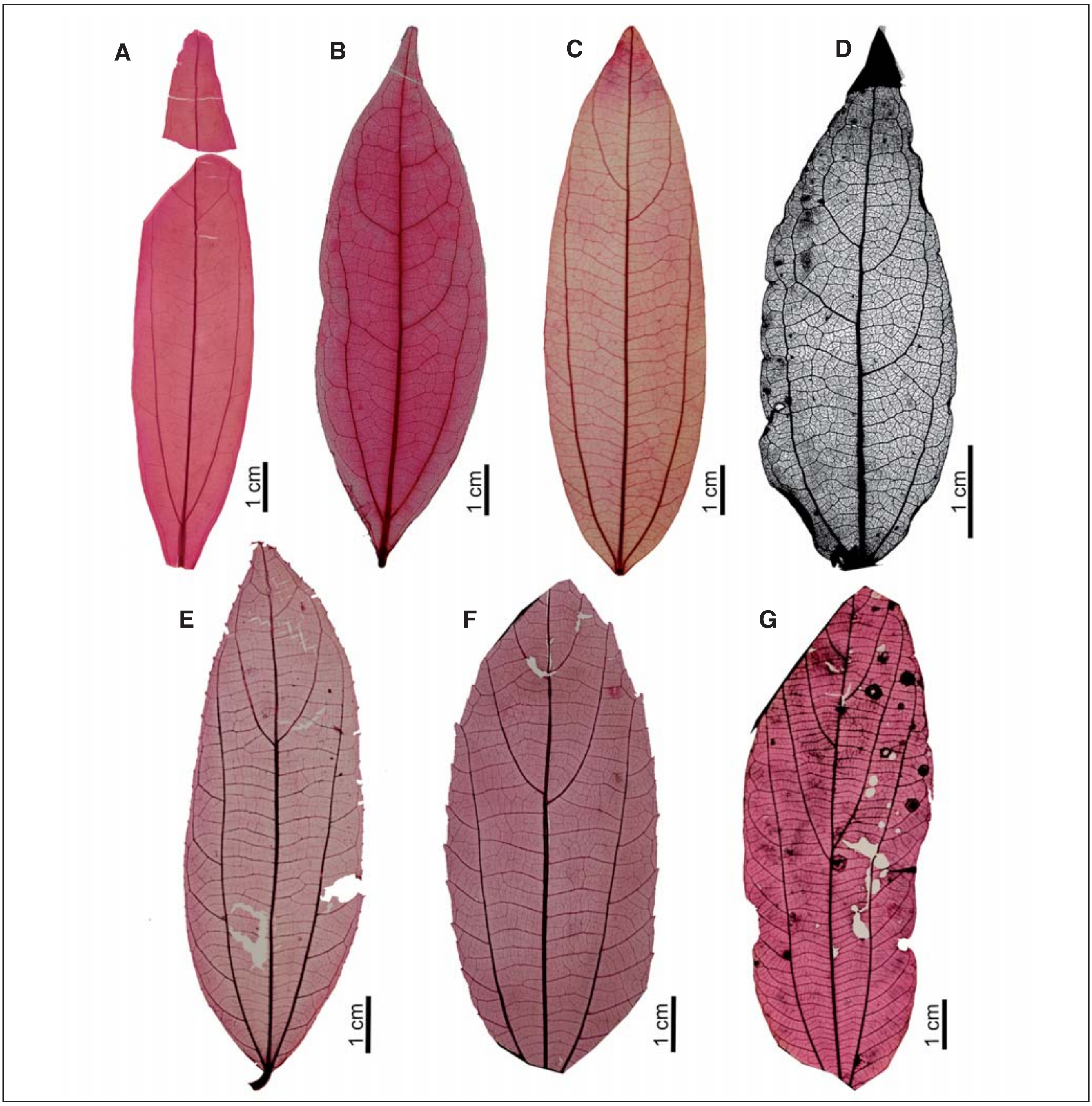


Fig. 19. Specimens of the National Cleared Leaf Collection-Wolfe (NCLC-W) compared to *Menispermophyllum isonensis* n. sp. from the Isona-*sud* site: A, Monimiaceae, *Hortonia angustifolia* Trimen, MO2059972; B, Lauraceae, *Phoebe trinervis* Lund, DS652549; C, Menispermaceae, *Hyperbaena hendunonsis* Standley, UCH519161; D, Hamamelidaceae, *Matudaea trinervia* Lund, SUDH343357; E, Malvaceae, *Trichospermum mexicanum* Baillon, UCH1389462; F, Malvaceae, *Goethalsia meiantha* (Donnell Smith) Burret, SUDH601759; G, Malvaceae, *Lueheopsis rosea* (Ducke) Burret, UCH1209194.

Fig. 19. Ejemplares de la National Cleared Leaf Collection-Wolfe (NCLC-W) comparados con *Menispermophyllum isonensis* n. sp. del yacimiento Isona-*sud*: A, Monimiaceae, *Hortonia angustifolia* Trimen, MO2059972; B, Lauraceae, *Phoebe trinervis* Lund, DS652549; C, Menispermaceae, *Hyperbaena hendunonsis* Standley, UCH519161; D, Hamamelidaceae, *Matudaea trinervia* Lund, SUDH343357; E, Malvaceae, *Trichospermum mexicanum* Baillon, UCH1389462; F, Malvaceae, *Goethalsia meiantha* (Donnell Smith) Burret, SUDH601759; G, Malvaceae, *Lueheopsis rosea* (Ducke) Burret, UCH1209194.

terminate at the margins (Fig. 17B; Fig. 18A–C). Quaternary and quinternary veins are reticulate, forming well-developed areoles (Fig. 17B–C; Fig. 18). Within areoles, once branched freely ending veinlets can be observed in the best preserved specimens (Fig. 17C). The marginal ultimate venation is looped (Fig. 17B; Fig. 18A).

Discussion. Vicente (2002) assigned most of the specimens to *Carya heerii* Ettingshausen, 1854. However, this species has dentate leaf margins instead of entire (cf. Heer, 1855-1859: pl. CXXXI, figs. 8–17). Specimen MGB 38390 was assigned to *Eucalyptus geinitzii* Heer, 1885 and MGB 38222 to *Cinnamomum affine* Lesquereux, 1868 by the same author. The former species has pinnate venation (cf. fig. 1375 in Dana, 1896) and the lamina of the latter species is elliptic (cf. Knowlton, 1922: pl. VIII, fig. 4). The venation in the middle of the lamina of the studied specimens closely resembles that of a partial leaf from the Upper Maastrichtian of Molí del Baró, in the same basin (figs. 7A, 8A in Marmi *et al.*, 2015) that was assigned to cf. *Cocculophyllum* sp. by the authors. However, in *Cocculophyllum*, exmedial primary veins connect with secondary veins which are brochidodromous (fig. 1N in Kvaček, 1983).

Elliptic to linear leaves with three basal veins and percurrent tertiary veins are found in several families like Monimiaceae (*Hortonia angustifolia* Trimen, Fig. 19A) and Lauraceae (*Phoebe trinervis* Lund; Fig. 19B) within Laurales, Menispermaceae (*Hyperbaena hendunonsis* Standley, Fig. 19C) within Ranunculales, Hamamelidaceae (*Matudaea trinervia* Lund, Fig. 19D) within Saxifragales and, Malvaceae (*Trichospermum mexicanum* Baillon, Fig. 19E; *Goethalsia meiantha* (Donnell Smith) Burret, Fig. 19F; *Lueheopsis rosea* (Ducke) Burret, Fig. 19G) within Malvales, representing Magnoliids, basal Eudicots and Core Eudicots. The veins arising from exmedial primary veins are brochidodromous in *Hortonia angustifolia* (Fig. 19A), *P. trinervis* (Fig. 19B), *M. trinervia* (Fig. 19D), *T. mexicanum* (Fig. 19E) and *Lueheopsis rosea* (Fig. 19G). This feature has not been observed in the leaf fossils from Isona. *Goethalsia meiantha* as well as *T. mexicanum* have dentate margins (Fig. 19E–F). Leaves of *H. hendunonsis* are the most similar to the studied specimens based on size, overall shape, entire margins and venation although, in this species, this last character is basal instead of suprabasal acrodromous (Fig. 19C). Based on this evidence, the specimens from Isona are attributed to a new species within the fossil-genus *Menispermophyllum* which was erected by Velenovský, *in* Fric & Bayer (1901).

Clade CORE EUDICOTS
Clade EUROSIDS I
Order FAGALES
Family BETULACEAE?

Genus *Alnophyllum* Staub, 1887

Type species. *Alnophyllum reussii* (Ettingshausen) Staub, 1887 by original designation (p. 267).

Alnophyllum sp.

Fig. 20; Fig. 21

Synonymy

2002 *Platanus aceroides* (Goeppert, *in* Lesquereux); Vicente: 75–76, pl. XVII, fig. 2
2002 *Betula protopendula* Vicente: 85–86, pl. XXII, fig. 1
2002 *Betula stevensonii* (Lesquereux); Vicente: 86–87, pl. XXII, figs. 4–5
2002 *Alnus corylifolia* (Lesquereux); Vicente: 87–88, pl. XXI, figs. 1–8; pl. XLIV, fig. 2
2002 *Corylus insignis* (Heer); Vicente: 89, pl. XXII, fig. 6
2002 *Acer quercifolium* (Hollick); Vicente: 118–119, pl. XXX, fig. 1
2014 Dicot type 7 Marmi *et al.*: 54, pl. III, fig. 7; pl. IV, fig. 7
2015 Eudicot form 2 Villalba-Breva *et al.*: 39, figs. 3E, H; 4C, H

Material. MGB 38146, MGB 38275, MGB 38280–82, MGB 38301, MGB 38314–15, MGB 38317–18, MGB 38320, MGB 38323–24, MGB 38330–32, MGB 38371, MGB 38409.

Occurrence. Isona-*sud* site (see Villalba-Breva *et al.*, 2015 for details).

Description. Leaves are petiolate, simple, microphyllous to notophyllous, 33.3–78.9 mm long and 23.3–86.6 mm wide. The petiole is marginal and, in the largest specimen (MGB 38324, Fig. 20K; Fig. 21K), it is 17.9 mm long and 2.4 mm wide. The most complete leaf blades are elliptic to oblong and medially symmetrical, giving a length/width ratio of 1.5–2.4. The apex is obtuse, convex to rounded (Fig. 20E–F; Fig. 21E–F) while the base is acute, decurrent and symmetrical (Fig. 20A, D–E, J; Fig. 21A, D–E, J). The leaf margin is crenate with two orders of irregularly spaced teeth giving a tooth density of three teeth per centimetre (Fig. 20I; Fig. 21I). Teeth are basally convex, whereas they are straight or convex apically (Fig. 20A, F, I–K; Fig. 21A, F, I–K). They are separated from each other by angular sinuses. A principal vein is present and terminates at the apex of each tooth (Fig. 20F; Fig. 21F). Venation is pinnate craspedodromous with secondary veins excurrently arising from a straight and stout midvein. Basal secondary veins are opposite but they become alternate towards the apex (Fig. 20D, F–G, I, K; Fig. 21D, F–G, I, K). The major secondary vein spacing gradually increases proximally while their angle of insertion smoothly decreases proximally (Fig. 20D; Fig. 21D). Intersecondary veins, when present, are perpendicular to the midvein and run parallel to the subjacent secondary vein, being more than a half as long as the latter (Fig. 20D; Fig. 21D). In some specimens, tertiary veins are preserved, forming a chevron or being sinuous opposite percurrent (Fig. 20H–I; Fig. 21C, H–I). Quaternary and quinternary veins are reticulate and form well-developed areoles (Fig. 20H; Fig. 21H–I).

Discussion. Vicente (2002) assigned most of the specimens to *Alnus corylifolia* Lesquereux, 1883 but also to *Corylus insignis* Heer, 1871, *Betula stevensonii* Lesquereux, *in* Brown, 1962, *Platanus aceroides* Goeppert, *in* Lesquereux, 1878, *Acer quercifolium* (Hollick, 1930), and to the new species *Betula protopendula*. *Alnus coryli-*

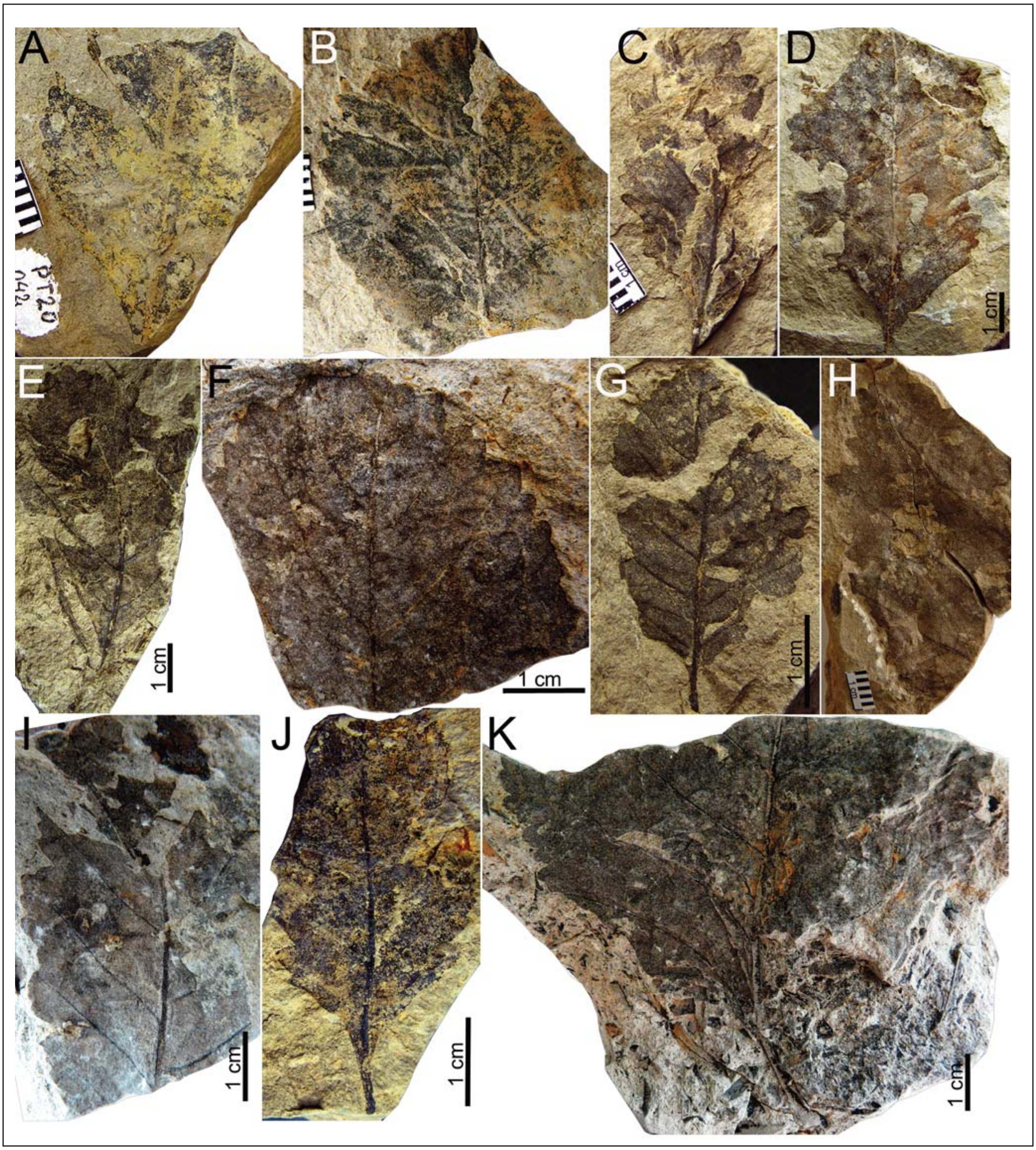


Fig. 20. *Alnophyllum* sp. from the Isona-*sud* site: A, MGB 38146, lamina base; B, MGB 38275, partial lamina; C, MGB 38280, broken lamina; D, MGB 38281, almost complete lamina; E, MGB 38282, almost complete lamina; F, MGB 38301, apical end of a lamina; G, MGB 38314, small leaf bearing the petiole attached; H, MGB 38371, fragment of lamina showing details of venation; I, MGB 38317, partial lamina showing two orders of teeth and details of venation; J, MGB 38318, small leaf with decurrent base, bearing the petiole attached; K, MGB 38324, basal end of a large leaf bearing the petiole attached. Scale in A, B, C and H, 1 cm.

Fig. 20. *Alnophyllum* sp. del yacimiento Isona-*sud*: A, MGB 38146, base de una lámina; B, MGB 38275, lámina incompleta; C, MGB 38280, lámina fragmentada; D, MGB 38281, lámina casi completa; E, MGB 38282, lámina casi completa; F, MGB 38301, parte apical de una lámina; G, MGB 38314, pequeña hoja con el peciolo en conexión; H, MGB 38371, fragmento de lámina mostrando detalles de la nervadura; I, MGB 38317, fragmento de lámina mostrando dos órdenes de dientes y detalles de la nervadura; J, MGB 38318, pequeña hoja con base decurrente y peciolo en conexión; K, MGB 38324, parte basal de una hoja grande con el peciolo en conexión anatómica. Escala en A, B, C y H, 1 cm.

folia was renamed as *A. corylina* by Knowlton & Cockerell (Knowlton, 1919) and, according to Hollick (1936), specimens were hardly distinguishable from other species such as *Alnus diluvianum* Unger, 1852 and *Corylus macquarii* (Forbes) Heer, 1869. In *A. corylina* the base is cordate instead of decurrent and the sinuses between teeth are rounded instead of angular (cf. Hollick 1936: pl. 46, fig. 1; pl. 49, figs. 8–9; pl. 50, fig. 1). *Corylus insignis* has serrate margins with a single order of teeth and the laminar base is convex (Heer, 1871: pl. LIX, fig. 5). *Betula stevensonii* also differs from the studied specimens in marginal features and the shape of the lamina base (Brown, 1962: pl. 20, figs. 1–2, 4–5, 8–9). The specimen MGB 38371 was erroneously assigned to a fragment of a large *Platanus*-like leave (*Platanus aceroides*) by Vicente (2002: pl. XVII, fig. 2). However, according to dentition and sinus shape, it

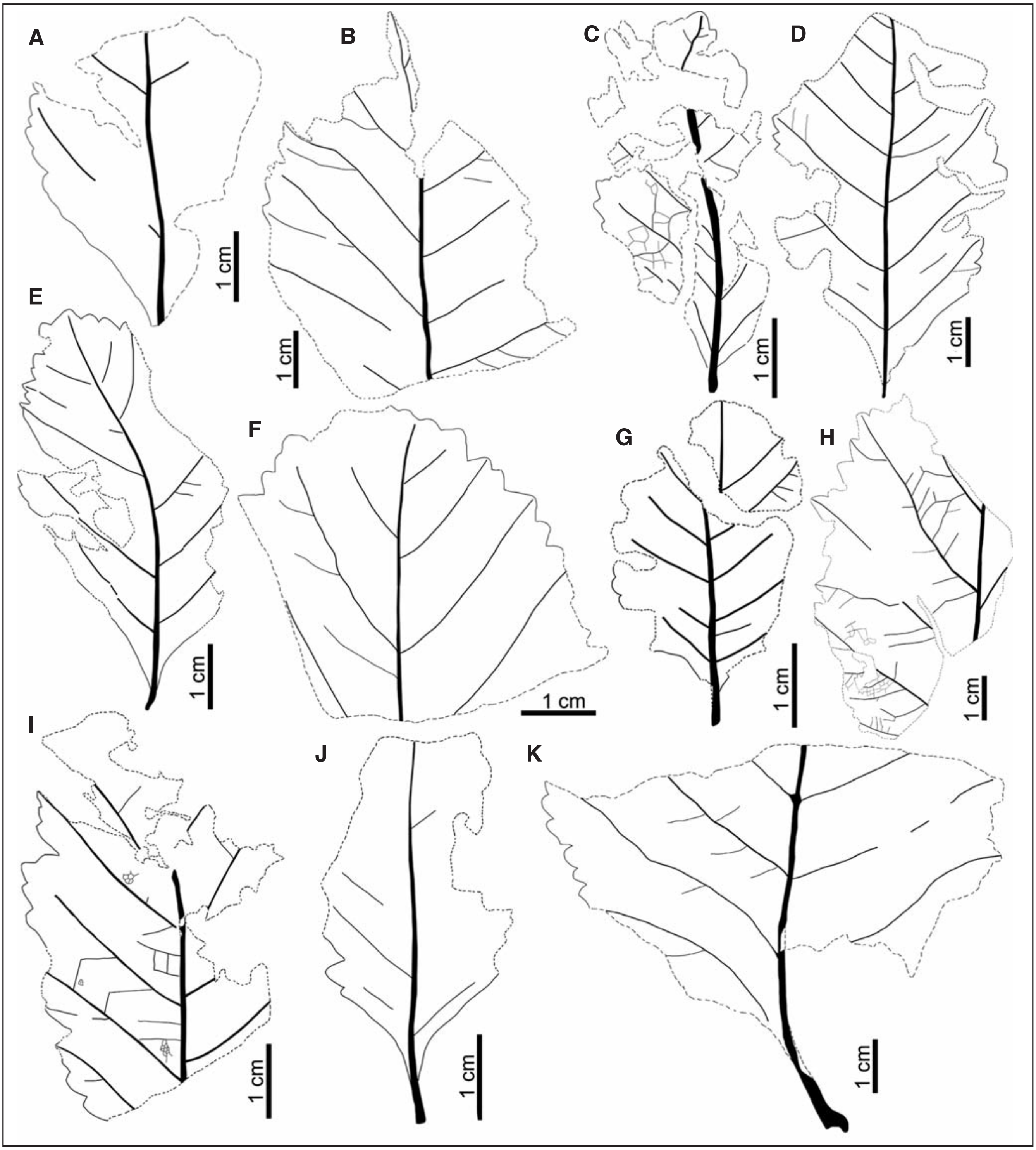


Fig. 21. *Alnophyllum* sp. from the Isona-*sud* site, interpretative drawings: A, MGB 38146; B, MGB 38275; C, MGB 38280; D, MGB 38281; E, MGB 38282; F, MGB 38301; G, MGB 38314; H, MGB 38371; I, MGB 38317; J, MGB 38318; K, MGB 38324.

Fig. 21. *Alnophyllum* sp. del yacimiento Isona-*sud*, dibujos interpretativos: A, MGB 38146; B, MGB 38275; C, MGB 38280; D, MGB 38281; E, MGB 38282; F, MGB 38301; G, MGB 38314; H, MGB 38371; I, MGB 38317; J, MGB 38318; K, MGB 38324.

clearly resembles the other leaves herein studied. The species *Rulac quercifolium* was firstly described by Hollick (1930) and renamed as *Acer quercifolium* by Vicente (2002). In *R. quercifolium* there is a single order of teeth and they are significantly larger than in the specimens from Isona (Hollick, 1930: pl. 29, fig. 1a; pl. 77, 1–10).

Marmi *et al.* (2014) assigned the studied specimens to uncertain Betulaceae and pointed out that they share the blade shape, venation and marginal characters with the extant species *Alnus glutinosa* (Linnaeus) Gaertner (Fig. 24A). The extant species *A. incana* (Linnaeus) Moench (Fig. 24B) and *Alnus tenuifolia* Nuttal (Fig. 24C), share the same features with the leaf fossils from Isona. Therefore, the specimens named Dicot type 7 and Eudicot form 2 by these authors and Villalba-Breva *et al.* (2015), respectively, are now assigned to the fossil-genus *Alnophyllum* which was erected by Staub (1887).

Order UNKNOWN
Family UNKNOWN

Core Eudicot indet. 1
Fig. 22A–C; Fig. 23A–C

Synonymy

2002 *Caesalpinites ripleyensis* (Berry); Vicente: 96–97, pl. XXVII, fig. 5
2002 *Caesalpinites wilcoxensis* (Berry); Vicente: 97, pl. XXVII, fig. 6
2002 *Gleditsiophyllum preovatum* (Berry); Vicente: 100, pl. XXVII, fig. 4
2014 Dicot type 8 Marmi *et al.*: 54, pl. III, fig. 8; pl. IV, fig. 8

Material. MGB 38349–50, MGB 38355.

Occurrence. Isona-*sud* site (see Villalba-Breva *et al.*, 2015 for details).

Description. Leaves are petiolate, nanophyllous to microphyllous, 13.7–32.1 mm long and 5.9–9.8 mm wide, giving a laminar length/width ratio of 3.3. Specimen MGB 38355 preserves a short petiole marginally attached that is 1.7 mm long and 1.2 mm wide (Fig. 22C; Fig. 23C). Laminae are elliptic, symmetrical, unlobed and entire-margined. Apices are convex and the bases are convex or straight, forming obtuse and acute angles respectively. Venation is pinnate with a straight and stout primary vein visible in all specimens. Two opposite secondary veins are weakly preserved in MGB 38350 (Fig. 22B; Fig. 23B).

Discussion. Vicente (2002) assigned the specimens to *Caesalpinites ripleyensis* Berry, 1925, *Caesalpinites wilcoxensis* Berry, 1930 and *Gleditsiophyllum preovatum* Berry, 1925. These three taxa resemble the specimens from Isona in size and shape but, among them, they show remarkable differences in secondary venation. For instance, in *C. ripleyensis* secondary veins are simple brochidodromous (Berry, 1925: pl. XI, fig. 6), while in *G. preovatum*, they are festooned brochidodromous (Berry, 1925: pl. XI, figs. 11–12). Marmi *et al.* (2014) assigned the specimens to Dicot type 8 and compared them with other leaf fossils from the Cretaceous of the Dakota Group (Kansas) and the Laramie Formation (Denver Basin) in the United States.

Leaves of similar shape with stout primary veins and short petioles are found in extant Eurosids orders Myrtales (Fig. 24D) and Sapindales (Fig. 24E–F) as well as in Asterids orders Ericales (Fig. 24G–H) and Gentianales (Fig. 24I–J). Based on these evidences, the parent plant of the fossil leaves from Isona likely belonged to Core Eudicots but, because of the lack of higher venation details, a more precise classification is not possible.

Order UNKNOWN
Family UNKNOWN

Core Eudicot indet. 2
Fig. 22D–I, Fig. 23D–I

Synonymy

2002 *Magnolia lakesii* (Knowlton & Cockerell); Vicente: 65, pl. X, fig. 3
2002 *Ficus juglandifolia* (Hollick); Vicente: 78, pl. XVII, fig. 1
2002 *Ficus pealei* (Knowlton); Vicente: 79, pl. XVIII, fig. 6
2002 *Byttneriophyllum tiliaefolium* (Knobloch & Kvaček); Vicente: 116, pl. XVI, fig. 3
2014 Dicot type 9 Marmi *et al.*: 54, pl. III, fig. 9; pl. IV, fig. 9

Material. MGB 38213, MGB 38263–67, MGB 38397.

Occurrence. Isona-*sud* site (see Villalba-Breva *et al.*, 2015 for details).

Description. In all cases, the leaf lamina is partially preserved and the general shape is unknown. However, specimens likely correspond to microphyllous to notophyllous leaves. Teeth are lacking in all preserved margins suggesting that leaves were entire-margined. In general, venation is pinnate brochidodromous, becoming occasionally semicraspedodromous (Fig. 22D–F; Fig. 23D–F). Secondary veins are alternate. Intersecondary veins, if present, are perpendicular to the midvein and run parallel to major secondary veins (Figs. 22E, G; Fig. 23E, G). Tertiary veins are prominent. Intercostal tertiary veins are straight, opposite percurrent and form obtuse angles compared to the midvein (Figs. 22D–I; Fig. 23D–I). The epimedial tertiary veins are opposite percurrent, with a proximal course perpendicular to the midvein and the distal course basiflexed (Fig. 22D–F, H–I; Fig. 23 D–F, H–I). Exterior tertiary veins are simple brochidodromous (Figs. 22H; Fig. 23H). In MGB 38213, quaternary and quinternary veins are preserved showing a reticulate framework and well-developed areoles (Fig. 22D; Fig. 23D).

Discussion. Vicente (2002) assigned the specimens from Isona to the following species: *Magnolia lakesii* Knowlton & Cockerell, in Knowlton, 1919, *Ficus juglandifolia* Hollick, 1930, *Ficus pealei* Knowlton, 1922 and

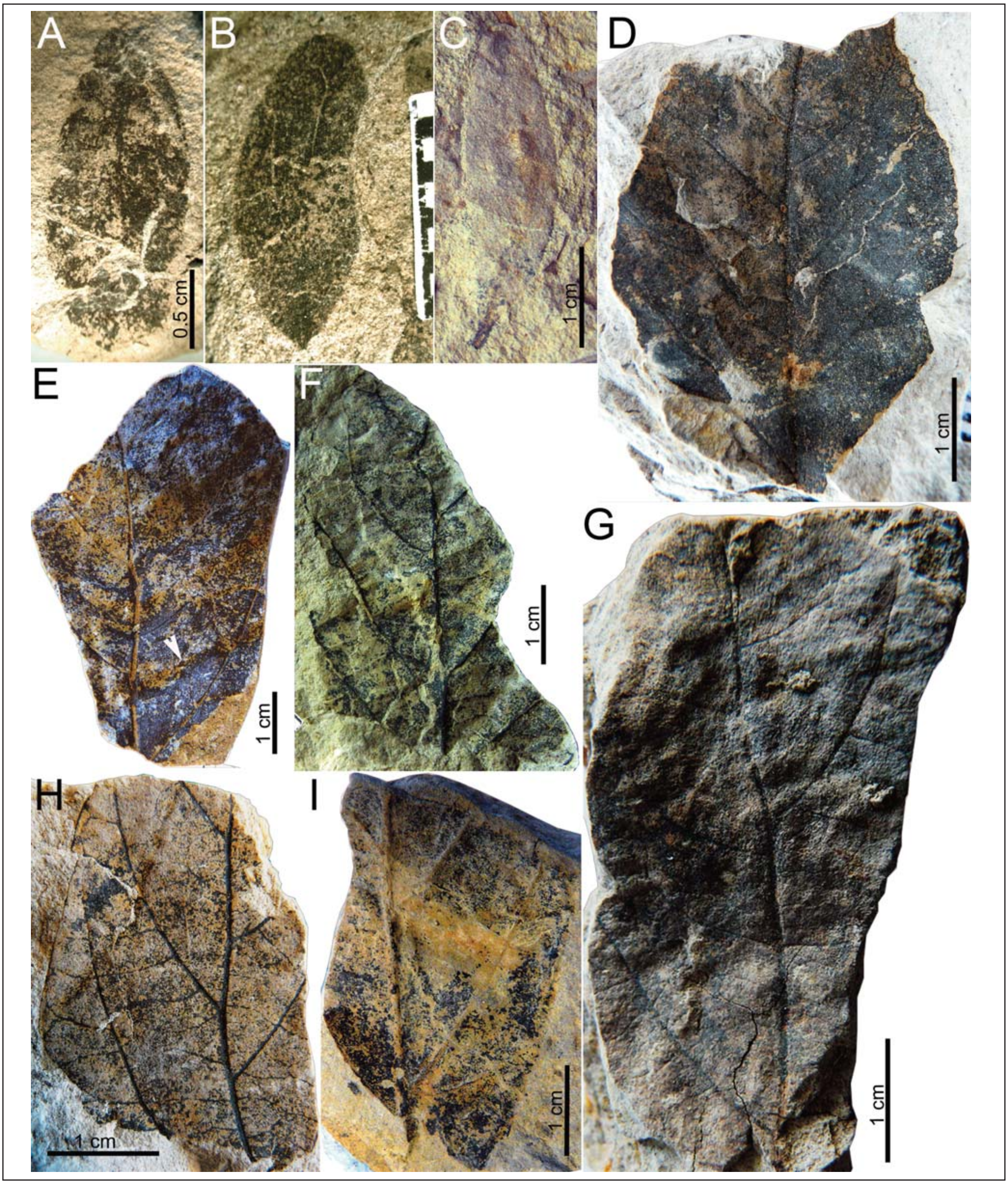


Fig. 22. Core Eudicot indet. 1 (A–C) and Core Eudicot indet. 2 (D–I) from the Isona-*sud* site: A, MGB 38349, lamina showing the midvein; B, MGB 38350, Lamina showing the midvein and two thin secondary veins (scale, 1 cm); C, MGB 38355, impression of a complete leaf; D, MGB 38213, lamina showing brochidodromous secondary veins; E, MGB 38263, partial lamina showing semicraspedodromous secondary veins and intersecondary veins (arrowed); F, MGB 38264, partial lamina showing brochidodromous secondary veins and percurrent tertiary veins; G, MGB 38267, partial lamina showing intersecondary veins and percurrent tertiary veins; H, MGB 38266, partial lamina showing exterior tertiary veins looped; I, MGB 38397, partial lamina showing percurrent tertiary veins.

Fig. 22. Core Eudicot indet. 1 (A–C) y Core Eudicot indet. 2 (D–I) del yacimiento Isona-*sud*: A, MGB 38349, lámina mostrando el nervio principal; B, MGB 38350, lámina mostrando el nervio principal y un par de nervios secundarios delgados (escala, 1 cm); C, MGB 38355, impresión de una hoja completa; D, MGB 38213, lámina mostrando nervios secundarios brochidodromos; E, MGB 38263, fragmento de lámina mostrando nervios secundarios semicraspedodromos y nervios intersecundarios (señalado con una flecha); F, MGB 38264, fragmento de lámina mostrando nervios secundarios brochidodromos y nervios terciarios percurrentes; G, MGB 38267, fragmento de lámina mostrando nervios intersecundarios y nervios terciarios percurrentes; H, MGB 38266, fragmento de lámina mostrando nervios terciarios exteriores en forma de lazo; I, MGB 38397, fragmento de lámina mostrando nervios terciarios percurrentes.

Byttneriophyllum tiliaefolium Knobloch & Kvaček, 1965. *Magnolia lakesii* resembles the studied specimens in venation but, in these latter, secondary veins arise from the midvein at more acute angles (see Knowlton, 1922: pl. XIII, fig. 2 for comparison). On the other hand, *Magnolia lakesii* is subcircular in outline but the shape is unknown in the specimens from Isona. The original descriptions of *F. juglandifolia* and *F. pealei* are based on elliptic or ovate leaves with secondary veins eucamptodromous and lacking details of tertiary veins (Hollick,

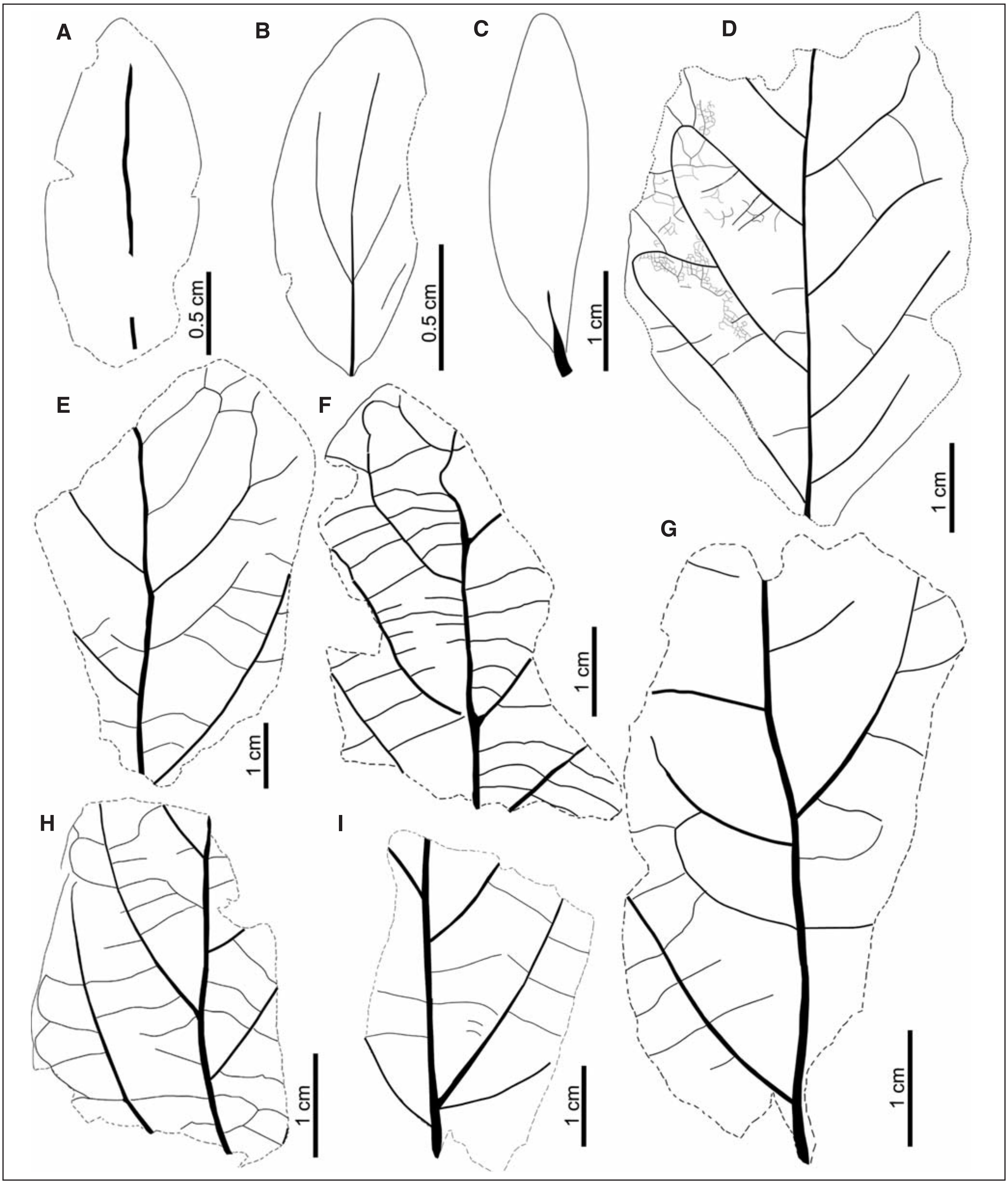
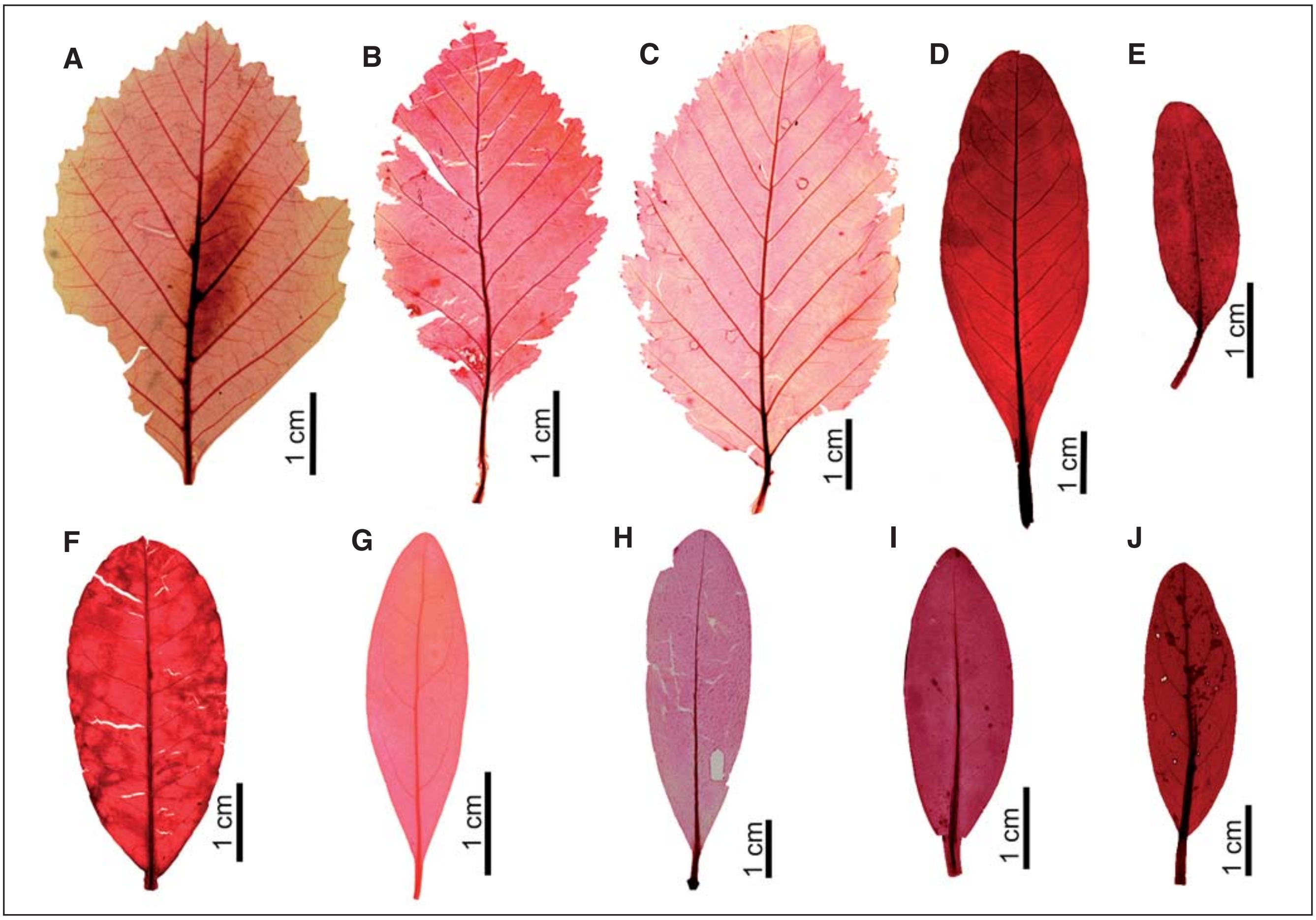


Fig. 23. Core Eudicot indet. 1 (A–C) and Core Eudicot indet. 2 (D–I) from the Isona-*sud* site, interpretative drawings: A, MGB 38349; B, MGB 38350; C, MGB 38355; D, MGB 38213; E, MGB 38263; F, MGB 38264; G, MGB 38267; H, MGB 38266; I, MGB 38397.
Fig. 23. Core Eudicot indet. 1 (A–C) y Core Eudicot indet. 2 (D–I) del yacimiento Isona-*sud*, dibujos interpretativos: A, MGB 38349; B, MGB 38350; C, MGB 38355; D, MGB 38213; E, MGB 38263; F, MGB 38264; G, MGB 38267; H, MGB 38266; I, MGB 38397.

1930: pl. 38, fig. 1; Knowlton, 1922: pl. XI, fig. 6, respectively). *Byttneriophyllum tiliaefolium* was previously assigned to *Ficus tiliaefolia* (Heer, 1855–1859) and it is abundant in the Tertiary of Europe (Vicente, 2002). The latter was figured in Heer (1855–1859: pl. LXXXIII, figs. 3–6; pl. LXXXIV, figs. 1–6) and shows large variability in shape and venation. Regarding to venation, leaves assigned to *F. tiliaefolia* have secondary veins brochidodromous and prominent, percurrent intercostal tertiary veins. However, within this species, some specimens are pinnate (Heer, 1855–1859: pl. LXXXIV, fig. 2) while others, including those assigned to *B. tiliaefolium*, are palmate actinodromous (Heer, 1855–1859: pl. LXXXIV, fig. 1; cf. figs. 3.1, 3.3, 3.6 in Hably, 1992). Marmi *et al.* (2014) compared the specimens from Isona to *Magnolia capellinii* Heer, 1867 from the Cretaceous of the Dakota Group, Kansas, USA. This species has percurrent intercostal tertiary veins and looped exterior tertiary veins but secondary veins are closer to each other compared to the studied specimens (see Heer, 1866: pl. III, figs. 5–6). In addition, secondary veins of a *M. capellinii* figured by Lesquereux (1892: pl. LXVI, fig. 1) seem eucamptodromous. The secondary and tertiary veins framework of Core Eudicot indet. 2 is also very similar to that of the central area of the platanoid-like leaf *Ettingshausenia onomastica* (Bayer) Kvaček & Halamski, 2015 (Popa *et al.*, 2016: fig. 4c). However, primary veins of the specimens from Isona seem pinnate instead of palinactinodromous.

Leaves with entire-margins and similar venation to the leaf fossils from Isona are found in several groups of extant Saxifragales (Fig. 25A), Eurosids (Fig. 25B–E) and Euasterids (Fig. 25F–G). This suggests that the studied specimens represent a Core Eudicot. However, because of the similarities with distantly related extant species and that general shape of the leaves is unknown, a more precise parataxonomic assignment is avoided. In fact, the possibility that specimens within Core Eudicot indet. 2 belong to more than a single taxon cannot be ruled out.



.Fig. 24. Specimens of the National Cleared Leaf Collection-Wolfe (NCLC-W) compared to the leaf fossils from Isona-*sud* (*Alnophyllum* sp. and Core Eudicot indet. 1): A, Betulaceae, *Alnus glutinosa* (Linnaeus) Gaertner, uncoded; B, Betulaceae, *A. incana* (Linnaeus) Moench, uncoded; C, Betulaceae, *Alnus tenuifolia* Nuttal, uncoded; D, Myrtaceae, *Randia aculeata* Linnaeus, DS635943; E, Rutaceae, *Correa glabra* Lindley, UC1222042; F, *Fagara chiloperone* Engler, UC1079771; G, Ebenaceae, *Diospyros dichrophyllum* (Gaud) Winter, UC1378428; H, Myrsinaceae, *Embelia laeta* (Linnaeus) Mez, uncoded; I, Rubiaceae, *Acrosynanthus latifolius* Standley, uncoded. J, Rubiaceae, *Coprosma rapensis* Forest Brown, UC805548.

Fig. 24. Ejemplares de la National Cleared Leaf Collection-Wolfe (NCLC-W) comparados con las hojas fósiles de Isona-*sud* (*Alnophyllum* sp. and Core Eudicot indet. 1): A, Betulaceae, *Alnus glutinosa* (Linnaeus) Gaertner, no codificado; B, Betulaceae, *A. incana* (Linnaeus) Moench, no codificado; C, Betulaceae, *Alnus tenuifolia* Nuttal, no codificado; D, Myrtaceae, *Randia aculeata* Linnaeus, DS635943; E, Rutaceae, *Correa glabra* Lindley, UC1222042; F, *Fagara chiloperone* Engler, UC1079771; G, Ebenaceae, *Diospyros dichrophyllum* (Gaud) Winter, UC1378428; H, Myrsinaceae, *Embelia laeta* (Linnaeus) Mez, no codificado; I, Rubiaceae, *Acrosynanthus latifolius* Standley, no codificado; J, Rubiaceae, *Coprosma rapensis* Forest Brown, UC805548.

Clade EUDICOTS
Order PROTEALES?
Family PLATANACEAE?

Genus *Ettingshausenia* Stiehler, 1857

Type species. *Ettingshausenia cuneifolia* (Bronn) Stiehler, 1857.

Ettingshausenia sp.
Fig. 26A–C; Fig. 27A–C

Synonymy
2002 *Magnolia amplifolia* (Heer); Vicente: 64, pl. X, fig. 1
2002 *Platanus aceroides* (Goeppert, *in* Lesquereux, 1878); Vicente: 75–76, pl. XVII, fig. 2; pl. XLV, fig. 3
2014 Dicot type 10 Marmi *et al.*: 54–55, pl. III, fig. 10; pl. IV, fig. 10

Material. MGB 38216, MGB 38368–69.

Occurrence. Isona-*sud* site (see Villalba-Breva *et al.*, 2015 for details).

Description. The specimens consist of three fragments of large, likely mesophyllous leaves the most complete of which (MGB 38368, Fig. 26A; Fig. 27A) is a large lamina base, 73.2 mm long and 140 mm wide, bearing an incomplete petiole 5.2 mm wide. Leaf margins are not preserved in any specimen. Venation is suprabasal actinodromous with five primary veins diverging radially from a single point (Fig. 26A; Fig. 27A). Likely compound agrophic veins are present (Fig. 26A–B; Fig. 27A–B). In MGB 38368, two opposite secondary veins arise from the midvein and some interior secondary veins are partially preserved (Fig. 26A; Fig. 27A). Specimen MGB 38216 is a more apical fragment of leaf showing opposite secondary veins and likely percurrent tertiary veins partially preserved (Fig. 26C; Fig. 27C).

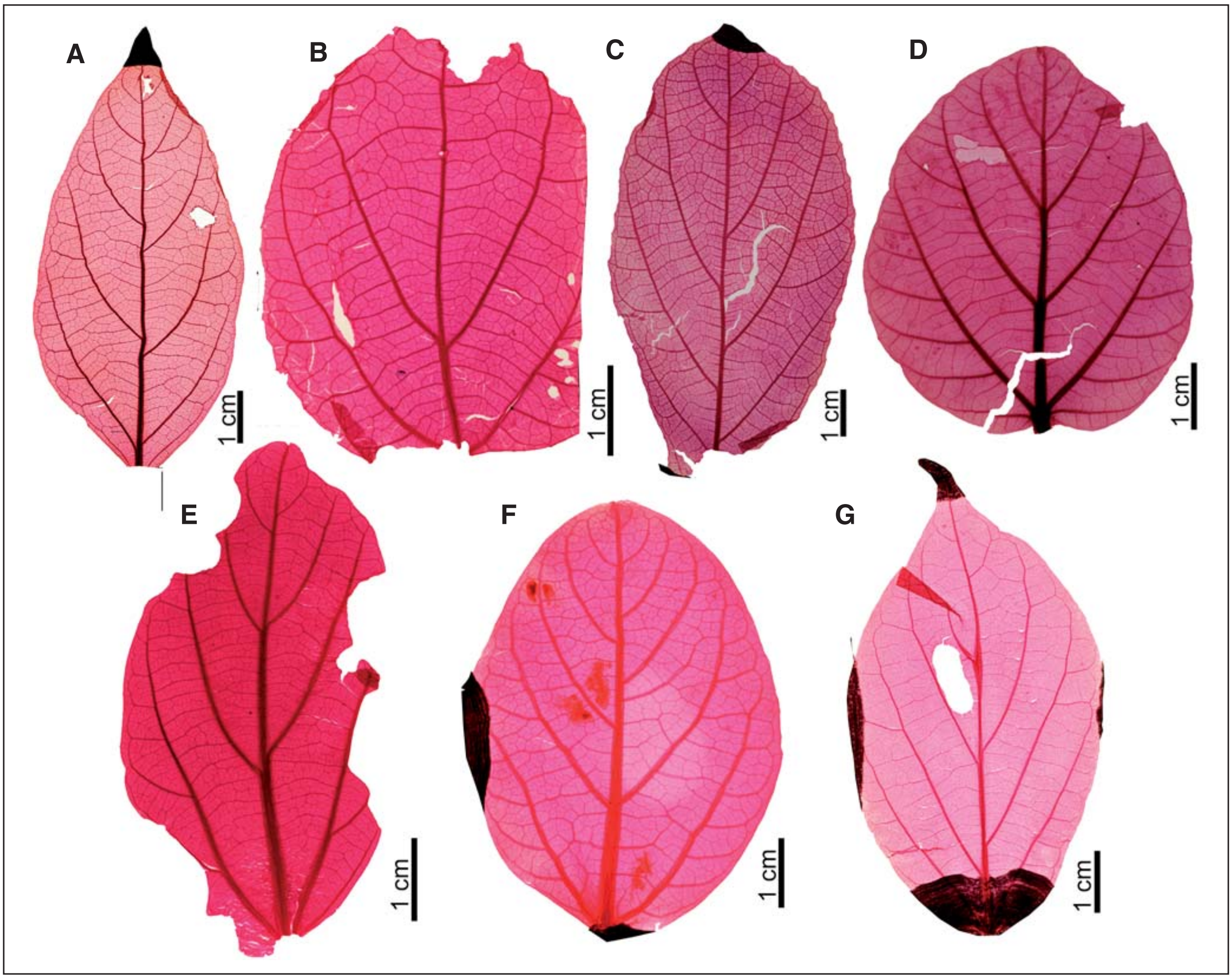


Fig. 25. Specimens of the National Cleared Leaf Collection-Wolfe (NCLC-W) compared to Core Eudicot indet. 2 from the Isona-*sud* site: A, Hamamelidaceae indet., uncoded; B, Passifloraceae, *Adenia cissampeloides* Hooker, uncoded; C, Moraceae, *Ficus hispida* Linnaeus, UC525376; D, Moraceae, *Ficus sycomorus* Linnaeus, UC802192; E, Tiliaceae, *Pentace curtisii* King, UC1003278; F, Bignoniaceae, *Delostoma lobbii* Seemann, DS336967; G, Bignoniaceae, *Distictella mansoana* (de Candolle) Urban, uncoded.

Fig. 25. Ejemplares de la National Cleared Leaf Collection-Wolfe (NCLC-W) comparados con Core Eudicot indet. 2 del yacimiento Isona-*sud*: A, Hamamelidaceae indet., no codificado; B, Passifloraceae, *Adenia cissampeloides* Hooker, no codificado; C, Moraceae, *Ficus hispida* Linnaeus, UC525376; D, Moraceae, *Ficus sycomorus* Linnaeus, UC802192; E, Tiliaceae, *Pentace curtisii* King, UC1003278; F, Bignoniaceae, *Delostoma lobbii* Seemann, DS336967; G, Bignoniaceae, *Distictella mansoana* (de Candolle) Urban, no codificado.

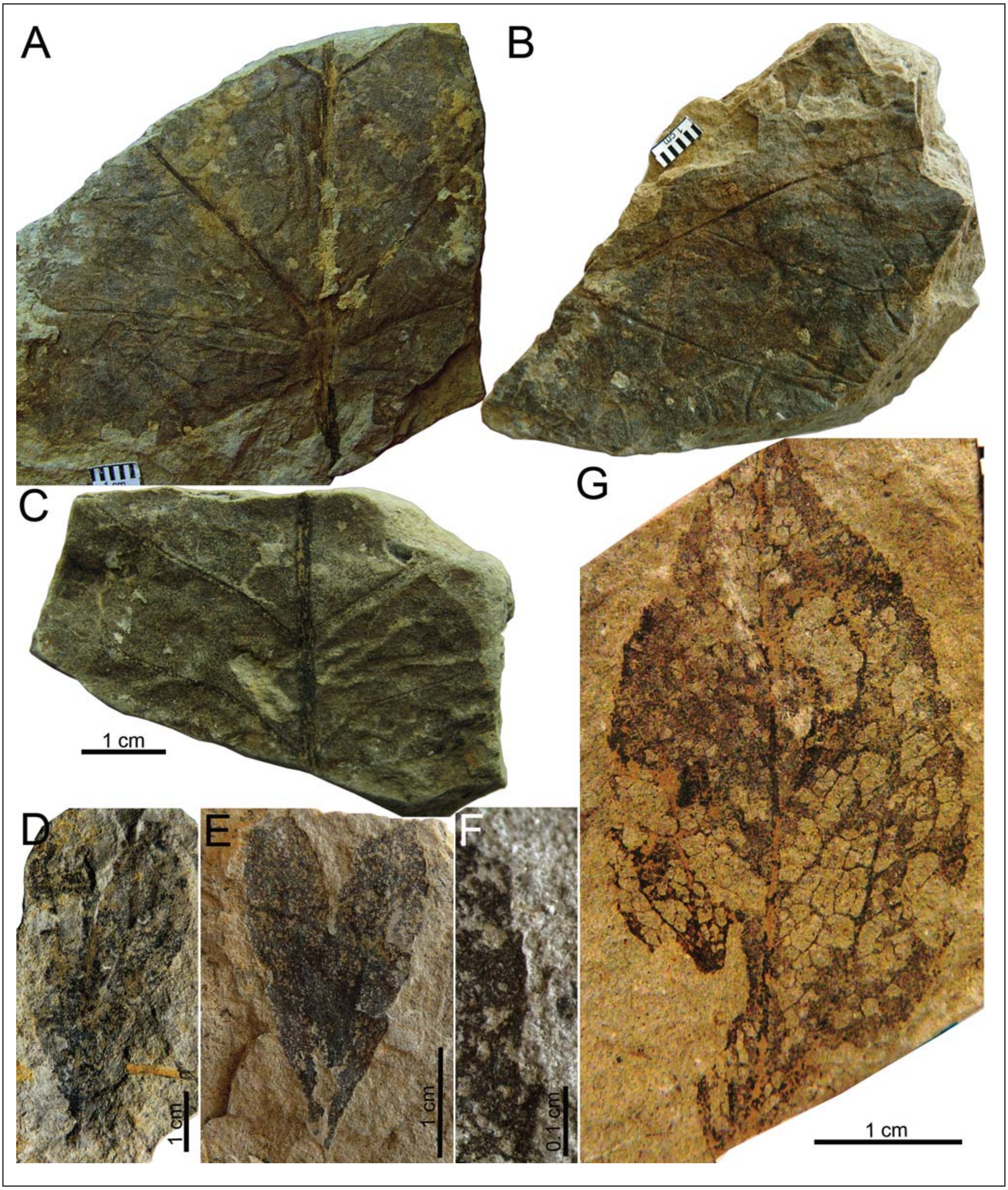


Fig. 26. *Ettingshausenia* sp. (A–C), *Celastrophyllum bilobatum* (Vicente, 2002) (D–F) and *Celastrophyllum* sp. (G) from the Isona-*sud* site: A, MGB 38368, base of a large leaf bearing petiole attached and five primary veins diverging from a single point; B, MGB 38369, partial leaf base showing likely compound agrophic veins; C, MGB 38216, more apical fragment of a leaf showing opposite secondary veins and partially preserved tertiary veins; D, MGB 38395, bi-lobed leaf; E, MGB 38396, bi-lobed leaf; F, MGB 38396 margin's detail showing tiny teeth; G, MGB 38407, leaf lamina showing details of venation.

Fig. 26. *Ettingshausenia* sp. (A–C), *Celastrophyllum bilobatum* (Vicente, 2002) (D–F) y *Celastrophyllum* sp. (G) del yacimiento Isona-*sud*: A, MGB 38368, base de una gran hoja con el peciolo en conexión anatómica y cinco nervios primarios divergiendo de un mismo punto; B, MGB 38369, fragmento de base de una hoja mostrando posibles nervios agróficos compuestos; C, MGB 38216, fragmento apical de una hoja mostrando nervios secundarios opuestos y nervios terciarios parcialmente conservados; D, MGB 38395, hoja bilobada; E, MGB 38396, hoja bi-lobada; F, MGB 38396, detalle del margen mostrando dientes diminutos; G, MGB 38407, hoja mostrando detalles de la nervadura.

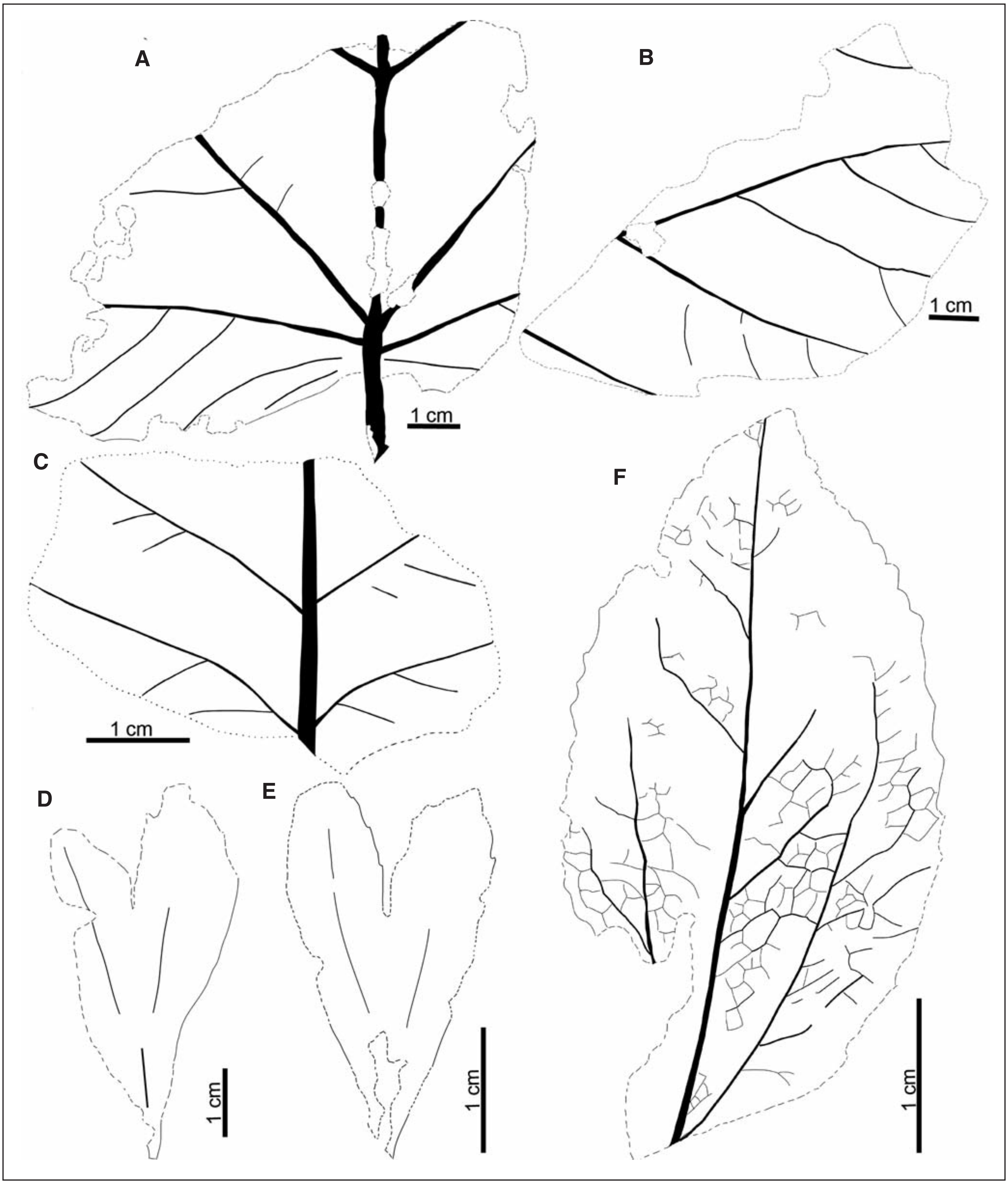


Fig. 27. *Ettingshausenia* sp. (A–C), *Celastrophyllum bilobatum* (Vicente, 2002) (D–E) and *Celastrophyllum* sp. (F) from the Isona-*sud* site, interpretative drawings: A, MGB 38368; B, MGB 38369; C, MGB 38216; D, MGB 38395; E, MGB 38396; F, MGB 38407.

Fig. 27. *Ettingshausenia* sp. (A–C), *Celastrophyllum bilobatum* (Vicente i Castells, 2002) (D–E) y *Celastrophyllum* sp. (F) del yacimiento Isona-*sud*, dibujos interpretativos: A, MGB 38368; B, MGB 38369; C, MGB 38216; D, MGB 38395; E, MGB 38396; F, MGB 38407.

Discussion. Vicente (2002) assigned specimen MGB 38216 to *Magnolia amplifolia* Heer, 1869. However, this specimen is interpreted here as a fragment of a platanoid-like leaf based on the thick midvein and opposite secondary veins, which are similar to those shown in MGB 38368 (see Fig. 26A, C for comparisons). The latter specimen and MGB 38369 were assigned to *Platanus aceroides* Goeppert, *in* Lesquereux, 1878 by Vicente (2002). Partial leaves belonging to this species were drawn in Heer (1885: pl. 12, fig. 1–5) and show opposite secondary veins diverging from a straight and stout midvein as well as likely compound agrophic veins. However, any of these specimens show clear actinodromous venation but see Hollick (1936: pl. 68, fig. 2).

Venation features observed in the studied specimens are found in species within the extant Platanaceae such as *Platanus* x *acerifolia* (Aiton) Willdenow (Fig. 28A) as well as in members of Eurosids (Fig. 28B–C) and Euasterids (Fig. 28D). However, species belonging to these two latter groups used for comparison (Fig. 28B–D) are mostly notophyll instead of mesophyll. Thus, a likely affinity to Platanaceae is proposed for the leaf fossils from Isona. Following Maslova *et al.* (2005) and Maslova & Herman (2015), the studied *Platanus*-like leaves are tentatively assigned to the genus *Ettingshausenia*.

Clade CORE EUDICOTS
Clade EUROSIDS I
Order CELASTRALES
Family CELASTRACEAE?

Genus *Celastrophyllum* Goeppert, 1854

Type species. *Celastrophyllum attenuatum* Goeppert, 1854 by original designation (p. 52, pl. 14, fig. 89).

Celastrophyllum bilobatum Vicente, 2002

Fig. 26D–F; Fig. 27D–E

Synonymy

2002 *Celastrophyllum bilobatum* Vicente: 115, pl. XXXI, figs. 8-9

2014 Dicot type 11 Marmi *et al.*: 55–56, pl. V, fig. 1; pl. VI, fig. 1

Material. MGB38395–96.

Occurrence. Isona-*sud* site (see Villalba-Breva *et al.*, 2015 for details).

Description. Leaves are microphyllous, 32.4–48.6 mm long and 15.4–25-4 mm wide, giving a length/width ratio of 1.9–2.1. Laminae are bi-lobed, heart-shaped and symmetrical (Fig. 26D–E; Fig. 27D–E). The apex is reflex and the base acute, becoming strongly narrow toward the petiole. Margins are poorly preserved but some tiny teeth are visible near the apex of specimen MGB 38396 (Fig. 26F; Fig. 27E). Teeth are 1.5–2.1 mm long and 0.2–0.4 mm in width. They are separated each other by rounded sinuses (Fig. 26F; Fig. 27E). The primary vein splits dichotomously into two veins that form the midvein of each lobe (Fig. 26D; Fig. 27D).

Discussion. Vicente (2002) assigned the specimens to the new species *Celastrophyllum bilobatum*. Genus *Celastrophyllum* is featured by small sized, elliptic leaves with decurrent bases, dentate margins and brochidodromous venation (Herman & Kvaček, 2010). However, leaves from Isona are bi-lobed and details of secondary venation are not preserved. Marmi *et al.* (2014) assigned the specimens to Dicot type 11 and compared them to *Liriophyllum obcordatum* Lesquereux, 1892. This species has the laminae bi-lobed but their margins are entire instead of dentate (Lesquereux, 1892: pl. XXVIII, fig. 7).

Similar bi-lobed leaves have been observed in extant Eurosids within Rosales (Fig. 28E) and Celastrales (Fig. 28F). Based on these evidences and the presence of dentate margins, the leaf fossils from Isona are assigned to Eurosids and the species proposed by Vicente (2002) maintained.

Celastrophyllum sp.

Fig. 26G; Fig. 27F

Synonymy

2002 *Celastrus splendidus* Saporta; Vicente: 113–114, pl. XXIX, fig. 2

2014 Dicot type 12 Marmi *et al.*: 56–57, pl. V, fig. 2; pl. VI, fig. 2

Material. MGB38407.

Occurrence. Isona-*sud* site (see Villalba-Breva *et al.*, 2015 for details).

Description. The single specimen is an almost entire leaf, elliptic in shape, with a symmetrical lamina 46.8 mm long and 23.8 mm wide (Fig. 26G). It only lacks the basalmost end of the lamina and the petiole. The apex is not completely preserved but seems acuminate (Fig. 26G). Margin is serrate in the middle of the lamina (concave/straight teeth separated each other by rounded sinuses), becoming crenate near the apex (convex/convex teeth separated each other by angular sinuses) (Figs. 26G; Fig. 27F). There is only one order of teeth which are regularly spaced giving a density of three to five teeth per centimeter. The primary vein is pinnate, and the secondary veins seem festooned semicraspedodromous (Figs. 26G; Fig. 27F). Secondary veins are not regularly spaced and arise from the primary vein forming inconsistent angles. There is less than one intersecondary vein per intercostal area. They are less than half shorter than the subjacent secondary veins and their courses are parallel to major secondary veins. Intercostal and epimedial tertiary veins, as well as quaternary tertiary veins, are reticulate (Figs. 26G; Fig. 27F).

Discussion. Vicente (2002) assigned this specimen to *Celastrus splendidus* de Saporta, 1867. However, in this species the apex is slightly emarginate and tertiary veins percurrent instead of reticulate (de Saporta, 1867: pl. 8, fig. 2). Marmi *et al.* (2014) pointed out that the specimen from Isona strongly resembles the extant species *Celastrus auriculatus* Vitman (Fig. 28G). These authors assigned the leaf fossil to *Celastrophyllum* based on similarities with *C. auriculatus* as well as the following features that are typical of the form-genus: small size, elliptic shape, dentate to crenate margins, venation pinnate and reticulate tertiary and quaternary veins.

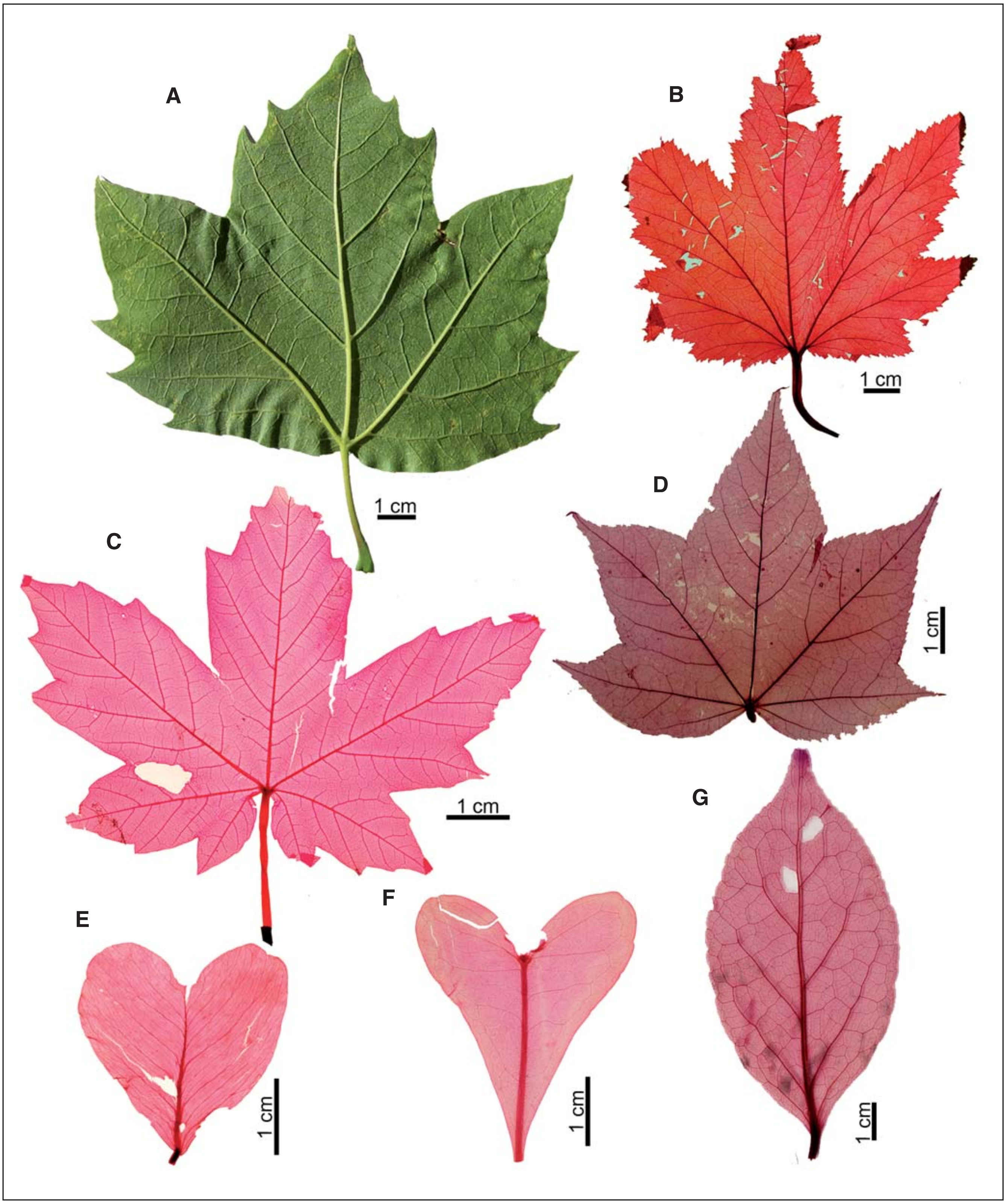


Fig. 28. *Platanus* x *acerifolia* (Aiton) Willdenow leaf (A) and specimens of the National Cleared Leaf Collection-Wolfe (NCLC-W) compared to *Ettingshausenia* sp. (B–D), *Celastrophyllum bilobatum* (E–F) and *Celastrophyllum* sp. (G) from the Isona-*sud* site: B, Rosaceae, *Filipendula occidentalis* (Watson) Howell, DS115757; C, Aceraceae, *Acer diabolicum* Blume, DS32878; D, Araliaceae, *Kalopanax pictus* (Thunberg) Nakai, uncoded; E, Fabaceae, *Haematoxylon campechianum* Linnaeus, uncoded; F, Celastraceae, *Polycardia phyllanthoides* (Lamarck) de Candolle, uncoded; G, Celastraceae, *Celastrus auriculatus* Vitman, ACL187 from the University of California Museum of Paleontology.

Fig. 28. Hoja de *Platanus* x *acerifolia* (Aiton) Willdenow (A) y ejemplares de la National Cleared Leaf Collection-Wolfe (NCLC-W) comparados con *Ettingshausenia* sp. (B–D), *Celastrophyllum bilobatum* (E–F) y *Celastrophyllum* sp. (G) procedentes de Isona-*sud* site: B, Rosaceae, *Filipendula occidentalis* (Watson) Howell, DS115757; C, Aceraceae, *Acer diabolicum* Blume, DS32878; D, Araliaceae, *Kalopanax pictus* (Thunberg) Nakai, no codificado; E, Fabaceae, *Haematoxylon campechianum* Linnaeus, no codificado; F, Celastraceae, *Polycardia phyllanthoides* (Lamarck) de Candolle, no codificado; G, Celastraceae, *Celastrus auriculatus* Vitman, ACL187 procedente del University of California Museum of Paleontology.

Order FAGALES?
Family BETULACEAE?

Genus *Betuliphyllum* Dusén, 1899

Type species. *Betuliphyllum patagonicum* Dusén, 1899 by original designation (p. 102, pl. 10, figs. 15,16).

Betuliphyllum sp.
Fig. 29; Fig. 30

Synonymy

2002 *Platanus aceroides* (Goeppert, *in* Lesquereux); Vicente: 75–76, pl. XVII, fig. 2
2002 *Betula protopendula* Vicente: 85–86, pl. XXII, fig. 2
2002 *Populus intermedia* Vicente: 91–92, pl. XXIV, fig. 4–5
2002 *Populus paleomutabilis* Vicente: 92–93, pl. XXIV, fig. 1–3
2002 *Populus rhomboidalis* Vicente: 93, pl. XXIII, fig. 1
2014 Dicot type 13 Marmi *et al.*: 57, pl. V, fig. 3; pl. VI, fig. 3

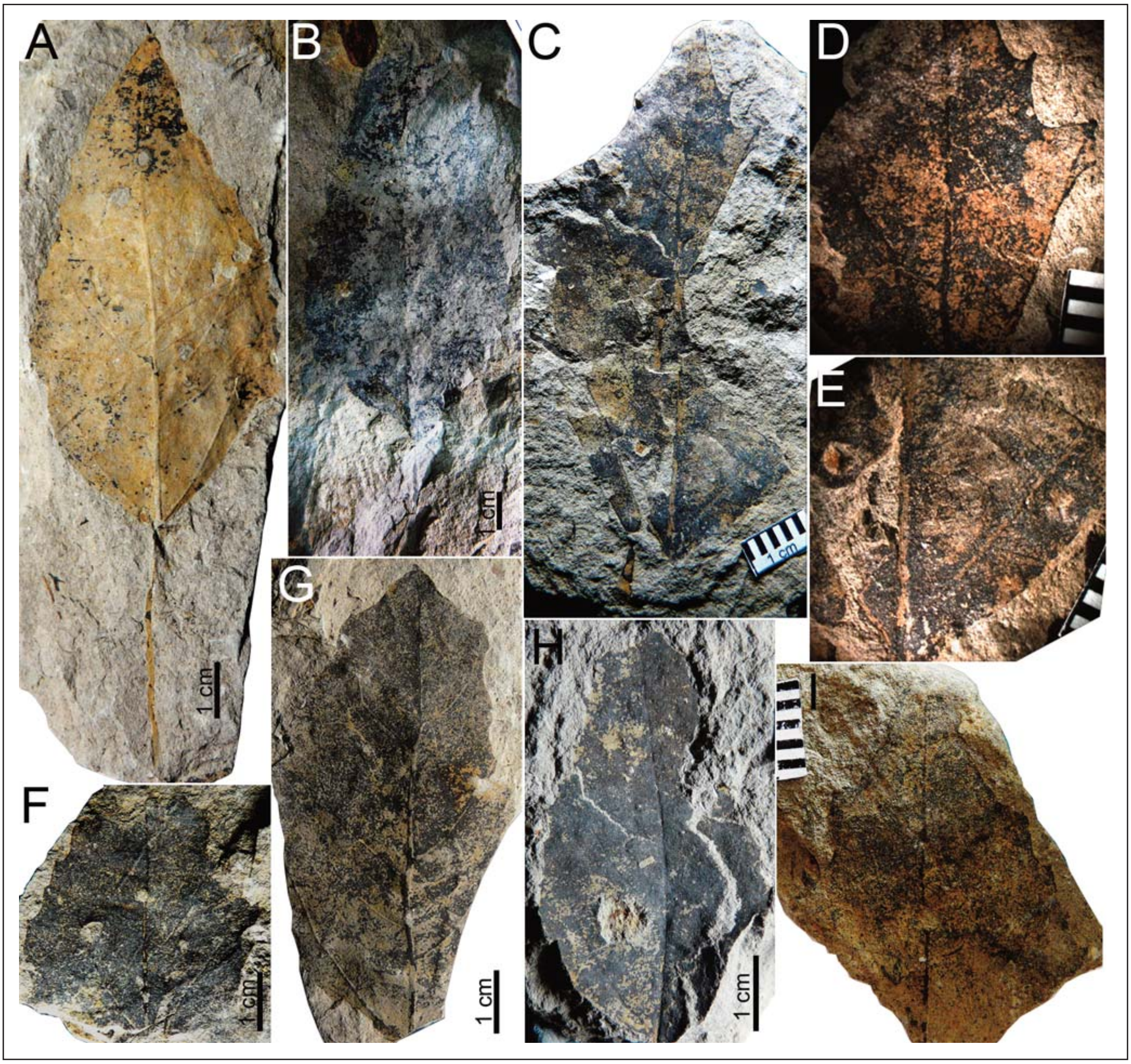


Fig. 29. *Betuliphyllum* sp. from the Isona-*sud* site: A, MGB 38341, complete leaf; B, MGB 38340, complete leaf; C, MGB 38375, partial lamina; D, MGB 38375 detail showing secondary veins terminating at mucronate tooth apices as well as epimedial percurrent tertiary veins forming a chevron; E, MGB 38375 detail showing mixed percurrent epimedial tertiary veins and exterior tertiary veins straight opposite percurrent; F, MGB 38327, apical fragment of a lamina with some marginal teeth preserved; G, MGB 38373, partial lamina showing intersecondary veins; H, MGB 38342, Apical end of a lamina showing some teeth at the margin; I, MGB 38372, detail of the apical end of a lamina. Scale in C and I, 1 cm; divisions in D and E, in millimetres.

Fig. 29. *Betuliphyllum* sp. del yacimiento Isona-*sud*: A, MGB 38341, hoja completa; B, MGB 38340, hoja completa; C, MGB 38375, fragmento de lámina; D, MGB 38375, detalle mostrando los nervios secundarios terminando en los ápices mucronados de los dientes del margen, además de nervios epimediales terciarios percurrentes chevronados; E, MGB 38375, detalle mostrando nervios terciarios epimediales percurrentes mezclados y nervios terciarios exteriores percurrentes y rectos; F, MGB 38327, fragmento apical de lámina con algunos dientes preservados; G, MGB 38373, fragmento de una lámina mostrando nervios intersecundarios; H, MGB 38342, fragmento apical de una lámina mostrando algunos dientes en el margen; I, MGB 38372, detalle del ápice de una lámina. Escalas en C e I, 1 cm.; divisiones en D y E, en milímetros.

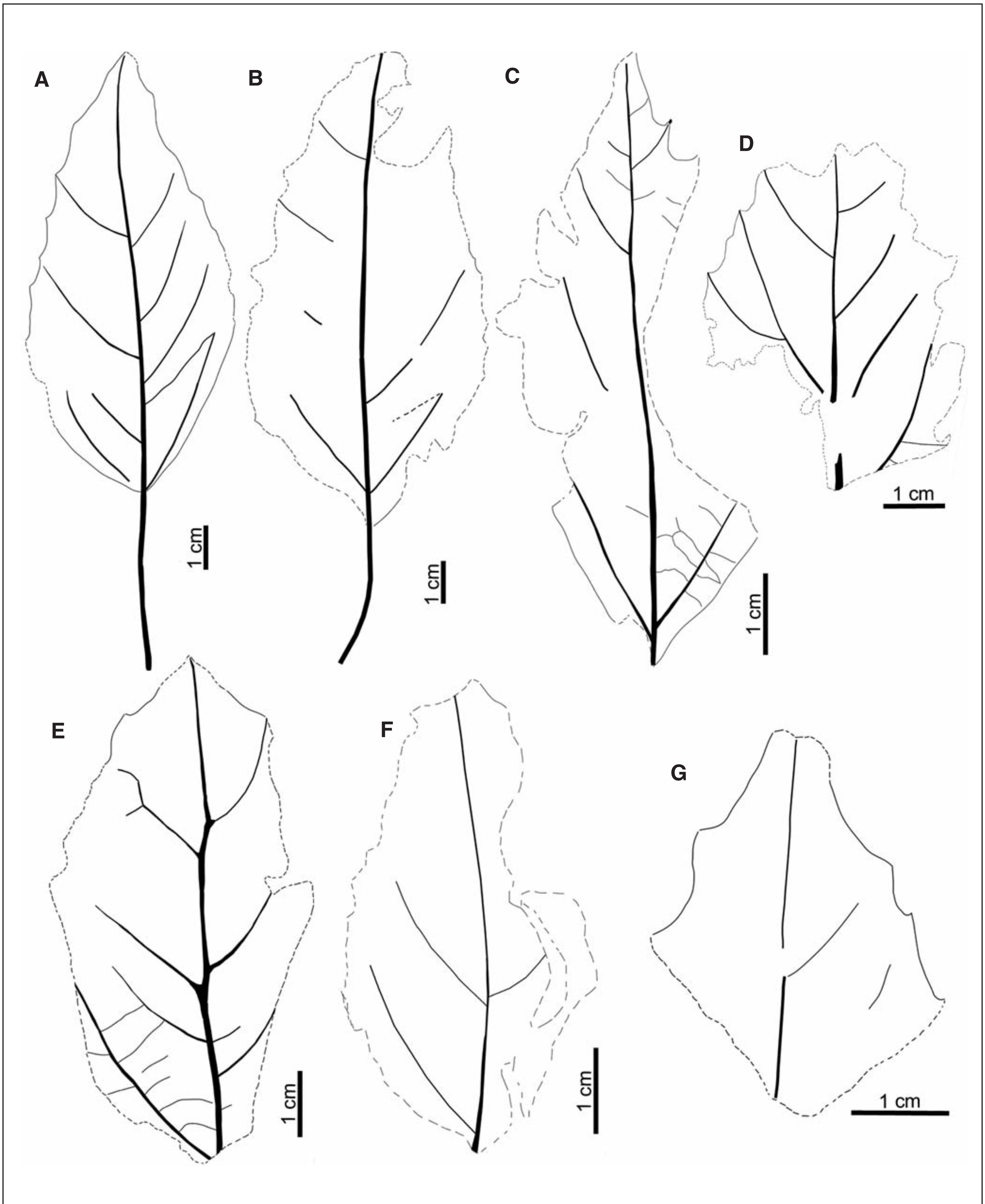


Fig. 30. *Betuliphyllum* sp. from the Isona-*sud* site, interpretative drawings: A, MGB 38341; B, MGB 38340; C, MGB 38375; D, MGB 38327; E, MGB 38373; F, MGB 38342; G, MGB 38372.

Fig. 30. *Betuliphyllum* sp. del yacimiento Isona-*sud*, dibujos interpretativos: A, MGB 38341; B, MGB 38340; C, MGB 38375; D, MGB 38327; E, MGB 38373; F, MGB 38342; G, MGB 38372.

Material. MGB 38327, MGB 38340–42, MGB 38372–73, MGB 38375.

Occurrence. Isona-*sud* site (see Villalba-Breva *et al.*, 2015 for details).

Description. The fossils consist of partial laminae except specimens MGB 38340 and MGB 38341, which are complete leaves bearing the petioles marginally attached (Fig. 29A–B; Fig. 30A–B). Leaves are notophyllous, with laminae 76.7–95.9 mm long and 41.5–44.7 mm wide. Laminae length/width ratio is 1.9–2.1. The petiole is 38 mm long and 1.2 mm wide in MGB 38341 (Fig. 29A; Fig. 30A). The shape of the lamina is ovate and symmetrical. The lamina base is slightly asymmetrical, convex and acute while the apex is symmetrical, straight and acute (Fig. 29A–C; Fig. 30A–C). The distal two thirds of the margins are slightly dentate. There is one order of regularly spaced teeth, giving a density of 1 to 2 teeth per cm (Fig. 29A–C, F, G; Fig. 30A–D, G). Teeth are generally concave/concave (Fig. 29A, C–

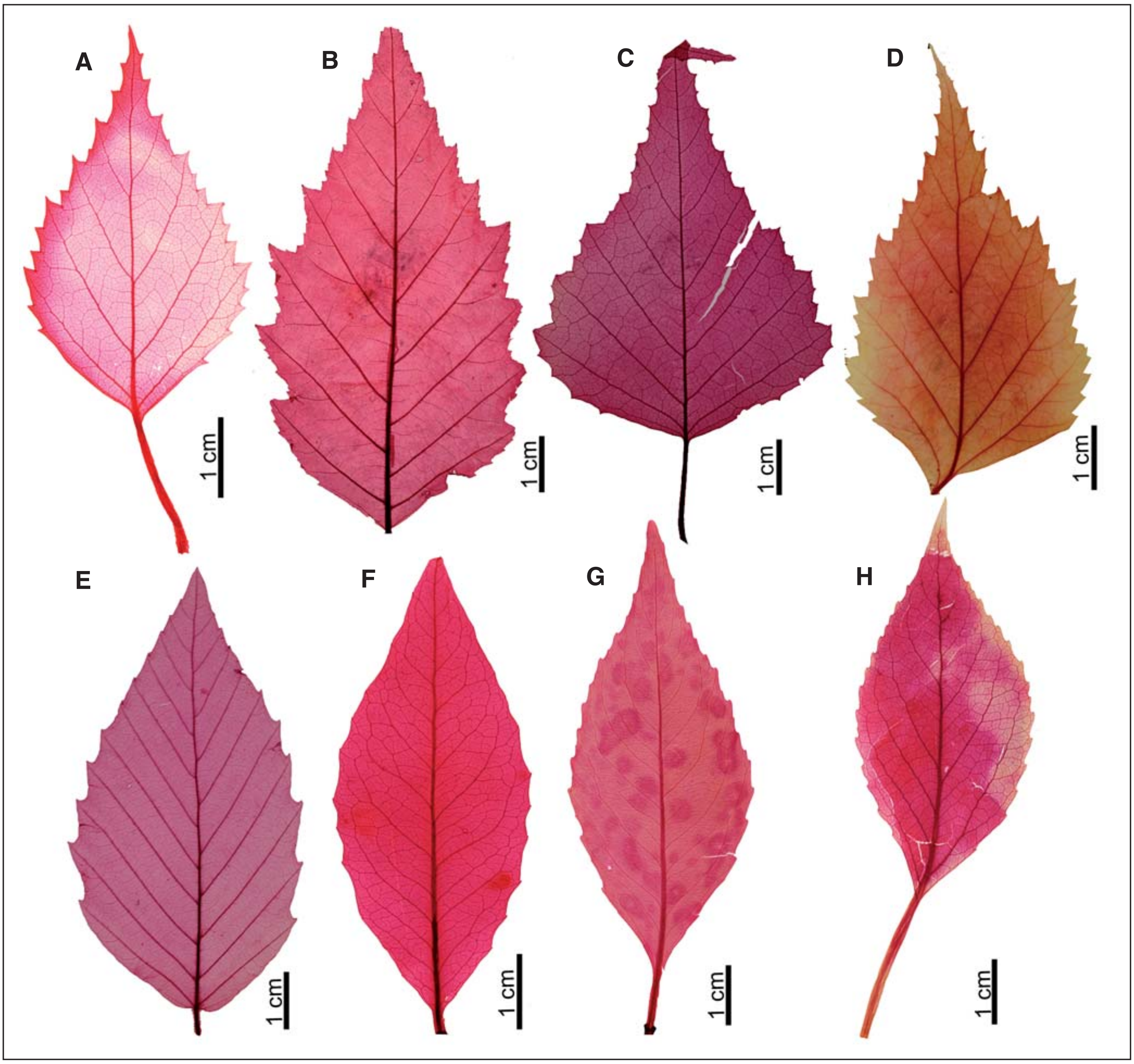


Fig. 31. Specimens of the National Cleared Leaf Collection-Wolfe (NCLC-W) compared to *Betuliphyllum* sp. from the Isona-*sud* site: A, Betulaceae, *Betula mandshurica* (Regel) Nakai, uncoded; B, Betulaceae, *Betula nigra* Linnaeus, uncoded; C, Betulaceae, *Betula platyphylla* Sukachev, uncoded; D, Betulaceae, *Betula verrucosa* Ehrhart, uncoded; E, Fagaceae, *Fagus grandifolia* Ehrhart, UCH M246360; F, Celastraceae, *Maytenus bilocularis* (von Mueller) Loesener, uncoded; G, Celastraceae, *Wimmeria concolor* Schlechtendal & Champion, DS628045; H, Salicaceae, *Populus acuminata* Rydberg, UCH212764.

Fig. 31. Ejemplares de la National Cleared Leaf Collection-Wolfe (NCLC-W) comparados con *Betuliphyllum* sp. del yacimiento Isona-*sud*: A, Betulaceae, *Betula mandshurica* (Regel) Nakai, no codificado; B, Betulaceae, *Betula nigra* Linnaeus, no codificado; C, Betulaceae, *Betula platyphylla* Sukachev, no codificado; D, Betulaceae, *Betula verrucosa* Ehrhart, no codificado; E, Fagaceae, *Fagus grandifolia* Ehrhart, UCH M246360; F, Celastraceae, *Maytenus bilocularis* (von Mueller) Loesener, no codificado; G, Celastraceae, *Wimmeria concolor* Schlechtendal & Champion, DS628045; H, Salicaceae, *Populus acuminata* Rydberg, UCH212764.

D) but, less frequently, they may also be convex/concave (Fig. 29F). They are separated each other by rounded sinuses (Fig. 29A, C–D, F, I; Fig. 30A, C–D, G) and their apices seem mucronate (Fig. 29D). Venation is pinnate craspedodromous. The secondary veins are alternate and not regularly spaced from each other. They arise from the midvein at acute angles, which smoothly decrease proximally, and end at the tooth apices (Fig. 29A, D; Fig. 30A). Intersecondary veins, when present, run parallel to major secondary veins and are less than half the length of the subjacent secondary vein (Fig. 29A, G; Fig. 30A–E). Specimens MGB 38373 and MGB 38375 preserve details of tertiary veins. Intercostal tertiary veins are opposite percurrent (Fig. 29G; Fig. 30E) and epimedial tertiary veins form a chevron or are mixed percurrent (Fig. 29C, E, G; Fig. 30C, E). Epimedial tertiary veins are proximally acute to midvein and distally basiflexed (Fig. 30E). Exterior tertiary veins are straight and terminate at the margin (Fig. 29C, E; Fig. 30C). Likely reticulate quaternary and quinternary veins are weakly preserved in MGB 38375 (Fig. 29D).

Discussion. Vicente (2002) assigned the studied material to four new species: *Populus paleomutabilis*, *P. intermedia*, *P. rhomboidalis* and *Betula protopendula*. However, Marmi *et al.* (2014) suggested that the specimens belong to a single leaf morphotype (Dicot type 13) which might represent the same taxon. Specimen MGB 38372 was assigned to *Platanus aceroides* by Vicente (2002) but it closely resembles the apical end of MGB 38341 in general shape and marginal features (Fig. 29A and I, respectively). Marmi *et al.* (2014) also compared the specimens from Isona to *Viburnum sphenophyllum* Knowlton, *in* Lesquereux, 1892 and *Quercus dakotensis* Lesquereux, 1892 from the Upper Cretaceous Dakota Group, United States. These species have laminar shapes and tooth features very similar to the studied specimens and also present pinnate craspedodromous venation. However, they lack intersecondary veins and the number of secondary veins is higher than in the fossil leaves from Isona (Lesquereux, 1892: pl. LIII, fig. 4; pl. VII, fig. 4).

The studied specimens share blade shape, venation and dentition features with different taxa included within the clade Eurosids 1 (Fig. 31). The laminar and tooth shapes of specimens from Isona strongly resemble those of the leaves of *Fagus grandifolia* Ehrhart (Fig. 31E) and *Maytenus bilocularis* von Mueller (Fig. 31G). However, the latter species has semicraspedodromous instead of craspedodromous secondary veins. Ovate leaves with dentate margins composed of concave/concave teeth separated from each other by rounded sinuses are also typical of species of genus *Betula* (Fig. 31A–D). Moreover, these leaves have pinnate craspedodromous venation, with secondary veins terminating at the tooth apices, and relatively long petioles as it was observed in the leaf fossils from Isona. However, in some extant species of *Betula*, two orders of teeth have been observed (e.g. *Betula nigra* Linnaeus, Fig. 31B; and *Betula verrucosa* Ehrhart, Fig. 31D). According to similarities with extant species of genus *Betula*, the studied specimens are assigned to genus *Betuliphyllum*, which was proposed by Dusén (1899) for naming Betulaceae-like fossil leaves.

Order UNKNOWN
Family UNKNOWN

Eurosid 1 indet.
Fig. 32A–B; Fig. 33A

Synonymy

2002 *Cercidiphyllum arcticum* (Brown); Vicente: 74, pl. XVI, fig. 2

2014 Dicot type 14 Marmi *et al.*: 57, pl. V, fig. 4; pl. VI, fig. 4

Material. MGB 38335.

Occurrence. Isona-*sud* site (see Villalba-Breva *et al.*, 2015 for details).

Description. Specimen MGB 38335 consists of a simple, microphyllous, partially preserved leaf that is 43.6 mm long and 41.2 mm wide (Fig. 32A). The lamina is nearly circular and entire-margined (Fig. 32A; Fig. 33A). The apex and the base are obtuse and rounded. The midvein is straight and stout. Secondary veins are thin and seem brochidodromous (Fig. 32A–B; Fig. 33A). Intercostal tertiary veins are straight opposite percurrent and form obtuse angles compared to the primary vein (Fig. 32B; Fig. 33A). Exterior tertiary veins are also straight and likely terminate at the margin (Fig. 32B; Fig. 33A). Quaternary venation is partially preserved and seems reticulate (Fig. 32B; Fig. 33A).

Discussion. Vicente (2002) assigned the specimen to *Cercidiphyllum arcticum* Brown, 1962. However, this species has acrodromous venation instead of pinnate venation and their margins are usually toothed (Brown, 1962: pl. 37, figs. 8–9, 13, 15, 17, 20, 22). *Leguminosites mucronatus* Herman & Kvaček, 2010 from the lower Campanian of Austria is similar in size, marginal features and venation to the studied specimen, although its blade shape is broadly elliptic instead of circular (fig. 35 in Herman & Kvaček, 2010). MGB 38335 also resembles the extant *Glyptopetalum orbiculare* Merrill in shape and venation (Fig. 34A). This species belongs to Celastraceae.

Clade CORE EUDICOTS
Order UNKNOWN
Family UNKNOWN

Core Eudicot indet. 3
Fig. 32C–F

Synonymy

2002 *Nilssonia annavilae* Vicente: 50–51, pl. VI, fig. 3–4; pl. XLIII, fig. 6–7

Material. MGB 38161, MGB 38163.

Occurrence. Isona-*sud* site (see Villalba-Breva *et al.*, 2015 for details).

Description. Leaves are linear, microphyllous, 62.3–62.8 mm long and 14.3–15.2 mm wide. In both specimens, the lamina base is lost (Fig. 32C–D). The lamina apex seems acute but its shape is difficult to discern because it is not well preserved in any specimen (Fig. 32C). The lamina is medially symmetrical and the margins are entire (Fig. 32C). The midvein is straight and stout (Fig. 32C, E). A great number of thin secondary veins arise from the midvein at nearly right angles (69º–87º) and terminate at the margins (Fig. 32E–F). Moreover, the secondary veins are very close and run parallel to each other (Fig. 32F).

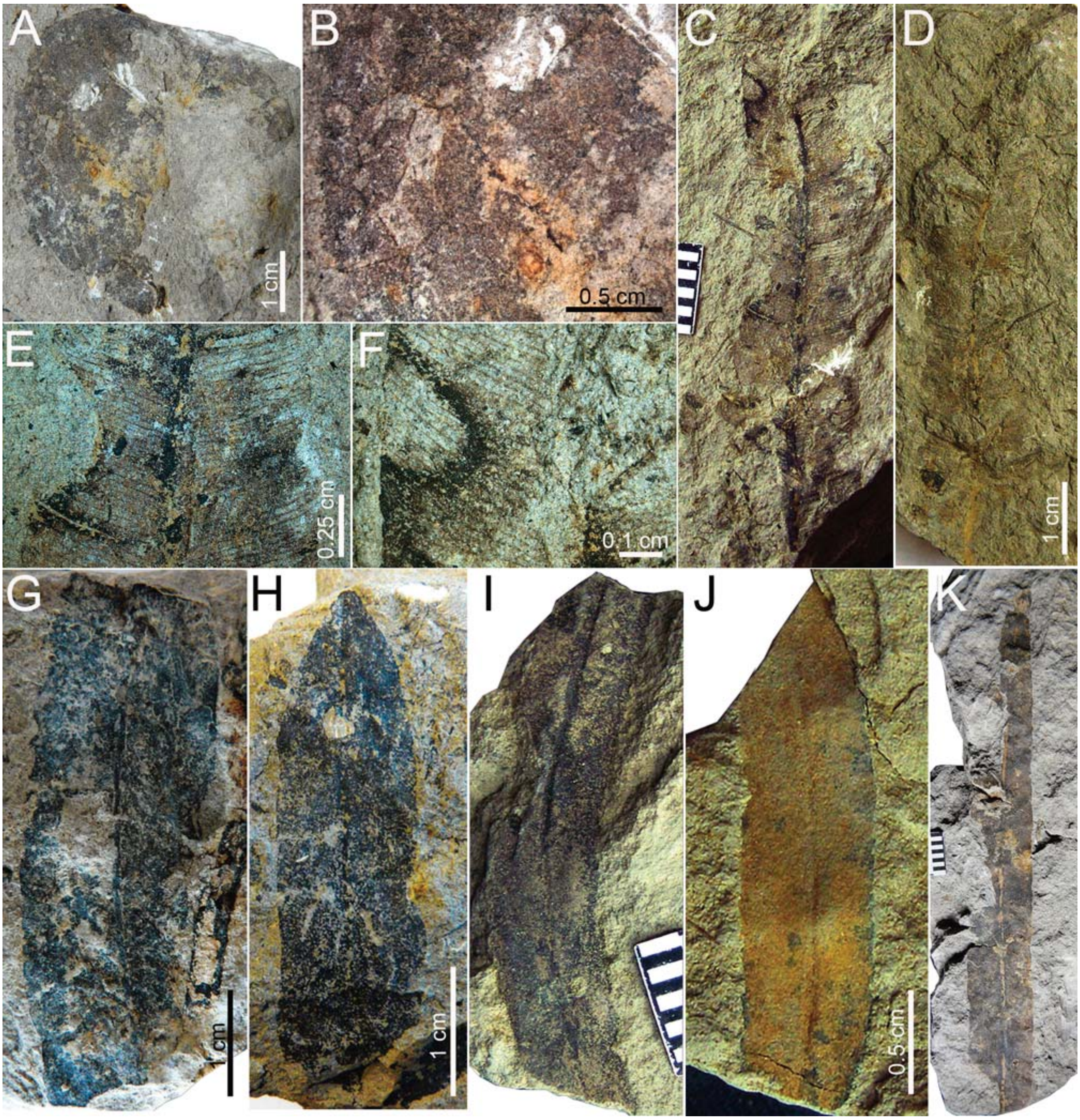


Fig. 32. Eurosid 1 indet. (A–B), Core Eudicot indet. 3 (C–F) and *Dicotylophyllum* cf. *proteoides* (Unger) Herman & Kvaček (2010) (G–K) from the Isona-*sud* site: A, MGB 38335, partial leaf; B, detail of this last showing tertiary as well as quaternary venation; C, MGB 38161, partial leaf; D, MGB 38163, partial leaf; E, MGB 38161 detail showing the stout midvein and thin secondary veins; F, detail of secondary veins and a likely mark of insect predation or damage by fungi in the same specimen; G, MGB 38219, fragment of leaf; H, MGB 38378, apical end of a leaf; I, MGB 38249, fragment of leaf; J, MGB 38359, fragment of leaf; K, MGB 38270, fragment of a long leaf. Scales in C, I and K, 1 cm.

Fig. 32. Eurosid 1 indet. (A–B), Core Eudicot indet. 3 (C–F) y *Dicotylophyllum* cf. *proteoides* (Unger) Herman & Kvaček (2010) (G–K) del yacimiento Isona-*sud*: A, MGB 38335, fragmento de hoja; B, detalle de esta última mostrando la nervadura terciaria y quaternaria; C, MGB 38161, fragmento de hoja; D, MGB 38163, fragmento de hoja; E, detalle de MGB 38161 mostrando un nervio principal grueso y nervios secundarios finos; F, detalle de los nervios secundarios y de una posible marca de depredación de insecto o de daño por la acción de los hongos, en el mismo ejemplar; G, MGB 38219, fragmento de hoja; H, MGB 38378, parte apical de una hoja; I, MGB 38249, fragmento de hoja; J, MGB 38359, fragmento de hoja; K, MGB 38270, fragmento de hoja elongada. Escalas en C, I y K, 1 cm.

Discussion. Vicente (2002) assigned both specimens to his new species *Nilssonia annavilae*. Elongated leaves with entire margins showing similar venation are usually found in the cycadalean genus *Nilssonia* (e.g. fig. 19 in Herman & Kvaček, 2010). However, this genus is also featured by lamina ruptures simulating segmentation, which has not been observed in the studied specimens. The particular venation of the leaf fossils from Isona is also found in living angiosperms within the clades Eurosids 1 (Fig. 34B) and Euasterids 1 (Fig. 34C–E). Accordingly, the specimens are tentatively assigned to indeterminate Core Eudicots.

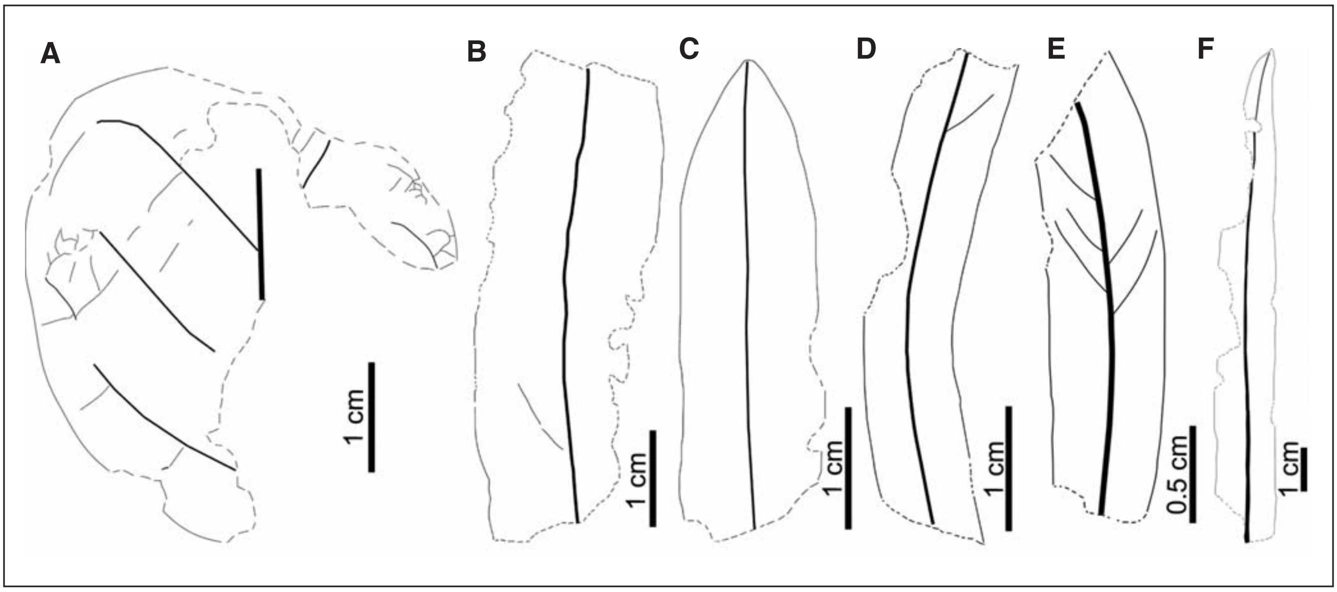


Fig. 33. Eurosid 1 indet. (A) and *Dicotylophyllum* cf. *proteoides* (Unger) Herman & Kvaček (2010) (B–F) from the Isona-*sud* site, interpretative drawings: A, MGB 38335; B, MGB 38219; C, MGB 38378; D, MGB 38249; E, MGB 38359; F, MGB 38270.
Fig. 33. Eurosid 1 indet. (A) y *Dicotylophyllum* cf. *proteoides* (Unger) Herman & Kvaček (2010) (B–F) del yacimiento Isona-*sud*, dibujos interpretativos: A, MGB 38335; B, MGB 38219; C, MGB 38378; D, MGB 38249; E, MGB 38359; F, MGB 38270.

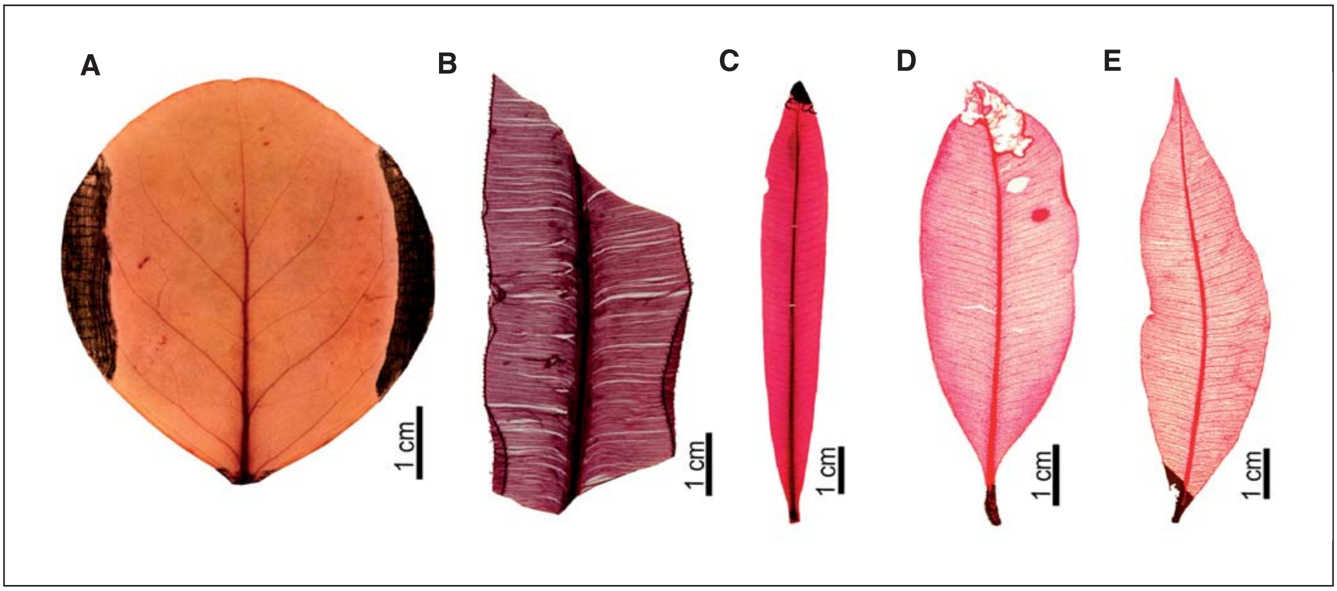


Fig. 34. Specimens of the National Cleared Leaf Collection-Wolfe (NCLC-W) compared to Eurosid 1 indet. and Core Eudicot indet. 3 from the Isona-*sud* site: A, Celastraceae, *Glyptopetalum orbiculare* Merrill, UC262807; B, Ochnaceae, *Euthemis leucocarpa* Jack, UCH267325; C, Apocynaceae, *Nerium oleander* Linnaeus, DS606231; D, Apocynaceae, *Alyxia concatenata* (Blanco) Merrill, UCH240652; E, Apocynaceae, *Alyxia forbesii* King, UCH259412.
Fig. 34. Ejemplares de la National Cleared Leaf Collection-Wolfe (NCLC-W) comparados con Eurosid 1 indet. y Core Eudicot indet. 3 del yacimiento Isona-*sud*: A, Celastraceae, *Glyptopetalum orbiculare* Merrill, UC262807; B, Ochnaceae, *Euthemis leucocarpa* Jack, UCH267325; C, Apocynaceae, *Nerium oleander* Linnaeus, DS606231; D, Apocynaceae, *Alyxia concatenata* (Blanco) Merrill, UCH240652; E, Apocynaceae, *Alyxia forbesii* King, UCH259412.

Clade EUDICOTS
Order UNKNOWN
Family UNKNOWN

Genus *Dicotylophyllum* Bandulska, 1923

Type species. *Dicotilophyllum stopesii* Bandulska, 1923 by original designation.

Dicotylophyllum cf. *proteoides* (Unger) Herman & Kvaček, 2010
Fig. 32G–K; Fig. 33B–F

Synonymy
2002 *Benzoin attenuatum* (Heer); Vicente: 65–66, pl. XI, fig. 2
2002 *Daphnogene lanceolata* (Unger); Vicente: 68, not figured
2002 *Nectandra prolifica* (Berry); Vicente: 70, pl. XI, figs. 7–9
2002 *Dewalquea isonensis* Vicente: 71–72, pl. XIV, fig. 1
2002 *Carya heerii* (Ettingshausen); Vicente: 82–83, pl. XIX, fig. 6
2002 *Myrica wadii* (Berry); Vicente: 83–84, pl. XX, fig. 1
2002 *Salix gardnerii* (Knowlton); Vicente: 89–90, pl. XXVI, figs. 1–3
2002 *Podogonium obtusifolium* (Heer); Vicente: 100–101, pl. XXVII, figs. 7–8
2002 *Eucalyptus angusta* (Velenovsky); Vicente: 106–107, pl. XXVIII, fig. 2
2002 *Eucalyptus geinitzii* (Heer); Vicente: 107–108, pl. XXVIII, fig. 4
2002 *Apocynophyllum ripleyensis* (Berry); Vicente: 121, pl. XXIX, fig. 7

Material. MGB 38219, MGB 38241–42, MGB 38246–47, MGB 38249–54, MGB 38270–72, MGB 38284–86, MGB 38295, MGB 38308–09, MGB 38311–12, MGB 38359, MGB 38378, MGB 38387, MGB 38389, MGB 38414.

Occurrence. Isona-*sud* site (see Villalba-Breva *et al.*, 2015 for details).

Description. The fossils are fragments of microphyllous, linear leaves that are medially symmetrical and have entire margins (Fig. 32G–K; Fig. 33B–F). The fragments are 28.4–122.6 mm long and 4.33–18.5 mm wide. Apex is acute and straight and is preserved in a very few specimens (e.g. Fig. 32H). The venation is pinnate. All specimens show a straight and stout midvein. Secondary veins are very thin and partially preserved in some specimens (Fig. 33B, D–E). They are excurrently attached to the midvein from which they arise forming acute angles (28.5º–43.9º).

Discussion. Vicente (2002) assigned the specimens to a variety of species: *Benzoin attenuatum* Heer, 1885–1859, *Daphnogene lanceolata* Unger, 1851, *Nectandra prolifica* Berry, 1925, *Dewalquea isonensis* Vicente, 2002, *Salix gardnerii* Knowlton, 1917, *Carya heerii* Ettingshausen, 1854, *Myrica wadii* Berry, 1925, *Podogonium obtusifolium* Heer, 1855–1859, *Eucalyptus angusta* Velenovsky, 1882–1887, *Eucalyptus geinitzii* Heer, 1885 and *Apocynophyllum ripleyensis* Berry, 1925. However, similarities in size, shape, marginal features and primary venation suggest that the specimens likely belonged to the same taxon. Similar leaves were described from the lower Campanian of the Grünbach Formation (Austria) by Herman & Kvaček (2010). These authors assigned such fossils to *Dicotylophyllum proteoides* (Unger) Herman & Kvaček (2010) and *Dicotylophyllum* sp. 7 (Herman & Kvaček, 2010: pl. 28, figs. 1–15; pl. 29, figs. 1–7; pl. 25, figs. 8–14). However, some specimens of *D. proteoides* show camptodromous secondary veins and percurrent tertiary veins (fig. 45H in Herman & Kvaček, 2010), features not preserved in the specimens from Isona. On the other hand, *Dicotylophyllum* sp. 7 has thin secondary veins closely spaced and running parallel to the midvein (Herman & Kvaček, 2010: pl. 25, fig. 11) unlike the studied specimens. Based on the strong similarities in size, shape, marginal features and primary venation, the leaf fossils from Isona are tentatively assigned to *Dicotylophyllum* cf. *proteoides*.

DISCUSSION

The new revision of the dicot leaf fossils of the Vicente collection has allowed assigning 131 specimens to 16 taxa. Two of them, Core Eudicot indet. 3 and *Dicotylophyllum* cf. *proteoides*, were not previously described by Marmi *et al.* (2014). In addition, these authors assigned several fragments of linear pinnatisect leaves in eight specimens to the Dicot type 15, which was considered dicot foliage of uncertain botanical affinity. This morphotype has not been revised here because of the lack of similar extant dicot leaves in the Cleared Leaf Databases. Thus, the plant fossil assemblage of the Isona-*sud* site could include up to a total of 17 dicot taxa. Hypotheses on the supra-generic taxonomy of 16 taxa were proposed on the basis of comparisons of leaf architecture features among fossil specimens and cleared leaves of extant taxa. Accordingly, two of them (*Daphnogene* cf. *lanceolata* and *Cinnamomophyllum vicente-castellum* n. sp.) could represent members of Magnoliids and the remaining are included within Eudicots. Within this latter clade, dicot leaves from Isona-*sud* could represent basal Eudicots such as Proteales (*Ettingshausenia* sp.) as well as likely members of Eurosids I (*Saliciphyllum serratum* n. sp., *Alnophyllum* sp., *Celastrophyllum bilobatum*, *Celastrophyllum* sp., *Betuliphyllum* sp. and Eurosid 1 indet.), Eurosids II (*Myrtophyllum*) and Asterids (*Cornophyllum herendeenensis*). Within the clade Rosids, the families Salicaceae, Betulaceae and Celastraceae are tentatively identified. The Salicaceae have a particularly extensive fossil record in the Cenozoic but the only secure Cretaceous record of their inclusive order (the Malpighiales) are the fossil flowers of *Paleoclusia* (Clusiaceae) (Friis *et al.*, 2011). Similarly, several leaves and seeds assigned to Celastraceae have been described from the Eocene onwards in Europe and North America (Collinson *et al.*, 1993). However, *Salix*-like and *Celastrus*-like leaves are common in the Late Cretaceous fossil record. In addition, recent molecular analyses suggest that stem Salicaceae and Celastrales evolved during the Cretaceous (Bell *et al.*, 2010; Xi *et al.*, 2012). On the contrary, the Fagales are well documented in the Late Cretaceous floras (Friis *et al.*, 2011) and are frequent in the sporomorph record of the uppermost Cretaceous of the Iberian Peninsula (Diéguez *et al.*, 2010). Pollen assigned to Fagales was also reported in the plant bearing beds of the Isona-*sud* site (Villalba-Breva *et al.*, 2015).

From a phytogeographical point of view, Vicente (2002) estimated that 72% of the taxa from the Isona flora were shared with North American floras and 35% and the 3% with Eurasian and Arctic floras, respectively.[1] Marmi *et al.* (2014) also suggested that the Isona flora was a mixture of elements from other Cretaceous floras of Europe and North America. This is suported by the presence of the fossil palm *Sabalites longirhachis* in Campanian-Maastrichtian localities from France, Austria and Romania in addition to the southern Pyrenees. *Sabalites* palms are also reported from the Upper Cretaceous of North America. Taxodioid conifers are shared with other Upper Cretaceous localities from Portugal, Austria as well as Central and Eastern Europe (see details in Marmi *et al.*, 2014). Current data agree with the previous studies. For instance, *Daphnogene* sp. and *Dicotylophyllum proteoides* are common in the Cretaceous and Tertiary of Central Europe (Hably, 1989; Herman & Kvaček, 2010) and *Cornophyllum* cf. *heredeenensis* suggests a relationship with Upper Cretaceous floras from North America. However, the three new species described in the present work together with *Celastrophyllum bilobatum* could reveal some degree of uniqueness in the flora from the Lower Maastrichtian of Isona. This is consistent with the palaeogeography of southern Europe during the latest Cretaceous. Emerged lands of the Iberian Peninsula and southern France formed a large island, the so called Iberoarmorican Domain, in the westernmost edge of the Southern European archipelago (Dercourt *et al.*, 2000). The Iberoarmorican Domain was isolated from landsmasses of Central and Eastern Europe by the Tethys seawaters. However, it is important to note that the Lower Maastrichtian flora of Isona is not coeval to some of the other Cretaceous floras used for comparisons; for instance, those of the Albian of Nazareth (Portugal), the Cenomanian of Bohemia (Czech Republic) or the lower Campanian of Grünbach (Austria). In addition, taxonomic composition of the fossil plant assemblages is strongly influenced by environment and taphonomy. Based on Villalba-Breva *et al.* (2015), plant remains from Isona were parautochthonous and allochthonous and deposited in a distal floodplain. Although it is likely that most of the parent plants grew somewhere in the floodplain and surronding environments, a more precise habitat was only possible to infer for trees or shrubs bearing *Alnophyllum* leaves. These alder-like plants probably inhabited river banks or environments close to the overflow point, forming riparian vegetation (Villalba-Breva *et al.*, 2015).

CONCLUSIONS

The paleobotanical collection of Mr. Joan Vicente i Castells is among the most important in Europe. It is composed of around 400 specimens including taxodioid and cheirolepidiacean conifers, likely pandanales, *Sabalites* palms and a variety of dicotyledoneous foliage. The 131 dicot leaf specimens of this collection have been tentatively assigned to 17 taxa representing Magnoliids, Proteales, Eurosids and Asterids.

In spite of the high convergence among leaf architecture features, the fragmentary nature of most of specimens and the lack of cuticular data, possible members of Salicaceae, Betulaceae and Celastraceae have been identified within the clade Rosids. Family Lauraceae has tentatively been identified within Magnoliids.

The Isona flora shares some taxa with other Upper Cretaceous-Tertiary localities from Europe and North America. However, there are some dicot taxa that seem unique in this Pyrenean locality. Many Cretaceous fossil floras from Europe and North America are pending revision. Among the few examples of revised floras in Europe there is the Grünbach (Austria) lower Campanian one (Herman & Kvaček, 2010). Thus, a better understanding of the diversity of Late Cretaceous floras from Europe and North America depends on a deep taxonomic revision of all the available fossil material in addition to a better knowledge of the taphonomy and geological setting of their original localities. Only then, the uniqueness of some Cretaceous floras, such as that of Isona, will be able to be rigorously evaluated.

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[1] Editor's note: The percentages fully correspond to those given in Vicente (2002: 144). The fact that their addition is over 100 per cent (110%) points only to the fact that the distribution of some species was not restricted to one of the three areas considered in that paper.

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