Foliar adaptations of *Rhus asymmetrica* sp. nov. from the Oligocene of Cervera (Catalonia, Spain). Palaeoclimatic implications

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Abstract

Rhus asymmetrica sp. nov. from the lower Oligocene of Cervera (Catalonia, Spain) is characterized by a trifoliate leaf with a symmetric sessile apical leaflet and asymmetric lateral leaflets. The apical leaflet displays a serrate margin and decurrent base with pinnate primary venation, craspedodromous secondary venation and an irregular reticulate tertiary framework. The lateral leaflets show a rounded base with a secondary basal vein in the distal part of the lamina, while the proximal part is straight or concave. Formerly, these specimens were accommodated within *Rhus pyrrhae* Unger. However, detailed study of the *Rhus pyrrhae* holotype has led us to emend its diagnosis to include its brochidodromous secondary venation pattern, which differs clearly from the venation pattern of the new species. Additionally, a number of leaf morphotypes from the Cervera palaeobotanical site that were erroneously attributed to *Rhus* by former authors have been segregated and related to *Acer* and *Toxicodendron*. The extant species *R. aromatica* displays the closest foliar structure to *Rhus asymmetrica* sp. nov. However, differences in the leaf morphology suggest that the new species grew under distinct palaeoclimatic conditions: (1) *R. asymmetrica* sp. nov. bears glands at the tips of the teeth of the lateral leaflets while *R. aromatica* is devoid of these glands. This character would help to prevent excessive evapotranspiration; (2) Lateral leaflets of *R. asymmetrica* sp. nov. are asymmetric while in *R. aromatica* they are symmetric, suggesting that *R. asymmetrica* sp. nov. grew under a greater environmental stress than *R. aromatica*; (3) *R. asymmetrica* sp. nov. displays fewer teeth with a larger tooth-area than *R. aromatica.* This would indicate growth under a warm climate with low seasonal contrast. These features are compatible with an open woodland habitat under subtropical palaeoclimatic conditions.

Keywords: Anacardiaceae; Paleogene; Ebro Basin; paleoenvironment; foliar architecture.

1. Introduction

Rhus is one of the most heterogeneous and controversial genera in the Anacardiaceae (Andrés-Hernández and Terrazas, 2009). Their foliar features are characterized by simple or compound leaves, with leaflets varying in number from three to twenty-one leaflets. Additionally, some species display a high intraspecific polymorphism. Barkley (1937) redefined this genus, based chiefly on the characters of the fruits and realized that a number of *Rhus* species should be segregated and included within *Malosma.* He also divided *Rhus* into the two subgenera: *Rhus* that includes *R. lanceolata, R. copalina, R. chinensis, R. sandwicensis, R. punjabensis, R. potaninii, R. typhina, R. glabra* and *R. michauxii,* and *Lobadium* that nests *R. ovata, R. integrifolia, R. vinens, R. choriophylla, R. pachirrachis, R. schiedeana, R. kearneyi, R. rubifolia, R. microphylla, R. trilobata* and *R. aromatica*. Finally, he erected the so-called "*Rhus* complex" to accommodate the genera which were considered to show affinity to *Rhus*. Heimsch (1940) studied the wood anatomy and pollen of *Rhus* revealing that some species that Barkley (1937) ranged within the genus *Rhus* would belong to *Actinocheta*, *Cotinus*, *Malosma*, *Metopium* and *Toxicodendron,* which he kept within the *Rhus* complex. Subsequently, studies of the morphology and anatomy (Gillis, 1971; Young, 1975; Andrés-Hernández and Terrazas 2006, 2009; Andrés-Hernández et al., 2014), biochemistry (Young, 1979) and ITS (internal transcribed spacer) sequences (Miller et al*.,* 2001) of *Rhus* were published. Phylogenetic studies combined with foliar features demonstrated that *Rhus* s.s. is a monophyletic genus composed of two subgenera i.e *Rhus* and *Lobadium* (Andrés-Hernández et al., 2014), with subgenus *Rhus* being paraphyletic, while subgenus *Lobadium* is monophyletic (Miller et al. 2001). According to these authors the results were consistent with previous studies in the terms of identity of the genus. However, the phylogenetic relationship between *Rhus* s.s. with the genera that were removed from it (*Actinocheita*, *Cotinus*, *Malosma*, *Searsia* and *Toxicodendron*) remains poorly known. Despite the significant progress in *Rhus* phylogeny during the last few years, some authors still keep within *Rhus* some species that correspond to *Searsia* (Yi et al., 2004).

The fossil record of *Rhus* is scarce. However, in a synthesis of the fossil Anacardiaceae, Edwards and Wonnacott (1935) pointed out that by the mid-20th century, 159 organ-species of *Rhus* fossils from Europe and North America had been reported (e.g. by Unger, 1847; Saporta, 1866; Lesquereux, 1891). This large number of taxa would seem to reflect a high degree of intraspecific polymorphism rather than real species richness.

The Oligocene of Cervera has provided what is so far the richest assemblage of *Rhus* fossils in Europe (Depape and Brice, 1965; Sanz de Siria, 1992), with dozens of well-preserved specimens, including two leaves with the three leaflets anatomically connected. The material studied by most authors to date was collected by Mr. Martí Madern, a schoolteacher from Cervera. Most of the leaves in his collection are housed in the Barcelona Natural History Museum (Museu de Ciències Naturals de Barcelona), while one of the two exceptionally complete leaves illustrated and briefly described by Depape and Brice (1965) is stored in the University Pierre et Marie Curie, specifically in the Boureau collection. These authors stated that the lateral leaflets were asymmetric, while the apical leaflet displayed bilateral symmetry and bore a petiolule. Comparison of specimens from the Rupelian of Cervera with those from upper Oligocene and Miocene European localities led these authors to conclude that the Catalan specimens were similar to the fossil organ-species *R. pyrrhae* Unger, "*R*". *herthae* Unger, *R. pluriloba* Boulay, *R. vexans* Lesquereux, *R. rhomboïdalis* Saporta, *R. subrhomboïdalis* Lesquereux, *R. paucidentata* Laurent, *R. membranacea* Lesquereux, "*R*". *quercifolia*

Goeppert and, *R. evansii* Lesquereux. In addition, Depape and Brice (1965) compared the Cervera specimens with trifoliate leaves of living *Rhus* (i.e. *R. aromatica*, *R. trilobata*, "*R.*" *toxicodendron* and *R. diversifolia*) from French herbaria, and concluded that the fossil specimens could be assigned to *R.* aff. *aromatica*. Part of this fossil material was studied by Broutin (1970). This author described into detail the specimens concluding that the lateral leaflets are basal asymmetric with a more developed side in the distal part of the lamina. Also, the lateral leaflets show a different number of the teeth in both side of the blade. Broutin (1970) also provided the first insight of the secondary venation pattern being craspedodromous. In turn, he recognized cuticle fragments in one specimen and suggested that the *Rhus* fossils from Cervera might display pilosity. Some years later, Fernández-Marrón (1971) collected and studied four specimens from the Oligocene plant beds of Cervera as a part of her PhD Thesis. Fernández-Marrón (1971) noticed that the original descriptions of the Cenozoic *Rhus* species were ambiguous and the degree of polymorphism of the specimens from Cervera was high, making their taxonomic affinity challenging. Nevertheless, she finally included them in *R. pyrrhae* and suggested that the basal shape of the leaflets may allow identification of isolated apical and lateral leaflets. The lateral leaflets would range from slightly lobate to lobate, while the general shape could be symmetric or asymmetric. In contrast, the apical leaflet base would be decurrent and bear a petiolule. Fernández-Marrón (1971) also reported that the venation pattern is homogeneous in the two types of leaflets; primary venation being pinnate, while the secondary veins are craspedodromous. Finally, Sanz de Siria (1992) studied thirty-four "*Rhus*" specimens from the Martí Madern collection housed in the Barcelona Natural History Museum. He realized that the specimens displayed strong medial asymmetry and that the size and leaf blade varied greatly. He also noticed that the diagnosis of *R. pyrrhae*, does not accommodate the whole range of variation of *R. pyrrhae* from the Martí Madern collection and proposed that the regular venation pattern should be the main diagnostic character. No further studies of the Cervera *Rhus* specimens have been performed since.

R. pyrrhae was defined by Unger (1847) based on the general shape of only one apical leaflet from the middle Miocene (Serravalian) of Radoboj (formerly Radobojum), in Croatia. This author compared the fossil specimen with living *R. aromatica* and concluded that it could correspond to a trifoliate leaf. During the 20th century, new plant localities containing *R. pyrrhae* were reported. For instance, the Palaeocene of Menat, France, would include the oldest record of the species (Piton, 1940; but see a critical review of the Menat fossil record in Wedmann et al., 2018). In spite of those taxonomic studies, the leaf architecture especially the venation pattern and the lateral leaflets of *R. pyrrhae* remained practically unknown. The aim of the present study is to describe in detail the leaf architecture of the *Rhus* from the Oligocene Ebro Basin in order to compare it with that of *R. pyrrhae* and selected extant species. Furthermore, the palaeoecology and palaeoclimatic conclusions concerning the *Rhus* specimens from Cervera are inferred on the basis of their adaptive leaf characters.

2. Material and methods

The studied collection of the Cervera paleobotanical site (also known as the Sant Pere dels Arquells site) contains dozens of specimens corresponding to *Rhus* and was gathered from five plant-bearing beds reported and analysed taphonomically by Tosal and Martín-Closas (2016). The present study focuses exclusively on the material collected by those authors from plant-bearing bed no. 2, which provided the richest assemblage of *Rhus*. This is intended to ensure that all the remains studied are coeval and grew under similar conditions. In total fifty-five isolated leaflets, all of them preserved as adpressions with poorly-preserved cuticular details, are studied and then housed in the Barcelona Natural History Museum under catalogue numbers MGB 84946 — MGB 85001.

The specimens were photographed using a Nikon 5300 camera with a 105 mm Macro lens. Up to 50 pictures were taken of each specimen and later compiled using the Helicon Focus 5.3 software (www.heliconsoft.com). The processed photographs were used to characterize the leaf morphology and venation pattern, using drawing software. Leaf morphology description followed the Manual of Leaf Architecture by Ellis et al. (2009) while the leaf measurements were taken using the free software "ImageJ" (https://imagej.net/Welcome).

The *Rhus* specimens studied were compared with the *Rhus* type material including *R. pyrrhae* from the Unger collection kept in the Johanneum Landesmuseum at Graz (Austria) and the Cenozoic flora collections stored in the Muséum National d'Histoire Naturelle de Paris (France). Finally, the fossil specimens from Cervera were also compared with the leaves of living *Rhus* from the Bonaparte Collection, stored in the herbarium LY–CERESE, of the University Claude Bernard Lyon 1 (Lyon, France), and the herbarium MPU, of the University of Montpellier (Montpellier, France).

Institutional abbreviations: LJG, Johanneum Landesmuseum Graz; LY, Herbarium of the University Claude Bernard Lyon 1 (Lyon, France); MGB, Barcelona Natural History Museum; MNHN, Paris National Natural History Museum (Paris, France); MPU, Herbarium of the University of Montpellier 2 (Montpellier, France); UPMC, University Pierre et Marie Curie (Paris, France).

3. Geological setting

The plant locality of Cervera is located in the eastern Ebro Basin (Fig. 1A), which is the foreland basin of the Pyrenees. This basin was shaped during the Palaeogene as a result of the collision between the Iberian and the Eurasian plates (Puigdefàbregas et al., 1992), resulting not only in the uplift of the Pyrenees but also of the Catalan Coastal Chain. Palaeogene marine sedimentation dominated in the eastern Ebro Basin and continued from the Ypresian until the late Eocene, when the entire Ebro Basin quite suddenly became endorheic (Costa et al., 2010). Several lacustrine systems were formed from the Priabonian to the late Miocene, when the Ebro Basin finally drained into the Mediterranean Sea (Anadón et al., 1989). The Cervera palaeobotanical site belongs to the third lacustrine system, called the La Segarra system, which is Rupelian in age, according to charophyte biostratigraphy (Feist et al., 1994; Sanjuan et al., 2012, 2014). Magnetostratigraphic studies allowed it to be more precisely attributed to chron C12, which is 32.4 Ma in age (Barberà et al., 2001). The evolution of these lacustrine systems was driven by the climate, mainly by long-period Milankovitch oscillation cycles (Valero et al., 2014). Sedimentation during the La Segarra lacustrine interval is composed of the Montmaneu Formation.

The Montmaneu Formation was defined by Colldeforns et al. (1994) and is composed of marls, marlstones and limestones, corresponding to sedimentation in a permanent, well-developed lake. In the study area, this formation is represented by the Civit Member, which is 14 m thick and consists of intercalations of pale grey and dark grey marlstones. The pale grey marlstones with plane-parallel lamination are rich in plant remains. They were formed by sedimentation in the distal part of a well-developed lake under poorly oxygenated lake bottom conditions (Tosal and Martín-Closas, 2016). In contrast, the dark grey marlstones with ripple lamination hardly contain plant remains or they are poorly preserved. This indicates an environment with relatively higher energy that would correspond to lake shore facies with occasionally oxygenate lake bottom conditions (Tosal and Martín-Closas, 2016).

4. Results

4.1. Systematic palaeobotany

Family Anacardiaceae Lindley, 1831

Genus *Rhus* Linnaeus, 1753

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Plates I, II, III and Fig. 2

4.1.1. Material

One complete leaf (UPMC nº5737a) from the Boureau collection of the University Pierre et Marie Curie (Paris) and fifty-five leaflets housed in the Natural History Museum of Barcelona (MGB 85946 — 85995). The later were collected in plant-bearing bed no. 2 of the Carulla quarry section near Cervera (Tosal and Martín-Closas, 2016).

Holotype. Specimen UPMC nº 5737a originally collected by Mr. Martí Madern in the Oligocene of Cervera (Fig. 2)

Paratypes. Specimens MGB 84946— 84948 housed in the Barcelona Natural History Museum corresponding to apical leaflets (Plate I, 1−3) and specimens from MGB 84964 to MGB 84967 corresponding to lateral leaflets (Plate II, 1−4).

Derivation of name: The epithet refers the characteristic asymmetric lateral leaflets.

4.1.2. Diagnosis

Trifoliate leaves. Apical leaflet symmetric and elliptic in shape with a serrate margin, largely decurrent base, no petiolule and an acute apex. Primary venation of the apical leaflet pinnate. Secondary vein framework craspedodromous, without branching. Major secondary vein attachment to the midvein decurrent. Intercostal tertiary vein fabric irregular reticulate. Exterior tertiary course and marginal ultimate venation looped.

Lateral leaflets basal asymmetric and ovate in shape, with an unequally serrate margin, rounded base in the distal part and concave or straight base proximally, no petiolule and an acute apex. Primary vein framework of the lateral leaflet pinnate with only one basal vein. Secondary venation pattern craspedodromous. One of the first secondary vein pairs basal. Attachment of secondary veins to the midvein decurrent. Intercostal tertiary vein fabric irregular reticulate. Exterior tertiary course and marginal ultimate venation looped.

4.1.3. Description

Leaf formed of three leaflets. Based on the anatomically connected UPMC 5737a from the Boureau collection, this leaf is 1. 8 cm long and 2.5 cm wide (Fig. 2). Petiole unknown.

Apical leaflets. These are symmetric, elliptic and measure 17.0–79.0 mm long and 12.5–41.0 mm wide. The apex is straight with an acute angle and the base is largely decurrent without a petiolule. The total number of teeth ranges from 5 to 10 (mean 7) with the same number on both sides of the lamina. Tooth spacing is irregular. In general only one order of teeth occurs. However, rarely, the first pair of teeth bears a second order of teeth. The tooth shape varies greatly with distal–proximal flanks being respectively convex–convex (76% of teeth, Plate I, 4), straight–straight (12%), straight–convex (9%), convex–straight (3%) and rarely retuse–convex (Plate I, 5); while the sinus is angular. The secondary venation is composed of 2−3 craspedodromous vein pairs distributed sub-opposite (Plate I, 6). They rise from the primary vein with variable acute angles, ranging 52.5° to 58.4° (mean 56.4°) and end at the tooth apex, of which they are the main vein. The major secondary attachment to the midvein is decurrent. In some specimens the junction between the midvein and the first pair of secondary veins might display trichomes which would correspond to the leaf hairiness (Plate III, 1). The presence of hairiness in *Rhus* from Cervera was already reported by Broutin (1970) in specimen 6439a of the Boureau collection. This author observed small rounded cells (13-14 μm across) in the leaf epidermis that he interpreted as the insertion point of hairs (lam. I.4, 8; lam II.5 and lam. III. 6 from Broutin, 1970). Two different types of tertiary veins are distinguished: (1) A tertiary venation connecting the primary vein to the secondary framework, or joining the secondary veins to each other, is irregular reticulate with approximately straight angles (82°−120°) between veins (Plate III, 2); (2) Exterior tertiary course is looped (Plate III, 3). The first pair of tertiary loops rises from the primary vein, approximately 34 mm below the first pair of secondary veins, at angles of 66° to the midvein (Plate III, 4).

Lateral leaflets. These measure 3.0–13.0 mm long and 7.6–15.5 mm wide and are devoid of petiolules. The blades are asymmetric, ovate in shape with serrate margin. The apex is acute. The base is regular asymmetric. It changes on the two sides of the lamina forming angles of about 8−45º with the midvein. The distal side of the laminadisplays a rounded base, while the proximal part of the lamina may be rounded (Plate II, 5), but is general straight (Plate II, 6) or concave (Plate II, 7). The teeth are rounded and distributed unequally on both sides of the lamina. In the proximal part, only one tooth occurs and it rises from the middle or the upper third of the lamina; while the distal part contains two teeth rising from the first third. The tooth shape is also variable and ranges from convex–convex (78% of the teeth) to straight–convex (15%); straight–straight (5%) and convex–straight (2%). Sometimes the tooth apex bears a gland (Plate III, 5) unlike the apical leaflet, which is devoid of glands. The sinus is angular. The primary venation of the lateral leaflets is pinnate. The secondary venation framework is mostly composed of 2−3 vein pairs rising from the midvein and always running towards the tooth apex, of which they form the main vein and where they reach the margin. A basal secondary vein emerges from the rounded, distal part of the lamina base, forming an acute angle (60°) with the midvein and ending at the apex of the first tooth. Attachment of secondary veins to the midvein is decurrent forming angles of approximately 50°. Two different types of tertiary veins are distinguished: (1) Tertiary veins connecting the primary vein to secondary veins, and the secondary veins to each other, which are irregular reticulate (Plate III, 6). They rise with acute angles (70°); (2) Looped exterior tertiary course raises at a mean 73° angle to the secondary veins (Plate III, 7).

4.1.4. Remarks

In the past, insufficient knowledge of the foliar architecture of *R. asymmetrica* sp. nov. along with the high polymorphism of their leaflets led Fernández-Marrón (1971) and Sanz de Siria (1992) to include within this species a number of leaves that probably belong to other taxa. A complete taxonomic revision of these leaves is beyond the scope of this study, but a brief description is provided below in an attempt to avoidfurther confusion. These leaves are segregated here in two sets, based on the shape of the base and the presence of a petiolule.

Group 1. This group is formed of leaves with a well-developed petiolule or petiole, and pinnate primary venation. Many of them are medially symmetric (Plate IV, 1−2), while others are slightly asymmetric (Plate IV, 3). The base is rounded, straight or rarely slightly concave. The apex is acute and the margin serrate. The primary venation is pinnate. The secondary venation is craspedodromous and the angle of the secondary venation to the midvein increases proximally. Some specimens display a gland at the tip of the teeth (Plate IV, 4).

Depape and Brice (1965) were the first to propose that the apical leaflets of *R.* aff. *aromatica* from Cervera*,* now *R. asymmetrica* sp. nov.*,* displayed a petiolule, and some of the specimens illustrated (Depape and Brice, 1965, pl. 9, Fig. 2) show this character. However, the complete *Rhus* leaf (Boureau collection UPMC nº5737a) does not display such a feature. Later, a specimen from Cervera that was assigned to an apical leaflet of *Rhus pyrrhae* by Fernández-Marrón (1971) also showed a petiolule (pl. 8, Fig. 3). Also, Sanz de Siria (1992) attributed some specimens with a petiolule to *R. pyrrhae* (specimens MGB 32772, MGB 32882 and MGB 33090 housed at the Barcelona Natural History Museum). However, Young (1979) and Cronquist (1981) based on the foliar architecture of living *Rhus,* concluded that species with a foliar architecture similar to this genus but bearing a petiolule should be reassigned to the genus *Toxicondendron.* This is the case of *Toxicodendron radicans* (Linnaeus) Kuntze, which was formerly called *Rhus radicans*, and *Toxicodendron pubescens* (Linnaeus) Miller, formerly *Rhus toxicodendron*. In consequence, this first group of leaves is considered to show an affinity to *Toxicodendron.*

Group 2. This group is characterized by symmetric, palmately lobed leaves. Their base is cordate and occasionally shows a short petiole (Plate V, 1). The apex is acute. The primary venation pattern is actinodromous, composed of three or five basal veins that represent the main vein of the lobes (Plate V, 2−3 respectively). The secondary venation framework is craspedodromous without branching. Major secondary attachment to the midvein is decurrent. The tertiary venation fabric is sinuous opposite percurrent (Plate V, 4). The exterior tertiary course is looped but occasionally ends at the apex of second order teeth (Plate V, 5). Rarely, trichomes are observed between the basal primary veins and also at junctions between primary and secondary veins (Plate V, 6). The leaf margin is serrate and shows two orders of teeth. Glands occur at the tips of the teeth.

Fernández-Marrón (1971) reported that the lateral leaflets of *Rhus* specimens from Cervera are basally cordate. However, the foliar features, especially the venation pattern, clearly differ from this genus. The symmetric blade suggests that they belong to a simple leaf. The general leaf morphology and the venation pattern show affinity to the genus *Acer*, although, the extant representatives of this genus always have petiolate leaves without glands.

4.2. Comparison of Rhus asymmetrica sp. nov. with other Cenozoic Rhus from Europe

The taxonomy of the *Rhus* specimens from Cervera has been debated for decades. Depape and Brice (1965) compared the *Rhus* population from Cervera with other Cenozoic species. The European taxa *R. pyrrhae*, "*R." herthae* Unger, *R. rhomboïdalis* Saporta, *R. paucidentata* Laurent, "*R." quercifolia* Goeppert and *R. pluriloba* Boulay share with the specimens from Cervera a serrate margin with rounded teeth. However, "*R. herthae", "R. quercifolia", R. pluriloba* and *R. paucidentata* are petiolate while the new species shows sessile leaflets. Other differences with *R. asymmetrica* are summarized in Table 1.

The two species showing most affinity to *R. asymmetrica* sp. nov. are *R. rhomboïdalis* and *R. pyrrhae*, with apical leaflets that are devoid of a petiolule and have a symmetric elliptic blade, serrate margin and decurrent base. However, their detailed foliar features, especially the secondary venation pattern, indicate that they also differ from the new species. The secondary veins of *R. rhomboïdalis* branch near the margin into a net of tertiary veins. One of them ends at the apex of the teeth as is their main vein (Fig. 3A). Special attention should be given to *R. pyrrhae*, to which the Cervera

Rhus specimens were assigned until now (Fernández-Marrón, 1971; Sanz de Siria, 1992). Detailed study of the type material reveals that the secondary veins of *R. pyrrhae* are brochidodromous unlike the craspedodromous secondary venation pattern of *R. asymmetrica* sp. nov. (Figs. 3B−C respectively). In what follows, an emendation of the diagnosis of *R. pyrrhae,* based on the study of its holotype is provided to clarify its differences with *R. asymmetrica* sp. nov.

Rhus pyrrhae Unger, 1847 emend. Tosal, Sanjuan et Martín-Closas

Fig. 4

1847 *Rhus pyrrhae* Unger, 84; lam. 22, fig. 1

1855 *Rhus pyrrhae* Unger, Heer, 84; lam. 76, figs. 22, 23, 24, 26, 27 (non figs. 20, 21, 25, 28)

1874 *Rhus pyrrhae* Unger, Schimper, 273

non 1886 *Rhus pyrrhae* Unger, Engelhardt, 364-368; lam. 23, figs. 25, 27; lam. 24, figs. 18, 19

non 1914 *Rhus pyrrhae* Unger, Engelhardt, 309; lam. 5, fig. 5 non 1926 *Rhus pyrrhae* Unger, Principi, 68; lam.6−8, figs. 23,19 non 1934 *Rhus pyrrhae* Unger, Weyland, 92; Lam. 16, figs. 4−5

?1940 *Rhus pyrrhae* Unger, Piton, 102; lam 6, fig. 5

1965 *Rhus* aff. *aromatica* Aiton, Depape and Brice, 118; lam. 9, figs. 1,1' and 3

non 1971 *Rhus pyrrhae* Unger, Fernández-Marrón, 93−95; lam. 7, figs. 1−3

non 1992 *Rhus pyrrhae* Unger, Sanz de Siria, 334; lam. 6, fig. 14

4.2.1. Material

One specimen from the Miocene deposits of Radoboj (Croatia) housed in the Johanneum Landesmuseum, Graz (Austria) with catalogue number 76698 and corresponding to the holotype (Fig. 4).

4.2.2. Original diagnosis (Unger, 1847)

Foliolis trifoliatis sessilibus, foliolo terminali obovato-rhombeo utrinque truncatim attenuato inaequaliter inciso-dentato.

(Trifoliate sessile leaves, the apical leaflet ovate-rhomboid in shape, in both extremes [base and apex respectively] truncate and attenuated, unequally incised-toothed).

4.2.3. Emended diagnosis

Apical leaflet symmetric, sessile, elliptic in shape, with a serrate margin, a decurrent base and an acute apex. Primary venation pinnate and secondary framework brochidodromous. The major secondary attachment to the midvein decurrent. Intercostal tertiary vein fabric irregularly reticulate. A tertiary vein is the main teeth vein. Exterior tertiary course and marginal ultimate venation looped.

4.2.4. Description of the holotype

The leaflet is symmetric and elliptic in shape, with a length of 3.5−4.2 cm and a width of 2.2−2.4 cm. The apex is straight, the base decurrent and devoid of petiolule. The margin is serrate with eight or nine teeth unequally distributed and ranked in two orders. Teeth occur from the middle part of the lamina to the apex. One side of the lamina is composed of 1–2 teeth while the other displays 4–5 teeth. The tooth shape varies. In general the distal flank is straight, rarely convex, while the proximal flank may be concave, convex, flexuous or straight. The sinus between the teeth is angular. The primary vein is pinnate. The secondary venation is composed of six brochidodromous pairs of veins rising from the midvein at angles of 50º. The junction of the secondary veins with the primary vein is decurrent. The tertiary vein fabric is irregular reticulate. At the maximum curvature of the secondary vein, which occurs near the margin, a tertiary vein proceeds straight to the tooth apex, of which it is the main vein. The exterior tertiary course is looped.

4.2.5. Remarks

Rhus pyrrhae leaflets were reported from a number of southern European localities in Spain, France, Italy, Germany and Croatia. However, aside from the type material, only one specimen from Oeningen (Germany) stored in the MNHN in Paris (catalogue number MNHN.F.5706) is confirmed here to correspond clearly to *R. pyrrhae*. Other specimens might also correspond to *R. pyrrhae*, but the available information is insufficient to confirm this. This is the case of the illustrations provided by Heer (1855, lam. 76, Figs. 22, 23, 24, 26, 27), where the secondary venation pattern is not drawn with precision and might be either craspedodromous or brochidodromous. Another such dubious case was reported and figured by Piton (1940), from the Palaeocene of Menat (France). That specimen, which lacks the apical part, is elliptic in shape and displays a serrate margin, a pinnate primary vein and brochidodromous secondary veins. A tertiary vein rises from the secondary veins and ends at the tooth tip. These features match with the holotype characters well. In contrast, other characters do not coincide: (1) the base is asymmetric, showing a distal rounded part and a convex proximal part; (2) a secondary vein rises directly from the leaflet base. Basal asymmetry of the leaflets has been observed in the lateral leaflets of *R. asymmetrica* sp. nov., suggesting that the specimen from Menat might correspond to a lateral leaflet of *R. pyrrhae*.

Unger (1847) remarked that *R. pyrrhae* would display high polymorphism, as happens in living *Rhus*. Based on this premise and the imprecise diagnosis of the species, some authors included within *R. pyrrhae* a number of specimens with different foliar features, which certainly correspond to other taxa. Thus, specimens with serrate margin, rounded teeth and a petiolule were considered to belong to *R. pyrrhae* by Heer (1855, lam. 76, figs. 20, 25, 28); Weyland (1934) and Fernández-Marrón (1971), however, the holotype is sessile.

4.3. Comparison of R. asymmetrica sp. nov. with living Rhus species

The genus *Rhus* s.s. and other genera showing a high affinity to it, forming the so-called *Rhus* complex, comprise about 250 species that are found all around the world except in Australia, the Pacific Islands and Antarctica (Yi et al., 2004). This wide geographic and ecological distribution has resulted in a wide range of leaf features. Unfortunately, studies of the foliar architecture of living species from the *Rhus* complex are scarce (Andrés-Hernández and Terrazas, 2009; Martínez-Millán and Cevallos-Ferriz, 2005; Hickey and Wolfe, 1975). In order to compare the fossil leaves of *R. asymmetrica* sp. nov. with living species we studied up to 51 taxa of the *Rhus* complex that are hosted in herbaria. Twelve species of the *Rhus* complex with trifoliate leaves showing serrate margins were selected for comparison (Table 2). Five leaf features were analysed (1) leaf shape; (2) apex shape; (3) lateral leaflet base; (4) secondary venation fabric; and (5) tertiary venation framework. The presence/absence of a petiolule and the primary vein pattern were excluded since they are homogeneous in the whole *Rhus* complex.

Rhus trilobata Nuttall (Plate VI, 1) and *Rhus dioica* Brousseau ex Willdenow (Plate VI, 2) share some characters with *R. asymmetrica* sp. nov., such as an apical leaflet with decurrent base, craspedodromous secondary venation and a straight apex. The lateral leaflets show a rounded base but in some occasions the base of *R. trilobata* is asymmetric. While the proximal side is straight, the distal part remains rounded. The trilobed apical leaflet of *R. trilobata* contrasts with the elliptic, non-lobed apical leaflet of *R. asymmetrica* sp. nov. Another difference is found in the tertiary framework, which is freely ramified in *R. trilobata*, while *R. asymmetrica* sp. nov. has an irregular reticulate pattern. In *R. dioica*, the margin shows occasionally two to three smooth teeth, contrasting with the serrate margin of *R. asymmetrica* sp. nov. Other living *Rhus* species, such as *R. dentata* Thunberg (Plate VI, 3) and *R. incisa* Linnaeus (Plate VI, 4), are characterized by a straight apex and basally asymmetric lateral leaflets. These foliar features are also observed in *R. asymmetrica* sp. nov. Nevertheless, *R. dentata* differs from *R. asymmetrica* sp. nov. in the teeth shape, which is acute (with straight distal and proximal flanks) and because it lacks the characteristic first pair of tertiary loops that occur in the apical leaflet of *R. asymmetrica* sp. nov. Meanwhile, the secondary veins of *R. incisa* reach both the teeth tips and the teeth sinuses, while in *R. asymmetrica* sp. nov these veins end exclusively at the teeth tip. In addition, the base of the lateral leaflets of *R. incisa* is decurrent in the proximal part and straight in the distal part, while in *R. asymmetrica* sp. nov. it is straight and rounded respectively.

Two more species that in former days were included in *Rhus* but were later transferred to the genus *Toxicodendron*, i.e "*R.*" *diversiloba* and "*R.*" *toxicodendron*, resemble *R. asymmetrica* sp. nov. However, the leaflets of the two living species bear a petiolule (Plate VI, 5) and their craspedodromous secondary veins branch at the margin unlike *R. asymmetrica* sp. nov.

The extant species showing most similarity with *R. asymmetrica* sp. nov. is *R. aromatica* (Plate VI, 6–7). Its leaflets display craspedodromous secondary, non-branched venation. Also, like *R. asymmetrica* sp. nov., the tertiary vein framework is irregular reticulate and the exterior tertiary course, including the marginal ultimate venation, is looped (Plate VI, 8–9 respectively). The first pair of tertiary loops of the apical leaflet rises from the primary vein below the first pair of secondary veins with acute angles to the midvein. Hence, extant *R. aromatica* leaves share most of the characters considered here to be diagnostic of *R. asymmetrica* sp. nov., supporting the view of Depape and Brice (1965) and of Fernández-Marrón (1971) that *R. aromatica* is the nearest living relative of the *Rhus* specimens from Cervera.

Despite this similitude, the species differ in significant characters: (1) The base of the lateral leaflets of *R. aromatica* is symmetric with a rounded, occasionally straight, shape, while the base of *R. asymmetrica* sp. nov. is clearly asymmetric, distally rounded and straight or convex in the proximal part; (2) In *R. aromatica* the angle between thelateral leaflets and the apical leaflet varies from 70–90º, while in *R. asymmetrica* sp. nov. it is much more acute (ca. 60º), as observed in the exceptional articulated specimen of the Boureau collection (UPMC nº5737a); (3) In *R. aromatica* the first pair of secondary veins of the lateral leaflets is opposite and rises 1-2 mm from the base (Plate VI, 10), while in *R. asymmetrica* sp. nov. these veins are alternate, with the distal vein arising from the very base; (4) *R. asymmetrica* sp. nov. apical leaflets display 5–7 teeth and the lateral leaflets 5 teeth, while the apical leaflet of *R. aromatica* contains 9–13 teeth and the lateral leaflet 5–9 teeth; (5) The leaf of *R. aromatica* is devoid of glands (Plate VI, 11) while in *R. asymmetrica* sp. nov. the lateral leaflets usually bear well- developed glands.

5. Discussion

A leaf bed from the lower Oligocene of Cervera in the eastern Ebro Basin (Catalonia, Spain) provided a large number of complete leaflets of *Rhus asymmetrica* sp. nov. allowing us to perform a detailed reconstruction of the leaf (Fig. 5). The number of leaflets of *R. asymmetrica* sp. nov. is known from one articulated specimens figured by Depape and Brice (1965, lam. 9 fig.1-1') and stored in the Boureau collection (UPMC nº 5737a). This exceptionally well-preserved fossil demonstrates that the leaf was trifoliate. Comparison with living *Rhus* from herbaria suggests that *R. aromatica* shows the closest leaf architecture to that of *R. asymmetrica* sp. nov. However, some differences between them are observed that supply palaeoecological information. *R. asymmetrica* sp. nov. is characterized by glands at the apex of the teeth of the lateral leaflet and additionally it may bear trichomes, as suggested by Broutin (1970). These features are absent in *R. aromatica*. The function of a gland is to secrete substances e.g. wax, water or salt (Quer, 2009). Some living *Rhus* species which grow in open woodlands have glands which secrete wax i.e. *R. glabra* Linnaeus*, R. michauxii* Sargent and *R. typhina* Linnaeus (Miller et al., 2001). Wax is a hydrophobic compound which acts as a barrier against water loss and could reflect excessive light (Holmes and Keiller, 2002). According to Percy et al. (1994) and Barnes et al. (1996) the development of epicuticular wax together with the trichomes provides the best external defense against adverse environmental conditions in terms of evapotranspiration. The presence of these features in *R. asymmetrica* sp. nov. would indicate that their leaves were adapted to minimize water loss by evapotranspiration. Another significant difference between the two species analysed can be found in the symmetry of the base of the lateral leaflets, which. could be a phenotypic response to environmental stress or a phylogenetically determined character. This alternative has been analysed by comparison with two living species, i.e. its nearest living relative, *R. aromatica* and the sister species of the latter, which is *R. trilobata* according to Miller et al. (2001) and Yi et al. (2004). Nowadays, the distribution of *R. aromatica* matches well with the Köppen Cfa climate (temperate with dry and hot summer) which is not considered a stressful environment for plants (https://www.gbif.org). In contrast, *R. trilobata* grows under seasonal steppe and Mediterranean climates (https://www.gbif.org) perceived as a stressful. If the two species would bear the same type of basal symmetry despite its contrasting environment, this character could be considered as potentially determined by the phylogeny. However, the base of *R. aromatica* is regularly symmetric while the base of *R. trilobata* is occasionally asymmetric, suggesting that this character is more controlled by the climate than by the phylogeny. In sum, all foliar evidences appear to indicate that *R. asymmetrica* sp. nov. was a water-stressed plant.

Finally, *R. asymmetrica* sp. nov. differs from *R. aromatica* is in the number of teeth and the size and shape of their surfaces. Based on the experiments by Royer et al.

(2009) these features would be related to the mean annual temperature. Those authors studied the leaf blade plasticity of *Acer rubrum* under different climate conditions in North America, from Ontario to California. They observed that leaves from northern latitudes display more teeth, with a sharper tooth apex and smaller area. Similar adaptive responses may have occurred in *R. asymmetrica* sp. nov., which displays fewer teeth (4-9) with a more rounded shape and with a larger tooth area (5% of the total leaflet area) than *R. aromatica* (5−12 teeth occupying 3% from the whole leaflet area). These differences suggest that *R. asymmetrica* sp. nov. grew under warmer climate conditions than *R. aromatica,* which tends to occur at high latitudes of North America with temperatures below zero several months each year (Barkley 1937).

Comparison of *R. asymmetrica* sp. nov. with other Cenozoic *Rhus* species from Europe suggests that the new species was restricted to the Ebro Basin. It would show particular adaptations to drought, such as glands and trichomes, which are absent in other European *Rhus* species. In the same palaeogeographic area and time a number of endemisms have been reported such as *Ailanthus cerverensis* (Bataller and Depape 1950; Broutin, 1970) , the micromammals *Theridomys calafensis* and *T. major* (Arbiol et al., 1996) and the charophytes *Nodosochara jorbae* Choi*, Sphaerochara labellata* Grambast and *Lychnothamnus longus* Choi (Sanjuan and Martín-Closas, 2014). High endemism in charophytes was interpreted as consequence of the palaeogeographic isolation of the endorrheic Ebro Basin from the upper Eocene until the upper Miocene. Furthermore, charophyte species that occurred both in the Ebro Basin and in other parts of Europe (e.g. Hampshire Basin and Paris Basin) showed smaller gyrogonites in the Ebro Basin, which has been attributed to harsh palaeoclimatic conditions, including seasonal desiccation of charophyte ponds during long drought seasons. The results obtained here based on *Rhus* are consistent with these conclusions.

In the past, *Rhus* specimens from Cervera, now *R. asymmetrica* sp. nov. were considered to belong to *R. pyrrhae,* but the secondary venation allowed us to distinguish the two species. According to Roth-Nebelsick et al. (2001) the venation pattern is genetically fixed and, consequently, it is a reliable character when it comes to distinguishing between species. In spite of the new data supplied here concerning the holotype of *R. pyrrhae*, details of its lateral leaflets remain unknown. A specimen from Menat (France) described by Piton (1940) may represent this part of the leaf since it fits in well with the holotype (apical leaflet) venation pattern and with some characters of the leaf blade morphology, while it differs in its unequally serrate margin and asymmetric base that are typical characters of the lateral leaflets. However, a larger population is needed to ensure this attribution.

A number of taxa from the Oligocene of Cervera with foliar features similar to those of the genus *Rhus* but possibly belonging to *Acer* and *Toxicodendron* were erroneously considered by former authors to be polymorphs of *R. asymmetrica* sp. nov. but have now been differentiated herein. Similar confusion was reported in other Cenozoic *Rhus* species from Europe. For instance, *Rhus quercifolia* described by Kornilova (1956) from the Eocene of western Kazakhstan, was later re-assigned to *Acer aegopodifolium* Goeppert by Ilyinskaya (1968). Another example can be in the Miocene floras from Central Europe (Austria and Czech Republic) where Kvaček and Walther (1998, 2004) concluded that *Rhus herthae* is to be newly combined with *Toxicodendron herthae*.

6. Conclusions

The trifoliate leaf of *Rhus asymmetrica* sp. nov. has been characterized on the basis of a specimen with anatomically connected leaflets and numerous isolated leaflets from the lower Oligocene of Cervera in the Ebro Basin (Catalonia, Spain). The apical leaflet has a symmetric blade with a decurrent base, serrate margin, pinnate primary venation, craspedodromous secondary venation, irregular reticulate tertiary venation pattern and looped exterior tertiary course. The lateral leaflets mainly differ from the apical leaflet in blade shape. They display a very asymmetric base, with a rounded distal part of the lamina while the proximal part is straight to concave. A gland may occur at the teeth tip.

The new species is similar to *R. pyrrhae* Unger 1847 which led Fernández-Marrón (1971) and Sanz de Siria (1992) to include the *Rhus* specimens from Cervera within this species. However, detailed study of the foliar architecture of the holotype of *R. pyrrhae* enabled an easy distinction between the species based on the secondary venation pattern that is craspedodromous in *R. asymmetrica* sp. nov. and brochidodromous in *R. pyrrhae.* The diagnosis of *R. pyrrhae* has therefore been emended in order to characterize this species better according to present-day standards.

The lateral leaflets of *R. pyrrhae* still need to be described. The two localities in Germany and Croatia, from which only the apical leaflet of *Rhus pyrrhae* has been recognized, may also contain the corresponding lateral leaflets, but to date they have either not been found and recorded, or have not been recognized as belonging to this species. The lateral leaflet is absent from the Unger collection in the Johanneum Landesmuseum at Graz, where the holotype of *R. pyrrhae* is stored, but new finds by Krklec (2010) suggest that the lateral leaflet may be recorded in the type locality. The opposite situation appears to occur in the leaf collection studied by Piton (1940) from the Palaeocene of Menat (France), which appears to contain the lateral leaflet of this species but not the apical leaflet. More material should be recollected in these localities so as to be able to describe the *R. pyrrhae* lateral leaflets. Comparison of *Rhus asymmetrica* sp. nov. with living *Rhus* species indicates that *R. aromatica* is the most similar. However, the two differ in a few characters with significant palaeoecological and palaeoclimatic implications. For instance, the glands at the tip of teeth in the lateral leaflets of *R. asymmetrica* sp. nov. would represent adaptations to cope with high evapotranspiration rates. The remarkable asymmetry of the lateral leaflets of *R. asymmetrica* sp. nov. in comparison with its living relative suggests a more stressful environment for *R. asymmetrica* sp. nov., which is congruent with an arid climate. Finally, *R. asymmetrica* sp. nov. shows fewer teeth but with a larger area interpreted as responding to a climate with low seasonal temperature contrast. These results fit well with the palaeoecological interpretation proposed by Tosal and Martín-Closas (2016) based on a taphonomic study of the Oligocene flora from Cervera, concluding that *Rhus* would grow in a savannah-like woodland in the context of subtropical palaeoclimatic conditions.

In comprehensive views of the European Cenozoic flora, Mai (1989) and Kvaček (2010), noted that plant distributions within the continent followed a latitudinal pattern including a Mediterranean Tethys bioprovince. The flora from Cervera would belong to the Célas Unit of this bioprovince as indicated by the occurrence of a characteristic assemblage with *Comptonia* and *Ailanthus*. However, within this bioprovince the plant distribution was heterogeneous as a response to local palaeoecological and palaeoclimatic conditions (Mai, 1989; Kvaček, 2010). This certainly appears to be the case with the lower Oligocene flora of the Ebro Basin which contains a number of endemic species including the new species introduced herein. The results provided here strengthen the potential of the Iberian Peninsula, and especially of the Ebro Basin, as a spot of high plant species endemism across the Eocene-Oligocene boundary. This opens up new lines of research into the evolution of European plants in a period of palaeoclimatic change.

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Figure captions

Fig. 1: Geological setting of the area studied. A: Geological sketch of the Ebro Basin with the location of the study area, modified from Vergés et al. (1998). B: Stratigraphic column of the Carulla quarry (Montmaneu Formation) with the plant-bearing bed studied arrowed. Modified from Tosal and Martín-Closas (2016).

Fig. 2: Holotype of *Rhus asymmetrica* with anatomically connected leaflets from Cervera (specimen UPMC 5737a stored in the Boureau collection, Paris, France.

Fig. 3: Line drawing of apical leaflets of three Oligocene *Rhus* species showing a high degree of affinity. A: Holotype of *R. rhomboïdalis* from Aix-en-Provence (France) with secondary veins branching into a net of tertiary veins, specimen MNHN.F. 14158. B: Holotype of *R. pyrrhae* from Radoboj (Croatia) with brochidodromous secondary veins, specimen LJG 76698. C: Paratype of *R. asymmetrica* sp. nov. from Cervera (Catalonia, Spain) with craspedodromous secondary veins, MGB 84990. Scale bar 1 cm.

Fig. 4: *Rhus pyrrhae* holotype corresponding to the apical leaflet, specimen LJG 76698 of the Johanneum Landesmuseum, Graz (Austria).

Fig. 5: Reconstruction of the complete leaf of *Rhus asymmetrica* sp. nov.

Plate I: Apical leaflets of *R. asymmetrica* stored in Barcelona Natural History Museum. 1: Paratype with well-preserved tertiary venation pattern MGB 84946. 2: Complete leaflet corresponding to paratype MGB 84947. 3: Paratype MGB 84948 showing the first pair of exterior tertiary veins rising below the secondary veins. 4: Convex teeth shape in distal and proximal flanks, MGB 84950. 5: Retuse tooth shape in the proximal flank (arrow), MGB 84962. 6: Leaflet with alternate secondary veins MGB 84963. Scale bar 1 cm.

Plate II: Lateral leaflets of *Rhus asymmetrica* sp. nov. housed in Barcelona Natural History Museum. 1: Paratype composed of four teeth with straight shape in both flanks, MGB 84964. 2: Paratype MGB 84967 with two teeth and apex. 3: Paratype MGB 84966 with convex teeth shape in both flanks. 4: Paratype MGB 84965 with rounded teeth shape. 5: Leaflet displaying slightly rounded base of the proximal flank, MGB 84966. 6: Specimen with straight base on the proximal side, MGB 84967. 7: Leaflet with concave base on the proximal side, MGB 84970. Scale bar 1 cm.

Plate III: Detailed foliar features of *Rhus asymmetrica* sp. nov. 1: Apical leaflet with possible trichomes near the junction between the primary and the first pair of secondary veins (arrow), MGB 84948. 2: Tertiary venation fabric of apical leaflet forming an irregular reticule, MGB 84948. 3: Apical leaflet with exterior tertiary venation pattern forming loops, MGB 84946. 4: Apical leaflet with the first pair of tertiary loops (arrow) rising below the first pair of secondary veins, MGB 84946. 5: Lateral leaflet with a gland at the tooth tip (arrow), MGB 84967. 6: Lateral leaflet with tertiary venation fabric forming an irregular reticule, MGB 84968. 7: Lateral leaflet with exterior tertiary veins forming loops (arrow), MGB 84966. Scale bar 1 cm.

Plate IV: Foliar characters of specimens with a petiole and pinnate primary vein erroneously attributed to the *Rhus* apical leaflets from Cervera and related here tentatively with the genus *Toxicodendron*. 1: Symmetric specimen with rounded base, MGB 85001. 2: Symmetric specimen with straight base, MGB 85002. 3: Asymmetric blade with one side of the lamina having a slightly concave base, while the other is rounded, MGB 85004. 4: Specimen with glands at the teeth tip, MGB 85006. Scale bars 1 cm.

Plate V: Group of specimens with cordate base and actinodromous venation pattern formerly attributed to the lateral leaflets of *Rhus* from Cervera and related here tentatively with the genus *Acer*. 1: Specimen with the petiole still attached, MGB 85007. 2: Specimen with three basal veins, MGB 85008. 3: Specimen with five basal veins, MGB 85009. 4: Detail of the tertiary venation fabric with sinuous percurrent veins, MGB 85010. 5: Exterior tertiary venation ending into second order teeth, MGB 85011. 6: Trichomes at the junctions between primary and secondary veins (arrow) and glands at teeth apex, MGB 85012. Scale bar 1 cm.

Plate VI: Foliar architecture of living *Rhus* species. 1: *R. trilobata* with the apical trilobate leaflet (LY0172412). 2: *R. dioica* with leaflets showing two or three smooth teeth (LY0172566). 3: *R. dentata* leaf showing acute teeth (LY0172563). 4: *R. incisa* leaf showing secondary venation ending either at the tooth apex or at the sinuses (MPU4991). 5: "*R. toxicodendron*" leaf with a long petiolule (LY0172547). 6: Branch of *R. aromatica* (LY0172369). 7: *R. aromatica* leaf (LY0172369). 8: Detail of apical leaflet of *R. aromatica* showing irregular reticulate tertiary venation. Specimen from Parc de la Tête d'Or (Lyon, France). 9: Preceding specimen showing looped exterior tertiary venation (arrow). 10: Symmetric base of lateral leaflets of *R. aromatica* collected at Parc de la Tête d'Or (Lyon, France). 11: Teeth devoid of glands from the previous specimen. Scale bar 1 cm.

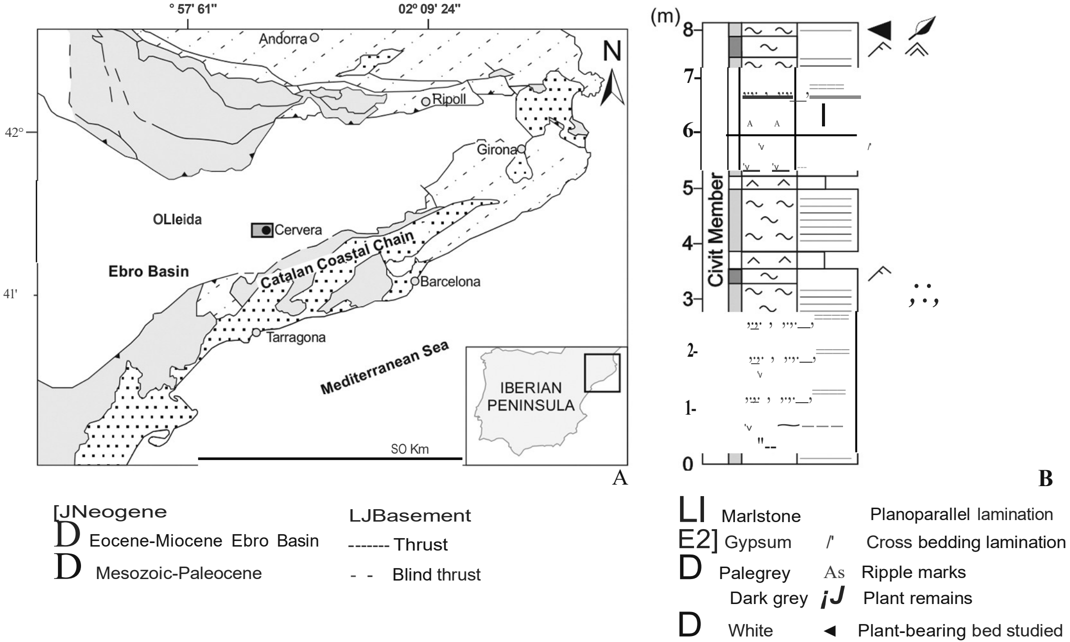
Table 1: Leaf characters of Cenozoic *Rhus* species from Europe considered affine of *R. asymmetrica* sp. nov.

Species	**Ocurrence**	**Leaflet shape**	**Petiolule**	**Base shape**	**Apex shape**	**Primary venation**	**Secondary venation**	**Tertiary venation**
R. pyrrhae	Oligocene-Miocene	elliptic	absence	decurrent	straight	pinnate	brochidodromous	not visible
"R. herthae"	Oligocene-Miocene	oblong	presence	rounded or straight	straight	pinnate	semicraspedodromous	irregular reticulate
R. rhomboïdalis	upper Oligocene	elliptic	absence	decurrent	straight	pinnate	reticulodromous	irregular reticulate
R. paucidentata	Oligocene	oblong	presence	-	straight-acuminate	pinnate	craspedodromous	not visible
"R. quercifolia"	Oligocene-Pliocene	oblong	presence	rounded	straight	actinodromous	craspedodromous	not visible
R. pluriloba	Miocene	obovate	presence	straight	rounded	pinnate	brochidodromous	not visible

Table 2: Leaf characters of living species of the *Rhus* complex with trifoliate leaves and serrate margin. Currently accepted species taxonomy obtained from the The Plant List (http://www.theplantlist.org, access date: 29/05/2018).

***Rhus* species names in the herbaria**	**Accepted names (The Plant List)**	**Habitat**	**Lateral leaflet base**	**Petiolule**	**Secondary venation pattern**	**Tertiary venation pattern**	**Apex**
R. aromatica	*R. aromatica*	Open woodlands	proximal: straight distal: straight	absent	craspedodromous	irregular reticulate	straight
R. aromatica var. *trilobata*	*R. trilobata*	Open woodlands (chaparral)	proximal: straight distal: straight	absent	craspedodromous	transversely freely ramified	straight
R. crenata	*R. crenata*	Coastal dunes	proximal: decurrent distal: straight	absent	semicraspedodromous	not visible	straight
R. dentata	*R. dentata*	Open woodlands	proximal: straight distal: rounded	absent	craspedodromous	alternate percurrent	straight
R. dioica	*R. dioica*	-	proximal: straight distal: straight	absent	craspedodromous	not visible	straight
R. dissecta	*R. dissecta*	Open woodlands	proximal: decurrent distal: decurrent	absent	craspedodromous branching at the margin	not visible	straight
R. diversiloba	*Toxicodendron diversilobum*	Woodland-chaparral	proximal: straight distal:	presence	craspedodromous branching at the margin	transversely freely ramified	straight

			straight				
R. incisa	*R. incisa*	Woodland	proximal: decurrent or concave distal: straight	absent	craspedodromous	not visible	round
R. natalensis	*Searsia natalensis*	Woodland-riparian	proximal: straight distal: straight	absent	brochidodromous	transversely freely ramified	round
R. oxyacanthoides	*R. oxyacanthoides*	Wetlands-lake shore	proximal: straight distal: decurrent	absent	craspedodromous	not visible	straight
R. toxicodendron	*Toxicodendron pubescens*	Woodland	proximal: straight distal: straight	presence	craspedodromous branching at the margin	transversely freely ramified	straight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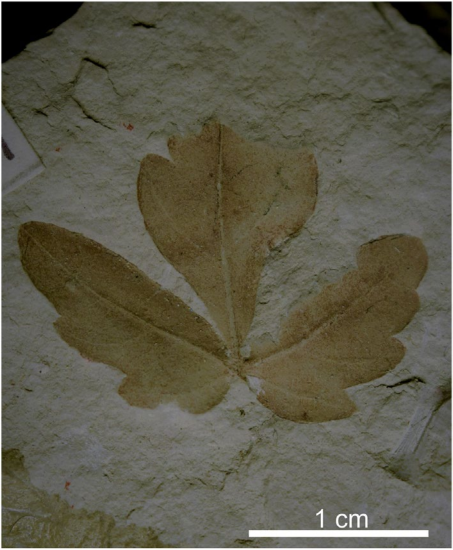
D Eocene-Miocene Ebro Basin
D Mesozoic-Paleocene
LJBasement
------- Thrust
- - Blind thrust
LI Marlstone
E2] Gypsum
D Palegrey
Dark grey
D White
Planoparallel lamination
/' Cross bedding lamination
As Ripple marks
¡J Plant remains
◄ Plant-bearing bed studied

Figure 1



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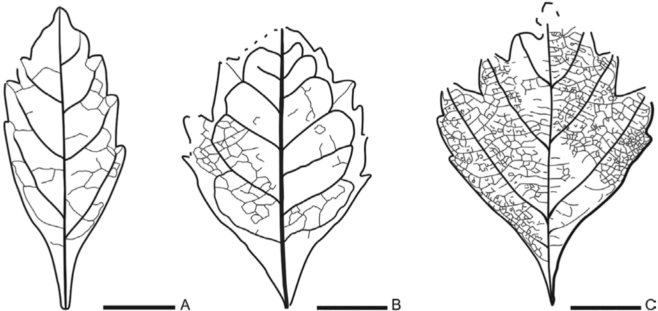


Figure 3

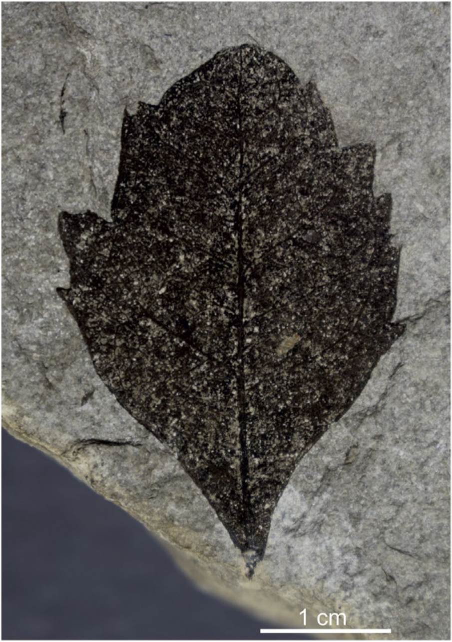
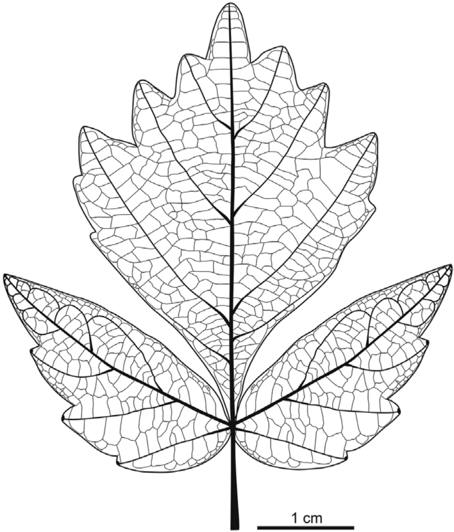


Figure 4



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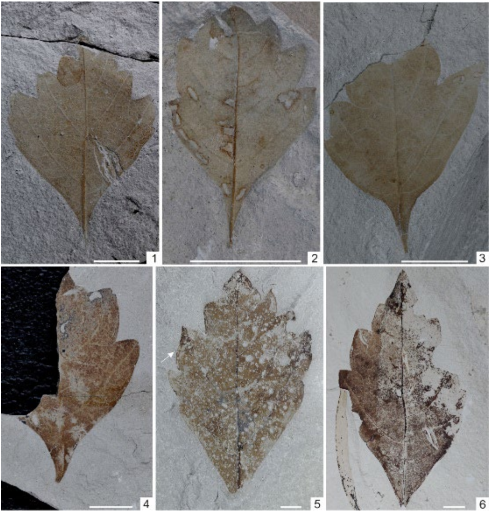
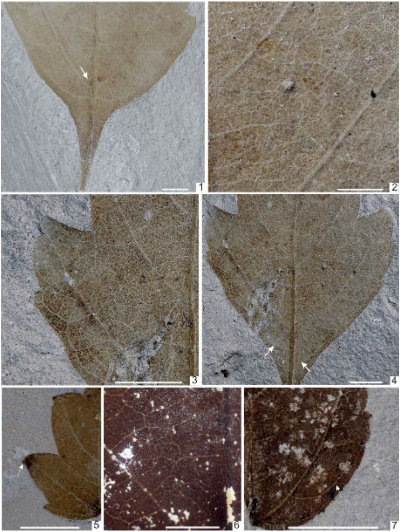


Plate I

Plate Ii



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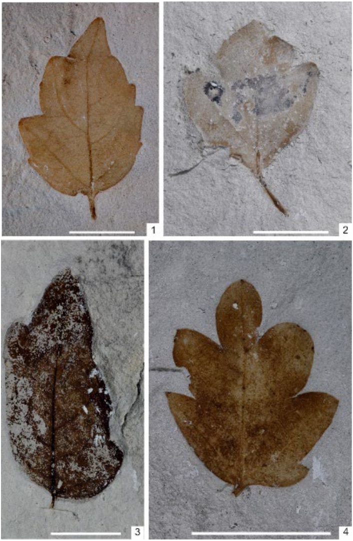

Plate IV

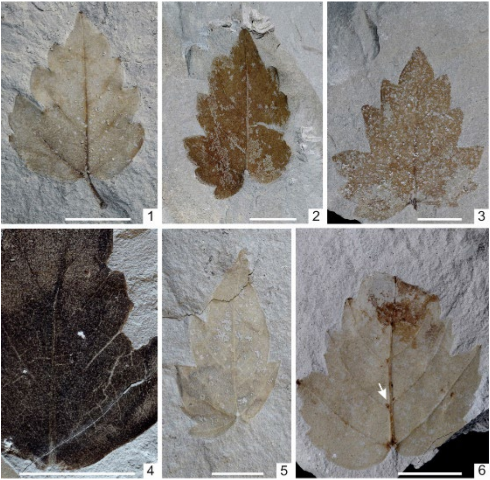

Plate V

Plate VI