



FOSSIL RECORD OF CELASTRACEAE: EVALUATION AND POTENTIAL USE IN MOLECULAR CALIBRATIONS

REGISTRO FÓSIL DE CELASTRACEAE: EVALUACIÓN Y USO POTENCIAL EN CALIBRACIONES MOLECULARES

ANA LILIA HERNÁNDEZ-DAMIÁN^{1*}, SANDRA LUZ GÓMEZ-ACEVEDO², AND SERGIO RAFAEL SILVESTRE CEVALLOS-FERRIZ³

¹ Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, CDMX, México.

² Unidad de Morfología y Función. Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, México.

³ Departamento de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, CDMX, México.

*Author for correspondence: hdez_damian@ciencias.unam.mx

Abstract

Background: Celastraceae is a morphologically heterogeneous family. For this reason, the inclusion of some taxa within this group is controversial. Recently this problem has become significant since its fossil record is recognized as an important source of information for evolutionary studies, especially those using molecular clocks which require a robust, reliable fossil record.

Questions: What are the most reliable fossil records of Celastraceae? What morphological characters are used to assign fossils in the family?

Study site and dates: Compilation of records contained in paleontological databases, and paleobotanical literature, covering publications from 1869 to 2018.

Methods: Published information on the Celastraceae fossil record was compiled and analyzed using the most recent classification system and specialized literature on the family.

Results: A total of 168 fossil records were examined, of which nine are proposed for use as molecular clock calibration points. Each specimen has a description based on a character set used for its identification, a photograph and/or illustration, their geological age is well supported, their geographic origin is known, and the specimens are in accredited home institutions with publicly accessible collections.

Conclusions: The identification and establishment of relationships between fossil and extant taxa have important limitations that depend on the critical interpretation of morphology in a phylogenetic context. Therefore, it is essential to incorporate only those morphological studies in Celastraceae that help clarify its fossil record.

Keywords: fossil plants, morphology, reliable record.

Resumen

Antecedentes: Celastraceae es una familia morfológicamente heterogénea. Por esta razón, la inclusión de algunos taxones actuales dentro de este grupo es controversial. Recientemente, este problema se ha acentuado en su registro fósil, considerado como una fuente importante de información para estudios evolutivos, como es el caso del reloj molecular, que requiere de un registro fósil confiable y robusto.

Preguntas: ¿Cuáles son los registros fósiles más confiables de Celastraceae? ¿Cuáles caracteres morfológicos son usados para asignar fósiles en la familia?

Sitio de estudio y fechas: Recopilación de registros contenidos en bases de datos paleontológicas y literatura paleobotánica, abarcando publicaciones de 1869 hasta el 2018.

Métodos: Se compiló y analizó la información publicada del registro fósil de Celastraceae usando el sistema de clasificación más reciente de la familia, así como literatura especializada del grupo.

Resultados: De un total de 168 registros fósiles examinados, sólo nueve son considerados como puntos de calibración confiables. Cada uno de los especímenes incluye una descripción del órgano de la planta a través del cual se identificó, una fotografía y/o ilustración, edad geológica y provincia geográfica, así como su acreditación en una institución de resguardo con colecciones públicas accesibles.

Conclusiones: La identificación y el establecimiento de las relaciones entre los taxones fósiles y actuales son limitantes importantes, y ambas dependen fundamentalmente de la interpretación de los caracteres morfológicos en un contexto filogenético. Por esta razón, es fundamental realizar estudios morfológicos profundos en Celastraceae, estos podrían permitir el esclarecimiento de su registro fósil.

Palabras clave: morfología, plantas fósiles, registros confiables.



Celastraceae *sensu lato* is a subcosmopolitan family composed of ca. 98 genera and 1,211 species. The most recent classification of Celastraceae proposed by [Simmons \(2004\)](#) is strongly supported by molecular data (e.g., [Simmons & Hedin 1999](#), [Simmons *et al.* 2001a, b](#), [Islam *et al.* 2006](#), [Zhang & Simmons 2006](#), [Coughenour *et al.* 2010, 2011](#)). It recognizes three monophyletic subfamilies: Hippocrateoideae, Salacioideae and Stackhousioideae, each one derived independently from Celastroideae, which is paraphyletic.

Traditionally, Celastraceae has been recognized as a morphologically variable group where the inclusion of some taxa is controversial. This problem has been particularly highlighted in its fossil record ([Estrada-Ruiz *et al.* 2012](#), [Bacon *et al.* 2016](#), [Zhu *et al.* 2020](#)). Since fossils rarely are preserved as complete plants or in organic connection their identification and classification is restricted and doubtful in comparison to extant plants ([Nixon 1996](#), [Crapet 2008](#)). Despite its inherent limitations, the fossil record has become highly relevant in supporting or refuting evolutionary scenarios including the dating of clades ([Donoghue & Benton 2007](#), [Parham *et al.* 2012](#), [Magallón *et al.* 2015](#)). Therefore, the availability of a reliable fossil record is crucial since errors in phylogenetic analyses have resulted from incorrect identifications and/or incorrect age assignments to fossil material ([Parham *et al.* 2012](#)).

According to the most recent revision of Celastraceae by [Bacon *et al.* \(2016\)](#), the family has an extensive fossil record. However, many of the fossils do not show diagnostic characters or their descriptions lack enough detail to consider them as reliable reports. Nevertheless, several newly published records are relevant for the history of the family (e.g., [Chambers & Poinar 2016](#), [Franco 2018](#)).

Therefore, our objective is to build on previous work by providing a review of the Celastraceae fossil record in order to establish reliable reports, which can potentially be used to calibrate molecular clocks.

Material and Methods

Revision of literature. We evaluated a total of 168 reports of fossils with affinity to Celastraceae or referred to the family, covering publication dates from 1869 to 2018. The reports of this revision were published in specialized literature and include the original descriptions (see [Supplementary Material](#), [Table S1](#)).

The consistency of the identification of the Celastraceae fossils was determined considering the criteria proposed by [Martínez-Millán \(2010\)](#), which are mentioned

in order of decreasing reliability: (1) inclusion of the fossil in a phylogenetic analysis, (2) discussion of key characters to place fossils in the group, (3) list of characters to include the fossil in a certain group, (4) complete description and diagnosis of the fossil, (5) photographs of the specimen, (6) drawings, diagrams and reconstructions of the fossils, (7) specimen information, home institution, collection number, and holotype designation, (8) collection information; locality, formation, and age. [Manches-ter *et al.* \(2015\)](#) indicated that the system proposed by [Martínez-Millán \(2010\)](#) is questionable since criteria (2) and (3) include similarities without indicating if they are unique and/or constitute a synapomorphy. For this reason, we included a discussion of these points. Furthermore, the selected fossils correspond to the oldest ones within the lineage ([Donoghue & Benton 2007](#), [Parham *et al.* 2012](#)), which is based on the Global Stratigraphic Chart 2020 ([Cohen *et al.* 2020](#)). Finally, the phylogenetic position of each fossil was established according to its comparison to extant taxa, recognizing that their similarity suggests a relationship between them ([Wiens 2003](#), [Sauquet *et al.* 2012](#)).

Results

A total of 168 records were found, of which 139 are vegetative, with 120 leaves and 19 woods. They have a temporal range that extends from the Cenomanian (Cretaceous) to the Pliocene (Neogene). Likewise, the record of reproductive structures that includes pollen (19), fruits and seeds (6), as well as inflorescences and flowers (4) have been recognized from the Maastrichtian (Cretaceous) to the Pliocene (Neogene) ([Figure 1A, B](#)).

In the next paragraphs, we discuss fossil taxa identified through vegetative and reproductive organs. Each one of them has a brief introduction and a discussion of the character or character set that supports their inclusion in Celastraceae. The results are summarized in [Table 1](#) with nine fossil record recognized here as reliable (see [Supplementary Material](#), [Table S2](#)). [Figure 2](#) displays the phylogenetic positions of each one based on the topology reported by [Coughenour *et al.* \(2010\)](#).

Leaves. Leaves are the most abundant fossil record of Celastraceae ([Bacon *et al.* 2016](#)). These have been related to extant members of Celastroideae ([Simmons 2004](#)) and they are widespread in strata of Cretaceous and Paleogene ([Figure 1A](#)). The fossil leaves of Celastraceae represent artificial forms because they had been described under

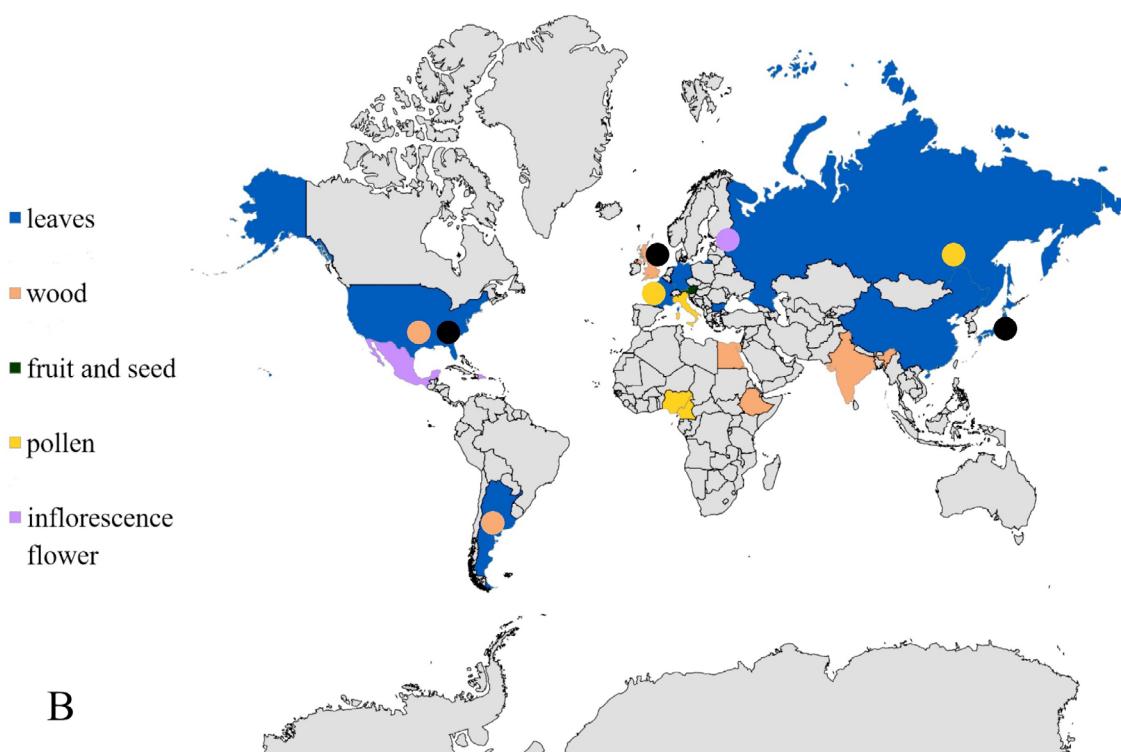
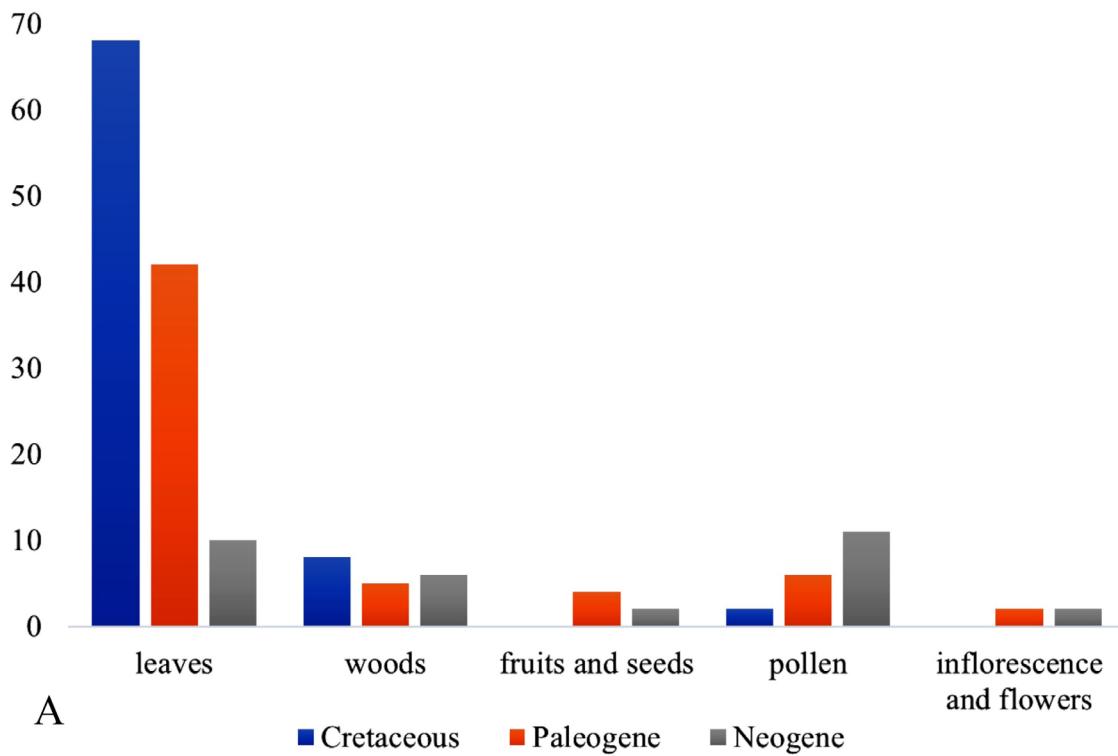


Figure 1. A. Abundance of leaves, woods, fruit-seeds, pollen, inflorescences, and flowers fossils assigned to Celastraceae by geologic time. B. Map showing the distribution of fossilized organs of plants identified as a member of Celastraceae.

strictly morphological criteria (Dilcher 1974). *Celastrophyllum* (Göppert 1854) and *Celastrinites* Saporta (Saporta 1865) represent extinct genera of Celastraceae that had been compared with *Celastrus*. They are mainly distributed in Europe (e.g., Vachrameev 1952, Samylina 1968, 1984) and high latitudes in America (e.g., Lee & Knowlton 1917, Knowlton 1919, 1922, Berry 1925). Doweld (2017) noted that there are two more descriptions associated with *Celastrophyllum*: *Celastrophyllum* Ettingsh. ex Saporta & Marion, and *Celastrophyllum* Ettingsh. ex Schimp.

Upchurch & Dilcher (1990) suggested that the type species of the genus should be *Celastrophyllum attenuatum* Göpp. It was described as a leaf with an entire margin and distinctive petiole, causing the expansion of the *Celastrophyllum* concept to include entire and toothed leaves, an apparently logical aspect since *Celastrus* has extreme foliar variation (Upchurch & Dilcher 1990, Mu *et al.* 2012, Liang *et al.* 2016). These include for example, the shape of the lamina ranging from elliptical to oblong or broadly ovate to orbicular; apex acute to obtuse or round and base rounded to acute (Bacon *et al.* 2016); however, morphologies overlap at intra and interspecific levels (Mu *et al.* 2012).

Recently, Herendeen (2020) suggested that *Celastrophyllum obtusum* Heer. is the species that validates the name *Celastrophyllum*, but its typification is necessary. Unfortunately, none of the three reports of *Celastrophyllum* are valid. Several of these reports are probably part of other families or genera since they have no diagnostic characteristics of the group (Doweld 2017, Herendeen 2020). Other members of Celastraceae have been reported from the Paleogene, including *Maytenus* (Berry 1938, Rüffle & Litke 2008) and *Euonymus* (Berry 1924, Brown 1937). Despite this, these records are also unresolved, because they are morphologically indistinguishable (Mu *et al.* 2012).

A diagnosis based on the foliar architecture of Celastraceae was proposed by Hickey & Wolfe (1975). Based on this, the leaves of Celastraceae *sensu stricto* typically have a theoid tooth, which has a median vein. This vein runs toward the apex and expands on the tooth, so that the apex is covered by an opaque deciduous seta. Moreover, brochidodromous secondary veins as well as percurrent tertiary veins are common in the group (Hickey & Wolfe 1975). Subsequently, Upchurch & Dilcher (1990) indicated that all these characters are enough evidence to establish the identification of fossil leaves to *Celastrus*. More recently, Liang *et al.* (2016) indicated that the secondary venation of *Celastrus* varies from camptodromous

to craspedodromous and semicraspedodromous types. Fossil leaves of the middle Eocene from the Green River Flora, USA, described by Hollick (1936) and reexamined by Wolfe (1977) are considered reliable records of *Celastrus* (Upchurch & Dilcher 1990).

Woods. Celastraceae often has woods with small, numerous and solitary vessels with simple or scalariform perforation plates; alternate bordered intervacular pits; and parenchyma variable in type and quantity, that sometimes can have scattered or even absent (Metcalfe & Chalk 1983). Additionally, the presence or absence of scalariform perforation plates is an informative character for the generic delimitation within the family (Archer & van Wyk 1993).

Family has few reports of fossil woods with Cretaceous age, and most of them are from Africa, Egypt, Ethiopia, and North America (Figure 1). As well as fossil leaves, the fossil record of woods have been related to extant genera of Celastroideae. For example, *Celastrinoxylon* (Schenk) Kräusel was identified by Schenk (1888) and reexamined by Kräusel (1939) (e.g., Kräusel 1939, Schönfeld 1955, Poole 2000, Kamal El-Din *et al.* 2006). It was recognized as a fossil wood with simple perforation plates, small vessels and rays composed entirely of square or erect cells, nevertheless, it has doubtful records. Such is the case of a fossil wood of *Celastrinoxylon* from India (Ramanujam 1960), which was reexamined and reassigned to *Ailan-thoxylon* (Simaroubaceae) by Awasthi (1975). Additionally, Kamal El-Din (2003) described *Celastrinoxylon* as a wood with scalariform perforation plates from the Cretaceous of Egypt, but it contrasts to the diagnosis proposed by Kräusel (1939).

According to Poole & Wilkinson (1999) *Celastrinoxylon* has more resemblance to *Catha* because both have small vessels, simple perforation plate, tiny intervacular pits with an opposite arrangement, thin-walled fibers, and uniseriate rays with erect cells. This combination of characters differs from *Celastrus*, which has vessel dimorphism, broad rays, and other forms of the parenchyma commonly present in scandents and lianas (Carlquist 1988).

Other fossil taxa that have a simple perforation plate are *Lophopetalumoxylon* (Mehrotra *et al.* 1983) and *Maytenoxylon* (Franco 2018). The first one is characterized by the presence of diffuse porosity, solitary vessels, bordered and alternate intervacular pits, thin apotracheal bands of parenchyma, uniseriate homocellular rays, non-septate thick-walled fibers, and intercellular canals. *Lophopeta-*

lumoxylon was compared closely to *Lophopetalum*, which commonly has multiple radial vessels ([Mehrotra et al. 1983](#)). [Wheeler et al. \(2017\)](#) suggested that *Lophopetalumoxylon* probably belongs to Sapindales since its features occur in other families.

On the other hand, *Maytenoxylon* is a wood with diffuse porosity, mainly solitary vessels, intervacular pits that vary from alternate to opposite, bands of fiber resembling parenchyma that alternate with ordinary fibers, both non-septate and septate ones, diffuse and scanty parenchyma, homocellular rays with some perforated cells ([Franco 2018](#)). The identification of *Maytenoxylon* is supported by the presence of perforated ray cells, which are restricted to *Maytenus* ([Joffily et al. 2007](#)).

Scalariform perforation plates have been rarely reported in the family ([Metcalfe & Chalk 1983](#), [Archer & van Wyk 1993](#)), such is the case of *Elaeodendroxylon* ([Gottwald 1992](#)). It has been closely compared to extant *Elaeodendron* because both have growth rings and numerous isolated or multiple radial vessels. *Baasia* ([Estrada-Ruiz et al. 2012](#)) is another taxon with a scalariform perforation plate. It has been considered as the most reliable record of Celastraceae until now, but its relationship to an extant taxon has not been established ([Bacon et al. 2016](#)).

Pollen. Celastraceae has spheroidal oblate or prolate radially symmetrical, isopolar, tricolporate pollen grains, and endoaperture monads that are generally elongated and sometimes oblong ([Bogotá & Sánchez 2001](#)). Typically, three types of pollen grains have been recognized in the family: (1) polyads in groups of four tetrads, (2) simple tetrads and (3) monads ([Erdtman 1952](#), [Campo & Hallé 1959](#), [Hallé 1960](#), [Hou 1969](#), [Lobreaux-Callen 1977](#)). All types have been recognized in the fossil record.

According to Ding [Hou \(1969\)](#) polyads and/or tetrads are common in Hippocrateoideae, Salacioideae, and *Lophopetalum*. For example, [Salard-Cheboldaeff \(1974\)](#) described *Polyadopollenites macroreticulatus*, *P. microreticulatus* and *P. micropoliada* from the Miocene of Cameroon as polyads of sixteen pollen grains, each one of them lacking an annulus and cross-linked exine, characters that are comparable to *Hippocratea volubilis* and *H. myriantha*. However, *Polyadopollenites* is a morphogenus assigned to circular and oval polyads, variable symmetry accounts for the aggrupation of sixteen monads, but it has been related with Fabaceae ([Barreda & Caccavari 1992](#)).

Furthermore, tetrads identified as *Triporotetradites campylostemonoides*, *T. hoekenii*, *T. letouzeyi*, and *T. sca-*

bratus ([Hoeken-Klinkenberg 1964](#), [Salard-Cheboldaeff 1974, 1978, 1979](#)) have been related to *Campylostemon*; however, similar tetrads are common in other families ([Copenhaver 2005](#)). *Retriticoporites* is another tetrad described by [Salard-Cheboldaeff \(1974\)](#) based on its tricolporate pollen grains with apparent endexin, whose morphology is close to *Loseneriella*.

Finally, [Muller \(1981\)](#) reported tricolporate monads recognized as *Microtropis* and *Peritassa* from the Oligocene of France ([Lobreaux-Callen & Caratini 1973](#)). Additionally, [Ramanujam \(1966\)](#) assigned tricolporate pollen grains with elongate ectoapertures to *Hippocrateace-aedites*, it was latter recognized from the Eocene of India by [Venkatachala & Kar \(1969\)](#).

Fruits and seeds. Celastraceae exhibits a substantial morphological variation in fruits and seeds. Traditionally these have been used to subdivide the family taxonomically (e.g., [Loesener 1942](#), [Takhtajan 1997](#), [Cronquist 1981](#)). According to [Simmons et al. \(2001a\)](#) the fruits can be capsules (with great variability in forms and types of dehiscence), schizocarpal mericarps (Stackhousiaceae), berries (e.g., *Cassine*, *Maurocenia*), drupes (e.g., *Acanthothamnus*, *Elaeodendron*), walnuts (e.g., *Mortonia*, *Pleurostylia*) or samaras (e.g., *Rzedowskia*, *Tripterygium*). Seeds are 1-12 in number, smooth or occasionally furrowed, albuminous or exalbuminous, sometimes winged, and the wing may be membranous or basal, exarillate or aril basal to completely enveloping the seed, and this can be membranous, fleshy, or rarely mucilaginous ([Ma et al. 2008](#)).

Reproductive organs have diagnostic characteristics, for this reason they have a high degree of reliability in taxonomic work and are highly useful for plant identification ([Tiffney 1990](#), [Wiens 2004](#)). [Berry \(1930\)](#) described a loculicidal capsule with three rough leaflets as *Celastrocarpus* from the Eocene of Tennessee. As well as, *Euonymus* was tentatively assigned to a dehiscent capsule with four round lobes and separated by a sinuate sulcus ([Berry 1930](#)). Likewise, *Euonymus moskenbergensis* a fruit with five lobes from the Miocene of Australia was reported by [Ettingshausen \(1869\)](#). Fruits with seeds from the early Eocene (52-49 Ma) were reported by [Reid & Chandler \(1933\)](#) in the London Clay Formation (United Kingdom). These reproductive structures were described as small, subovoid and lobate fruits, containing seeds with a winged extension. In the same work, *Canthicarpum celastroides* was recognized as a loculicidal capsule with three leaflets and seeds whose testa has three layers, the outermost composed of large polygonal cells, and a fourth layer interpreted as a possible aril.

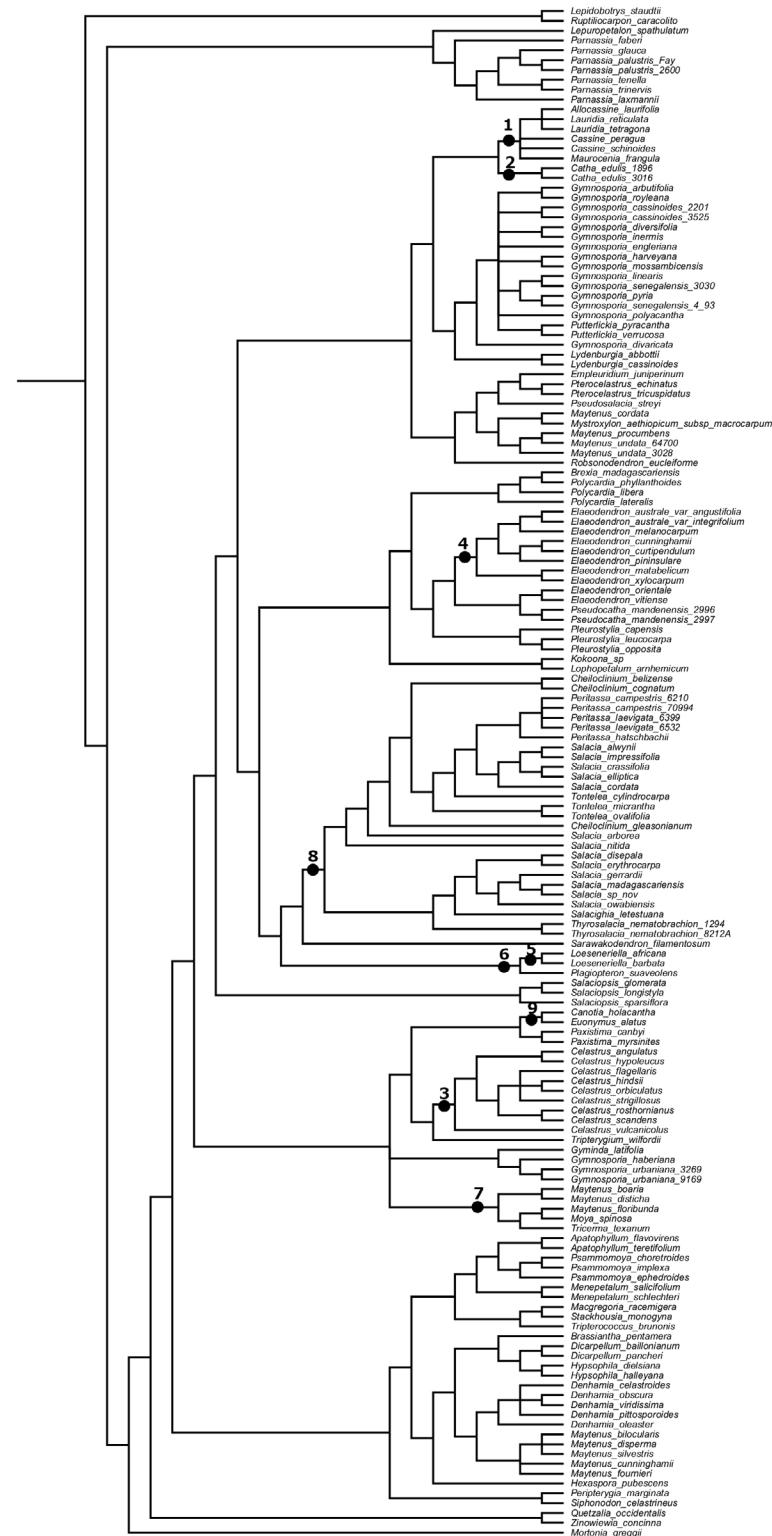


Figure 2. Assignment of Celastraceae fossils as molecular clock calibration points based on topology of [Coughenour et al. \(2010\)](#). 1. *Baasia armendari-sense* ([Estrada-Ruiz et al. 2012](#)), 2. *Cathispernum pulchrum* ([Reid & Chandler 1933](#)), 3. *Celastrus comparabilis* ([Wolfe 1977](#)), 4. *Elaeodendroxylon* sp. ([Gottwald 1992](#)), 5. *Hippocrateaceaedites* sp. ([Venkatachala & Kar 1969](#)), 6. *Lobocyclas anomala* ([Chambers & Poinar 2016](#)), 7. *Maytenoxylon perforatum* ([Franco 2018](#)), 8. *Salacia lombardii* ([Hernández-Damián et al. 2018](#)), 9. *Wuyuananthus hexapetalus* ([Wang et al. 2001](#)).

Tripterygium kabutoiwanum from the Pliocene of Japan ([Ozaki 1991](#)) was described as composed of winged fruits and leaves closely comparable with *Tripterygium regelii*. We were not able to obtain the original publication; however, other fossil records of the genus have been reexamined and assigned to *Craigia* (Malvaceae) ([Kvaček et al. 2005](#), [Manchester et al. 2009](#)).

Flowers. The flowers are generally bisexual, with a conspicuous nectarial disk, five or fewer stamens immersed in the ovary ([Stevens 2001](#)). However, this general pattern is modified within the lineage, because the number of parts of the floral whorls, or merism, has been changed in some members ([Matthews & Endress 2005](#)). For example, flowers with a pentamerous perianth and a trimerous androecium are common in Hippocrateoideae and Salacioideae. It has been considered as a distinctive pattern in Celastraceae ([Ronse De Craene 2010, 2016](#)). Even more, modifications in the number of stamens have been reported in Salacioideae. Flowers with five (e.g., *Cheiloclinium anomalum*) or two (e.g., *Salacia annetiae* and *S. lebrunii*) ([Hou 1969](#), [Hallé 1986, 1990](#), [Coughenour et al. 2010](#)) stamens are well known, and each type had an independent origin ([Coughenour et al. 2010](#)).

There are few records of fossil flowers of Celastraceae, among them the oldest one is *Celastrinanthium hauchecornei*, a cymose inflorescence preserved in Baltic amber ([Conwentz 1886](#)). According to [Conwentz \(1886\)](#) it includes bisexual flowers with a differentiated perianth with four sepals and petals, a disk, and an ovary with four locules. Other flower reports include *Wuyuananthus hexapetalus* from the Paleocene of China ([Wang et al. 2001](#)), *Lobocyclas anomala* (Hippocrateoideae) preserved in Miocene amber from the Dominican Republic ([Chambers & Poinar 2016](#)), and *Salacia lombardii* (Salacioideae) from Miocene of Simojovel de Allende, Mexico ([Hernández-Damián et al. 2018](#)). All these records have the general structural pattern of the family as they are bisexual flowers with a biseriate perianth and a conspicuous disk ([Stevens 2001](#), [Simmons 2004](#)).

Discussion

Fossil record of Celastraceae has been recognized in the early scientific literature. It has abundant and diverse fossil evidence, but only a few records have enough information to be recognized as credible records. They are relevant in comparative analysis as dated phylogenies since these provide important information for the inference of

the origin and diversification of a lineage. Different origin ages of the crown group Celastraceae have been estimated as 71.6 Ma ([Magallón & Castillo 2009](#)), (89) 76-71(60) Ma ([Bell et al. 2010](#)) and (109.85) 92.61 (76.98) ([Magallón et al. 2015](#)), but none of these analyses had as their main objective the family Celastraceae.

The most recently dated phylogeny of Celastraceae was proposed by [Bacon et al. \(2016\)](#). This work is relevant because it includes a revision of the fossil record of Celastraceae. But does not include newly reported fossil taxa that can change the phylogenetic interpretations when considering such taxa as *Maytenoxylon perforatum* ([Franco 2018](#)), *Lobocyclas anomala* ([Chambers & Poinar 2016](#)), and *Salacia lombardii* ([Hernández-Damián et al. 2018](#)).

In this revision, we recognize nine fossil records of Celastraceae as potential calibration points as each one represents the oldest age recognized for a lineage to date ([Table 1](#)). Most of these fossils have an age established through correlation rather than direct dating. Therefore, it is necessary to consider that these could change in the future. These nine fossil records have most of the criteria established by [Martínez-Millán \(2010\)](#) (see [Supplementary Material, Table S2](#)), but their acceptance for calibrating points needs to be carefully evaluated. The first criterion of [Martínez-Millán \(2010\)](#) refers to the inclusion of the fossils in a phylogenetic analysis, but none of the fossil records of Celastraceae have been subject to this type of study since the use of morphological data has been limited in a phylogenetic context ([Simmons & Hedin 1999](#), [Simmons et al. 2001a, b](#)).

On the other hand, the second and third criteria refer to the character or character set that supports the identification of the fossil as a member of Celastraceae. This information requires an interpretation within a phylogenetic context ([Manchester et al. 2015](#)), because the morphological synapomorphies are considered critical data to establish the relationship between fossil and extant taxa ([Parham et al. 2012](#)). Unfortunately, few morphological characters have been identified as synapomorphies in the lineage (e.g., [Simmons & Hedin 1999](#)), and most of them are restricted to reproductive structures. For example, Hippocrateoideae is easily recognized by the synapomorphies of transversely, flattened, deeply lobed capsules and seeds with membranous basal wings or narrow stipes, while Salacioideae is identified by berries with mucilaginous pulp ([Coughenour et al. 2010, 2011](#)).

Due to the above, the phylogenetic position of the nine fossil taxa is supported through morphological compari-

Table 1. Fossils records proposed as molecular clock calibration points arranged in alphabetic order.*Absolute age is available.

Fossil name	Plant part	Geological Age (Ma)	System Series	Provenance	Reference	Relationship Compared to
<i>Baasia armendarisense</i>	wood	73.5*	Upper Cretaceous	McRae Formation, USA	Estrada-Ruiz <i>et al.</i> 2012	<i>Cassine</i>
<i>Cathispermum pulchrum</i>	fruit and seeds	33.9	Eocene	London Clay, England	Reid & Chandler 1933	<i>Catha edulis</i>
<i>Celastrus comparabilis</i>	leaves	33.9	middle Eocene	Kushtaka Formation, USA	Wolfe 1977	<i>Celastrus</i>
<i>Elaeodendroxylon</i> sp.	wood	33.9	Eocene	Braunkohlen-Tagebau, Germany	Gottwald 1992	<i>Elaeodendron</i>
<i>Hippocrateaceaedites</i> sp.	pollen	33.9	Eocene	Laki Basin, India	Venkatachala & Kar 1969	<i>Loseneriella</i>
<i>Lobocyclas anomala</i>	flower	23-30*	middle Oligocene-lower Miocene	Dominican Republic	Chambers & Poinar 2016	<i>Prionostemma, Hippocratea</i>
<i>Maytenoxylon perforatum</i>	wood	5.3	Miocene	Ituzaingó Formation, Argentina	Franco 2018	<i>Maytenus</i>
<i>Salacia lombardii</i>	flower	23-15*	middle-early Miocene	Simojovel de Allende, Mexico	Hernández-Damián <i>et al.</i> 2018	<i>Salacia</i>
<i>Wuyuananthus hexapetalus</i>	flower	66.0-61.6*	lower Paleocene	Wuyun, China	Wang <i>et al.</i> 2001	<i>Euonymus, Celastrus</i>

son with extant taxa ([Figure 2](#)). Morphological similarity recognized in fossil and extant taxa suggests a relationship between them, but this situation may change drastically as more in-depth morphological studies are integrated into a phylogenetic context. Such is the case of *Cathispermum pulchrum* [Reid & Chandler \(1933\)](#) a five-lobed fruit with winged seeds that have been interpreted as a potential aril. However, presence of an aril is difficult to discern among extant plants and even more difficult in the fossil material. The definition of an aril is complicated to establish ([Simmons & Hedin 1999](#), [Simmons 2004](#), [Zhang *et al.* 2012, 2014](#)). Nevertheless, it typically has been defined for the family as a structure that derives from the funiculus during development ([Loesener 1942](#), [Corner 1976](#)). Thus, *C. pulchrum*, while morphologically like Celastraceae, needs a closer morphological comparison of the aril as discussed in the next paragraph.

According to [Simmons \(2004\)](#), winged seeds have been interpreted as homologues to arilated seeds, as in the case of *Catha edulis*, which was compared to *Cathispermum pulchrum*. However, [Zhang *et al.* \(2012, 2014\)](#) recognized that the tissue surrounding the seed in *Catha edulis* derives from the micropyle, not from the funiculus. For this reason, it is necessary to consider that the interpretation of

C. pulchrum could change as new morphological data or interpretations become available. The biased, incomplete nature of the fossil record is a limitation for its interpretation. In the same way, the lack of detailed morphological studies of extant taxa limits the identification of the fossil record. In Celastraceae, the study of the development of the winged seed is essential to interpret the evolution of this structure ([Zhang *et al.* 2014](#)), as well as the fossil record.

In general, the fossils of reproductive structures are considered reliable records, such is the case of fossil flowers of Celastraceae. All of them are bisexual flowers, with biserial perianth and nectarial disk. Nevertheless, *Wuyuananthus* has been considered a doubtful record due to its merosity, or the number of parts of the perianth (6 vs. 4-5, [Friis *et al.* 2011](#)). The meristic pattern within the group has modifications that have been little explored ([Ronse De Craene 2016](#)).

Identification of fossil flowers could be supported with higher reliability through the recognizing of potential morphological synapomorphies, these include a bulge in the dorsal part of the ovary with an apical septum, and the presence of calcium oxalate druses in floral tissue ([Matthews & Endress 2005](#)), but the type of fossilization is

a limiting factor for what anatomical characters get preserved. Flowers preserved in amber such as *Lobocyclas anomala* and *Salacia lombardii* are exceptional records because they are in three dimensions with relatively little distortion. Access to anatomical characters of plant inclusions in amber has been documented through non-destructive techniques such as microtomography (e.g., [Moreau et al. 2016](#)). Further observations on these fossil flowers will help to add support to our suggestion of good calibration point fossils.

Pollen is the most abundant part of the plant fossil record. It is generally identified with relatively low taxonomic resolution ([Sauquet et al. 2012](#)). According to [Hallé \(1960\)](#) the characters of pollen have a higher value at the infrageneric level, but these require the integration of information from other organs of the plant for a reliable taxonomic determination.

Tetrads and polyads have been considered as diagnostic characters of Hippocrateoideae, but these are not exclusive to the group. For example, *Triporotetradites* sp. was related to *Campylostemon*, but this record has been reexamined and related to other taxa. Such is the case of *Triporotetradites letouzeyi* from the lower of Miocene of Cameroon ([Salard-Cheboldaeff 1978](#)), which is comparable to the pollen of species of *Gardenia* ([Muller 1981](#)). Additionally, unlike in extant plants, it is often difficult to determine in fossil pollen taxa their range of morphological variation ([Cleal & Thomas 2010](#)), as in the case of *Lophopetalum* an extant genus that has both polyads and tetrads ([Hou 1969](#)).

Macrofossils are abundant in the fossil record of Celastraceae ([Bacon et al. 2016](#)). Specifically, the leaves have been rejected in taxonomic work because they are plastic organs that respond to environmental pressures ([Hickey 1973](#), [Hickey & Wolfe 1975](#)). Furthermore, leaf dimorphism is a factor that complicates the taxonomic determination in Celastraceae ([Simmons 2004](#)). For instance, *Elaeodendron orientale* has lanceolate leaves with an entire margin, but when it is a mature plant, its leaves are elliptical with a serrated margin ([Simmons 2004](#)). In addition, the lack of a precise description and diagnosis, such is the case of *Celastrophylgium*, has generated a highly doubtful abundant record in North America and Europe ([Doweld 2017](#), [Herendeen 2020](#)). Despite of these limitations, the presence of *Celastrus* based on fossil leaves can be considered a reliable record based on consistent characters, such as the theoid tooth and camptodromous, craspedodromus or semicraspedodromus venation ([Liang et al. 2016](#)).

Woods are recognized as the second organ most abundant in the fossil record of Celastraceae. Their structure and cellular organization under fossilization preserves well providing detailed anatomical data for their identification ([Poole 2000](#)). A combination of characters that includes small to medium-sized vessels, apotracheal bands of parenchyma, fine homogeneous rays, and non-septate fibers strongly indicate its affinities with the family Celastraceae ([Mehrotra et al. 1983](#)). Moreover, the scalariform perforation plate has been considered diagnostic for the group; however, the phylogenetic context of anatomical data has changed the interpretation of some records. For example, *Perrottetioxylon mahurzari* ([Chitaley & Patel 1971](#)) and *Gondwanoxylon* ([Saksena 1962](#)) were closely compared to *Perrottetia*, a genus traditionally considered an atypical member of Celastraceae. Its inclusion within Celastraceae was supported by anatomical characters, such as the presence of scalariform perforation plate, paratracheal parenchyma and absence of fiber tracheids ([Metcalfe & Chalk 1983](#), [Simmons & Hedin 1999](#)). However, [Zhang & Simmons \(2006\)](#) determined the exclusion of *Perrottetia* from this family through a phylogenetic analysis using molecular characters.

Although the fossil record of Celastraceae is scarce as point calibration according to criteria proposed by [Martínez-Millán \(2010\)](#), their geographic distribution suggest the dispersion between North America, Europe and Asia during the early Paleogene to the Pliocene ([Wolfe 1975](#), [Tiffney & Manchester 2001](#), [Graham 2018](#)). This hypothesis is supported by [Magallón et al. \(2019\)](#) that suggested that the diversification of the lineage was as a relevant event for angiosperms during the Paleogene ca. (68.40) 51.1 (42.83) Ma.

The selection of reliable fossils as calibration points is critical for reconstructing robust phylogenies. Unfortunately, the inherent fragmentary nature of fossil plants limits access to molecular characters and other sources of information, with morphology and anatomy being the most frequent source of information available for study ([Wiens 2004](#)). Consequently, an in-depth study of the morphological characters in a phylogenetic context in Celastraceae is essential (e.g., [Simmons & Hedin 1999](#)), since only through this will it be possible to generate a better interpretation and evaluation of their fossil record. It is also necessary to increase the value of fossils through the reconstruction of complete plants, as this work will significantly complement the understanding of plants in terms of variability and distribution of characters over time. After detailed evaluation and discussion, we propose

nine fossil reports of Celastraceae as reliable and well supported to be used as calibration points. However, further studies need to be conducted towards phylogeny of the family.

Acknowledgments

The authors recognize the guidance and comments of Drs. S. A. Quiroz Barroso, H. Flores-Olvera, S. Vásquez-Santana, H. Ochoterena and M. Martínez-Gordillo, Universidad Nacional Autónoma de México (UNAM). English grammar was improved with assistance of Dr. D. Erwin, University of California, Berkeley. We thank Dr. T. Terrazas chief editor and Dra. Silvia Aguilar Rodríguez associated editor of Botanical Sciences, Dr. M.P. Simmons, University of Colorado, Boulder, and two anonymous reviewers for several suggestions that improved the manuscript. This work was supported by the Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México (UNAM), PAPIIT-UNAM (project IN 210416) and the Consejo Nacional de Ciencia y Tecnología (CONACYT) projects 221129 and CF61501 and a scholarship (325158) for postgraduate studies to ALHD.

Supplementary material

Supplemental data for this article can be accessed here: <https://doi.org/10.17129/botsci.2802>

Literature cited

Archer RIL, van Wyk AE. 1993. Wood structure and generic status of some southern African Cassinoideae (Celastraceae). *International Association of Wood Anatomists Journal* **14**: 373-389. DOI: <https://doi.org/10.1163/22941932-90000592>

Awasthi N. 1975. Revision of some dicotyledonous woods from the Tertiary of South India. *The Palaeobotanist* **22**: 186-191.

Bacon CD, Simmons MP, Archer RH, Zhao LC, Andrianiana J. 2016. Biogeography of the Malagasy Celastraceae: Multiple independent origins followed by widespread dispersal of genera from Madagascar. *Molecular Phylogenetics and Evolution* **94**: 365-382. DOI: <https://doi.org/10.1016/j.ympev.2015.09.013>

Barreda VD, Caccavari M. 1992. Mimosoideae (Leguminosae) occurrences in the Early Miocene of Patagonia (Argentina). *Palaeogeography, Palaeoclimatology, Palaeoecology* **94**: 243-252. DOI: [https://doi.org/10.1016/0031-0182\(92\)90121-K](https://doi.org/10.1016/0031-0182(92)90121-K)

Bell CD, Soltis DE, Soltis, PS. 2010. The age and diversification of the angiosperms re-revisited. *American Journal of Botany* **97**: 1296-1303. DOI: <https://doi.org/10.3732/ajb.0900346>

Berry EW. 1924. The Middle and Upper Eocene floras of south eastern America. *United States Geological Survey Professional Paper* **92**: 1-206. DOI: <https://doi.org/10.3133/pp92>

Berry EW. 1925. The flora of the Ripley Formation. *United States Geological Survey Professional Paper* **129**: 199-226. DOI: <https://doi.org/10.3133/pp136>

Berry EW. 1930. Revision of the lower Eocene Wilcox flora of the southeastern States, with descriptions of new species, chiefly from Tennessee and Kentucky. *United States Geological Survey Professional Paper* **156**: 1-189. DOI: <https://doi.org/10.3133/pp156>

Berry EW. 1938. Tertiary Flora from the Rio Pichileufu, Argentina. *Geological Society of America Special Papers* **12**: 1-149. DOI: <https://doi.org/10.1130/SPE12>

Bogotá ARG, Sánchez LR. 2001. Caracterización palinológica de la familia Celastraceae para Colombia. *Caldasia* **23**: 269-280.

Brown RW. 1937. Additions to some fossil floras of the western United States. *United States Geological Survey Professional Paper* **186**: 163-206. DOI: <https://doi.org/10.3133/pp186J>

Campo M, Hallé Nv. 1959. Lees grains de pollen des Hippocrateacées d'Afrique de l'Ouest. *Pollen et Spores* **1**: 191-192.

Carlquist S. 1988. *Comparative Wood Anatomy Systematic, Ecological, and Evolutionary Aspects of Dicotyledon Wood*. Germany, Berlin: Springer Series in Wood Science. ISBN: 978-3-662-21714-6.

Chambers KL, Poinar Jr GO. 2016. *Lobocyclas anomala*, a new genus and species of Celastraceae subfamily Hippocrateoideae in Dominican amber. *Journal of the Botanical Research Institute of Texas* **10**: 137-140.

Chitaley SD, Patel MZ. 1971. A fossil dicotyledonous stem from the Deccan Intertrappean cherts of Mohgaon Kalan, India. *Journal of Biological Sciences (Bombay)* **14**: 50-57.

Cleal CJ, Thomas BA. 2010. Botanical nomenclature and plant fossils. *Taxon* **59**: 261-268.

Cohen KM, Finney SC, Gibbard PL, Fan JX. 2020. The ICS International Chronostratigraphic Chart. *Episodes* **36**: 199-204.

Copenhaver GP. 2005. A compendium of plant species producing pollen tetrads. *Journal of the North Carolina Academy of Science* **121**: 17-35.

Conwentz H. 1886. Die Angiospermen des Bernsteins. In: Göppert HR, Menge A, eds. *Die Flora des Bernsteins und ihre Beziehungen zur Flora der Tertiärformation und der Gegenwart* 2. Danzig: Engelmann, pp. 1-140.

Corner EJH. 1976. *The Seeds of Dicotyledons*. United Kingdom, London: Cambridge University Press. ISBN: 0521116058

Cougenour JM, Simmons MP, Lombardi JA, Cappa JJ. 2010. Phylogeny of Celastraceae subfamily Salacioidae and tribe Lophopetalae inferred from morphological characters and nuclear and plastid genes. *Systematic Botany* **35**: 358-366. DOI: <https://doi.org/10.1600/036364410791638289>

Cougenour JM, Simmons MP, Lombardi JA, Yakobson K, Archer RH. 2011. Phylogeny of Celastraceae subfamily Hippocrateoideae inferred from morphological characters and nuclear and plastid genes. *Molecular Phylogenetics and Evolution* **59**: 320-330. DOI: <https://doi.org/10.1016/j.ympev.2011.02.017>

Crepet WL. 2008. The Fossil record of angiosperms: requiem or renaissance? *Annals of the Missouri Botanical Garden* **95**: 3-33. DOI: <https://doi.org/10.3417/2007065>

Cronquist A. 1981. *An Integrated System of Classification of Flowering Plants*. USA, New York: Columbia University Press. ISBN: 0-231-03880-1.

Dilcher DL. 1974. Approaches to the identification of angiosperm leaf remains. *The Botanical Review* **40**: 1-157. DOI: <https://doi.org/10.1007/BF02860067>

Donoghue PCJ, Benton MJ. 2007. Rocks and clocks: calibrating the Tree of Life using fossils and molecules. *Trends in Ecology & Evolution* **22**: 424-431. DOI: <https://doi.org/10.1016/j.tree.2007.05.005>

Doweld AB. 2017. (60-62) Requests for binding decisions on the descriptive statements associated with *Celastrophyllum* Göpp., *Celastrophylleum* Ettingsh. ex Saporta & Marion, and *Celastrophylleum* Ettingsh. ex Schimp. (fossil plants). *Taxon* **66**: 1484-1485. DOI: <https://doi.org/10.12705/666.28>

Erdtman G. 1952. *Pollen Morphology and Plant Taxonomy-Angiosperms*. Stockholm: Almqvist and Wiksell.

Estrada-Ruiz E, Upchurch GR, Wheeler EA, Mack GH. 2012. Late cretaceous angiosperm woods from the crevasse canyon and McRae formations, south-central New Mexico, USA: Part 1. *International Journal of Plant Sciences* **173**: 412-428. DOI: <https://doi.org/10.1086/664714>

Ettingshausen C. von. 1869. Beiträge zur Kenntniss der Tertiärfloren Steiermarks. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften* **60**: 17-100.

Ettingshausen C. von. 1883. Beiträge zur Kenntniss der Tertiärfloren Australiens. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche* **47**: 1-48.

Ettingshausen C von. 1887. Beitraege zur Kenntnis der Fossilen Flora Neuseelands. *Denkschriften der Akademie der Wissenschaften, Wien* **53**: 143-194.

Franco MJ. 2018. Small Celastraceae and Polygonaceae twigs from the Upper Cenozoic (Ituzaingó Formation) of the La Plata Basin, Argentina. *Historical Biology* **30**: 646-660. DOI: <https://doi.org/10.1080/08912963.2017.1313840>

Friis EM, Pedersen KR, Crane PR. 2011. *Early Flowers and Angiosperm*. United Kingdom, London: Cambridge University Press. ISBN: 9780521592833.

Göppert HR. 1854. *Die Tertiärfloren auf der Insel Java nach den Entdeckungen des Herrn Fr. Junghuhn beschrieben und erörtert in ihrem Verhältnisse zur Gesamtflora der Tertiärperiode*. Germany: Nabu Press. ISBN: 978-1276014632.

Gottwald H. 1992. Hölzer aus marinen Sanden des oberen Eozän von Helmstedt (Niedersachsen). *Palaeontographica Abteilung B* **225**: 27-103.

Graham A. 2018. The role of land bridges, ancient environments, and migrations in the assembly of the North American flora. *Journal of Systematics and Evolution* **56**: 405-429. DOI: <https://doi.org/10.1111/jse.12302>

Hallé N. 1960. Essai de clé pour la détermination des pollens des Hippocrateacées Ouest-Africaines. *Pollen et Spores* **2**: 5-12.

Hallé N. 1986. Celastraceae-Hippocrateoideae. In: Morat P, ed. *Flore du Gabon (avec compléments pour d'autres pays d'Afrique et Madagascar)* (avec compléments pour d'autres pays d'Afrique et Madagascar). France, Paris: Bulletin du Museum National d'Histoire Naturelle, Laboratoire de Phanérogamie. pp 1-287.

Hallé N. 1990. Celastracées (Hippocrateoïdées). In: B. Satabie, Morat P, eds. *Flore du Cameroun*. France, Paris: Ministere de l'Enseignement Supérieur de l'Informatique et de la Recherche Scientifique Mesires, Yaoundé. pp. 3-243.

Herendeen P. 2020. Report of the Nomenclature Commit-

tee for Fossils: 13. *TAXON* **69**: 398-402. DOI: <https://doi.org/10.1002/tax.12218>

Hernández-Damián AL, Gómez-Acevedo SL, Cevallos-Ferriz SRS. 2018. Fossil flower of *Salacia lombardii* sp. nov. (Salacioideae-Celastraceae) preserved in amber from Simojovel de Allende, Mexico. *Review of Palaeobotany and Palynology* **252**: 1-9. DOI: <https://doi.org/10.1016/j.revpalbo.2018.02.003>

Hickey LJ. 1973. Classification of the architecture of dicotyledonous leaves. *American Journal of Botany* **60**: 17-33. DOI: <https://doi.org/10.1002/j.1537-2197.1973.tb10192.x>

Hickey LJ, Wolfe JA. 1975. The bases of angiosperm phylogeny: vegetative morphology. *Annals of the Missouri Botanical Garden* **62**: 538-589. DOI: <https://doi.org/10.2307/2395267>

Hoeken-Klinkenberg PMJ van. 1964. A palynological investigation of some Upper-Cretaceous sediments in Nigeria. *Pollen et Spores* **6**: 209-231.

Hou D. 1969. Pollen of *Sarawakodendron* (Celastraceae) and some related genera, with notes on techniques. *Blumea* **17**: 97-120.

Islam MB, Simmons MP, Archer RH. 2006. Phylogeny of the *Elaeodendron* group (Celastraceae) inferred from morphological characters and nuclear and plastid genes. *Systematic Botany* **31**: 512-524. DOI: <https://doi.org/10.1043/05-68.1>

Joffily A, Freire Domingues D, Cardoso Vieira R. 2007. Perforated ray cells in the root and stem of *Maytenus* (Celastroideae-Celastraceae). *International Association of Wood Anatomists Journal* **28**: 311-314. DOI: <https://doi.org/10.1163/22941932-90001642>

Kamal El-Din MM. 2003. Petrified wood from the Farafra Oasis, Egypt. *International Association of Wood Anatomists Journal* **24**: 163-172. DOI: <https://doi.org/10.1163/22941932-90000329>

Kamal El-Din MM, Wheeler EA, Bartlett JA. 2006. Cretaceous Woods from the Farafra Oasis, Egypt. *International Association of Wood Anatomists Journal* **27**: 137-143. DOI: <https://doi.org/10.1163/22941932-90000143>

Knowlton FH. 1919. A catalogue of the Mesozoic and Cenozoic plants of North America. *United States Geological Survey Professional Paper* **696**: 1-815. DOI: <https://doi.org/10.3133/b696>

Knowlton FH. 1922. The Laramie Flora of the Denver basin with a review of the Laramie problem. *United States Geological Survey Professional Paper* **130**: 1-175. DOI: <https://doi.org/10.3133/pp130>

Kräuse R. 1939. Der Bayerischen Akademie der Wissenschaften Ergebnisse der Forschungsreisen Prof. E. Stromers. *Abhandlungen der Bayerischen Akademie der Wissenschaften Mathematisch-naturwissenschaftliche Abteilung* **47**: 1-140.

Kvaček Z, Manchester SR, Akhmetiev MA. 2005. Review of the fossil history of *Craigia* (Malvaceae s.l.) in the northern hemisphere based on fruits and co-occurring foliage. In: Akhmetiev MA, Herman AB, eds. *Modern Problems of Palaeofloristics, Palaeophytogeography, and Phytostratigraphy*. Russia: Moscow: GEOS, Moscow. pp. 114-140.

Lee TW, Knowlton FH. 1917. Geology and paleontology of the Raton Mesa and other regions in Colorado and New Mexico. *United States Geological Survey Professional Paper* **101**: 1-561. DOI: <https://doi.org/10.3133/pp101>

Liang XQ, Ferguson DK, Jacques FMB, Su T, Wang L, Zhou ZK. 2016. A new *Celastrus* species from the middle Miocene of Yunnan, China and its palaeoclimatic and palaeobiogeographic implications. *Review of Palaeobotany and Palynology* **225**: 43-52. DOI: <https://doi.org/10.1016/j.revpalbo.2015.11.005>

Lobrea-Callen D. 1977. Les pollens des Celastrales (illustrations, commentaries). *Mémoires et travaux de l'Institut de Montpellier* **3**: 1-116.

Lobrea-Callen D, Caratini C. 1973. Pollens de "Celastraceae" à l'Oligocène en Gironde (France). *Bulletin de la Société Linnéenne de Bordeaux* **3**: 227-231.

Loesener T. 1942. Celastraceae. In: Engler A, Prantl K, eds. *Die natürlichen Pflanzenfamilien von A. Engler und K. Prantl, zweite stark vermehrte und verbeserte Auflage herausgegeben von Adolf Engler*. Germany, Berlin: Duncker & Humblot. pp. 87-197.

Ma M, Zhang Z, Quanru L, Peng H, Funston M. 2008. Celastraceae. In: Wu ZY, Raven PH Hong DY, eds. *Flora of China*. Vol. 11 (Oxalidaceae through Aceraceae). Beijing: Science Press, and St. Louis: Missouri Botanical Garden Press, pp. 439-492. ISBN: 1930723733

Magallón S, Castillo A. 2009. Angiosperm diversification through time. *American Journal of Botany* **96**: 349-365. DOI: <https://doi.org/10.3732/ajb.0800060>

Magallón S, Gómez-Acevedo SL, Sánchez-Reyes LL, Hernández-Hernández T. 2015. A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytologist* **207**: 437-453. DOI: <https://doi.org/10.1111/nph.13264>

Magallón S, Sánchez-Reyes LL, Gómez-Acevedo SL.

2019. Thirty clues to the exceptional diversification of flowering plants. *Annals of Botany* **123**: 491-503. DOI: <https://doi.org/10.1093/aob/mcy182>

Manchester SR, Chen ZD, Lu AM, Uemura K. 2009. Eastern Asian endemic seed plant genera and their paleogeographic history throughout the Northern Hemisphere. *Journal of Systematics and Evolution* **47**: 1-42. DOI: <https://doi.org/10.1111/j.1759-6831.2009.00001.x>

Manchester SR, Grímsson F, Zetter R. 2015. Assessing the fossil record of Asterids in the context of our current phylogenetic framework. *Annals of the Missouri Botanical Garden* **100**: 329-363. DOI: <https://doi.org/10.3417/2014033>

Martínez-Millán M. 2010. Fossil record and age of the Asteridae. *The Botanical Review* **76**: 83-135. DOI: <https://doi.org/10.1007/s12229-010-9040-1>

Matthews ML, Endress PK. 2005. Comparative floral structure and systematics in Celastrales (Celastraceae, Parnassiaceae, Lepidobotryaceae). *Botanical Journal of the Linnean Society* **149**: 129-194. DOI: <https://doi.org/10.1111/j.1095-8339.2005.00445.x>

Mehrotra RC, Prakash U, Bande MB. 1983. Fossil woods of *Lophopetalum* and *Artocarpus* from the Deccan Intertrappean beds of Mandla District, Madhya Pradesh, India. *The Palaeobotanist* **32**: 310-320.

Metcalfe C, Chalk L. 1983. *Anatomy of the Dicotyledons*, 2nd Ed. Vol. II. Wood structure and conclusion of the general introduction. United Kingdom, Oxford: Clarendon Press. ISBN: 978-0198545590.

Moreau JD, Néraudeau D, Perrichot V, Tafforeau P. 2016. 100-million-year-old conifer tissues from the mid-Cretaceous amber of Charente (western France) revealed by synchrotron microtomography. *Annals of Botany* **119**: 117-128. DOI: <https://doi.org/10.1093/aob/mcw225>

Mu XY, Zhao LC, Zhang ZX. 2012. Phylogeny of *Celastrus* L. (Celastraceae) inferred from two nuclear and three plastid markers. *Journal of Plant Research* **125**: 619-30. DOI: <https://doi.org/10.1007/s10265-012-0484-8>

Muller J. 1981. Fossil pollen records of extant angiosperms. *The Botanical Review* **47**: 1-141. DOI: <https://doi.org/10.1007/BF02860537>

Nixon KC. 1996. Paleobotany in cladistics and cladistics in paleobotany: enlightenment and uncertainty. *Review of Paleobotany and Palynology* **90**: 361-373. DOI: [https://doi.org/10.1016/0034-6667\(95\)00092-5](https://doi.org/10.1016/0034-6667(95)00092-5)

Ozaki K. 1991. Late Miocene and Pliocene floras in central Honshu, Japan. *Bulletin of Kanagawa Prefectural Museum*. Special Issue. **1**: 1-188.

Parham JF, Donoghue PCJ, Bell CJ, Calway TD, Head JJ, Holroyd PA, Inoue JG, Irmis R B, Joyce WG, Ksepka DT, Patané JSL, Smith ND, Tarver JE, van Tuinen M, Yang Z, Angielczyk KD, Greenwood JM, Hipsley CA, Jacobs L, Makovicky PJ, Müller J, Smith KT, Theodor JM, Warnock RCM, Benton MJ. 2012. Best practices for justifying fossil calibrations. *Systematic Biology* **61**: 346-359. DOI: <https://doi.org/10.1093/sysbio/syr107>

Poole I. 2000. Fossil angiosperm wood: its role in the reconstruction of biodiversity and Palaeoenvironment. *Botanical Journal of the Linnean Society* **134**: 361-381. DOI: <https://doi.org/10.1006/bojl.2000.0377>

Poole I, Wilkinson HP. 1999. A celastraceous twig from the Eocene London Clay of south-east England. *Botanical Journal of the Linnean Society* **129**: 165-176. DOI: <https://doi.org/10.1006/bojl.1998.0215>

Ramanujam CGK. 1960. Silicified woods from the Tertiary rocks of South India. *Palaeontographica Abteilung B* **106**: 99-140.

Ramanujam CGK. 1966. Palynology of the Miocene Lignite from south Arcot District, Madras, India. *Pollen et Spores* **8**: 149- 203.

Reid EM, Chandler MEJ. 1933. *The London Clay Flora*. United Kingdom, London. The British Museum.

Ronse De Craene LP. 2010. *Floral Diagrams an Aid to Understanding Flower Morphology and Evolution*. United Kingdom, London: Cambridge University Press. ISBN: 9780521729451

Ronse De Craene LP. 2016. Meristic changes in flowering plants: How flowers play with numbers. *Flora* **221**: 22-37. DOI: <https://doi.org/10.1016/j.flora.2015.08.005>

Rüffle L, Litke R. 2008. Ergänzungen zur Eozän-Flora des Geistales, Deutschland, und einigir weiterer Eozän-Fundstätten. *Feddes Repertorium* **111**: 449-463. DOI: <https://doi.org/10.1002/fedr.20001110711>

Saksena S. 1962. On two fossil dicotyledonous woods from south Rewa, Central India. *The Palaeobotanist* **11**: 30-37.

Salard-Cheboldaeff M. 1974. Pollens Tertiaires du Cameroun rapportés à la famille des Hippocrateacées. *Pollen et Spores* **16**: 499-506.

Salard-Cheboldaeff M. 1978. Sur la palynoflore Maestrichtienne et Tertiaire du bassin sedimentaire littoral du Cameroun. *Pollen et Spores* **20**: 215-260.

Salard-Cheboldaeff M. 1979. Palynologie maestrichtienne et tertiaire du cameroun. Etude qualitative et répartition verticale des principales espèces. *Review of Palaeo-*

botany and Palynology **28**: 365-388. DOI: [https://doi.org/10.1016/0034-6667\(79\)90032-0](https://doi.org/10.1016/0034-6667(79)90032-0)

Samylina VA. 1968. Early Cretaceous angiosperms of the Soviet Union based on leaf and fruit remains. *Botanical Journal of the Linnean Society* **61**: 207-218. DOI: <https://doi.org/10.1111/j.1095-8339.1968.tb00119.x>

Samylina VA. 1984. Late Cretaceous flora of the Tap River (Northern part of the sea of Okhotsk area). *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva* **27**: 236-247.

Saporta G de. 1865. Etudes sur la végétation du Sud-Est de la France à l'époque tertiaire. *Annales des Sciences Naturelles Botanique* **4**: 5-264.

Sauquet H, Ho SYW, Gandolfo MA, Jordan GJ, Wilf P, Cantrill DJ, Bayly MJ, Bromham L, Brown GK, Carpenter RJ, Lee DM, Murphy DJ, Sniderman JMK, Udovicic F. 2012. Testing the impact of calibration on molecular divergence times using a fossil-rich group: The case of *Nothofagus* (Fagales). *Systematic Biology* **61**: 289-313. DOI: <https://doi.org/10.1093/sysbio/syr116>

Schenk A. 1888. Fossile Hölzer aus Ostasien und Aegypten. *BihangKunglia Svenska Vetmkapsakadiens* **14**: 1-24.

Schönfeld E. 1955. Die Kieselhölzer aus der Braunkohle von Böhle bei Leipzig. *Palaeontographica Abteilung B* **99**: 1-83.

Simmons MP. 2004. Celastraceae. In: Kubitzki K, ed. *The Families and Genera of Vascular Plants. VI. Flowering Plants: Dicotyledons. Celastrales, Oxalidales, Rosales, Cornales, Ericales*. Berlin Germany: Springer, pp. 29-64.

Simmons MP, Clevinger CC, Savolainen V, Archer RH, Mathews S, Doyle JJ. 2001a. Phylogeny of the Celastraceae inferred from Phytochrome B gene sequence and morphology. *American Journal of Botany* **88**: 313-325. DOI: <https://doi.org/10.2307/2657021>

Simmons MP, Hedin JP. 1999. Relationships and morphological character change among genera of Celastraceae sensu lato (including Hippocrateaceae). *Annals of the Missouri Botanical Garden* **86**: 723-757. DOI: <https://doi.org/10.2307/2666152>

Simmons MP, Savolainen V, Clevinger CC, Archer RH, Davis JI. 2001b. Phylogeny of the Celastraceae inferred from 26S nuclear ribosomal DNA, phytochrome B, rbcL, atpB, and morphology. *Molecular Phylogenetics and Evolution* **19**: 353-366. DOI: <https://doi.org/10.1006/mpev.2001.0937>

Stevens PF. 2001. Onwards. Angiosperm Phylogeny Web-siteVersion. <http://www.mobot.org/MOBOT/research/APweb/> (accessed July 14, 2017)

Takhtajan AL. 1997. *Diversity and Classification of Flowering Plants*. USA, New York: Columbia University Press. ISBN: 9780231100984

Tiffney BH. 1990. The collection and study of dispersed angiosperm fruits and seeds. *Palaeos* **5**: 499-519. DOI: <http://dx.doi.org/10.2307/3514859>

Tiffney BH, Manchester SR. 2001. The use of geological and paleontological evidence in evaluating plant phylogeographic hypotheses in the Northern Hemisphere Tertiary. *International Journal of Plant Science* **162**: S3-S17 DOI: <https://doi.org/10.1086/323880>

Upchurch GR Jr, Dilcher DL. 1990. Cenomanian angiosperm leaf megafossils, Dakota Formation, Rose Creek locality, Jefferson County, southeastern Nebraska. *United States Geological Survey Professional Paper* **1915**: 1-55. DOI: <https://doi.org/10.3133/b1915>

Vachrameev VA. 1952. Stratigrafiya i iskopaemaya flora melovyh otlozenij zapadnogo Kazahstana. *Regional'naya stratigrafiya SSSR* **1**:1-340.

Venkatachala BS, Kar RK. 1969. Palynology of the Tertiary sediments of Kutch-1. Spores and pollen from Borehole No.14. *The Palaeobotanist* **17**: 157-178.

Wang YF, Li Fls CS, Li ZY, DZ Fu. 2001. *Wuyunanthus* gen. nov., a flower of Celastraceae from the Paleocene of north-east China. *Botanical Journal of the Linnean Society* **136**: 323-327. DOI: <https://doi.org/10.1111/j.1095-8339.2001.tb00576.x>

Wheeler EA, Srivastava R, Manchester SR, Baas P. 2017. Surprisingly modern latest Cretaceous-earliest Paleocene woods of India. *International Association of Wood Anatomists Journal* **38**: 456-542. DOI: <https://doi.org/10.1163/22941932-20170174>

Wiens JJ. 2003. Missing data, incomplete taxa, and phylogenetic accuracy. *Systematic Biology* **52**: 528-538. DOI: <https://doi.org/10.1080/10635150390218330>

Wiens JJ. 2004. The role of morphological data in phylogeny reconstruction. *Systematic Biology* **53**: 653-61. DOI: <https://doi.org/10.1080/10635150490472959>

Wolfe JA. 1975. Some aspects of plant geography of the Northern Hemisphere during the late Cretaceous and Tertiary. *Annals of the Missouri Botanical Garden* **62**: 264-279. DOI: <https://doi.org/10.2307/2395198>

Wolfe JA. 1977. Paleogene floras from the Gulf of Alaska region. *United States Geological Survey Professional Paper* **997**: 1-108. DOI: <https://doi.org/10.3133/pp997>

Zhang LB, Simmons MP. 2006. Phylogeny and delimita-

tion of the Celastrales inferred from nuclear and plastid genes. *Systematic Botany* **31**, 122-137. DOI: <https://doi.org/10.1600/036364406775971778>

Zhang X, Zhang Z, Stützel T. 2012. Aril development in Celastraceae. *Feddes Repertorium* **122**: 445-455. DOI: <https://doi.org/10.1002/fedr.201200007>

Zhang X, Zhang Z, Stützel T. 2014. Ontogeny of the ovule and seed wing in *Catha edulis* (Vahl) Endl.

(Celastraceae). *Flora* **209**: 179-184. DOI: <https://doi.org/10.1016/j.flora.2014.01.002>

Zhu YX, Lei FW, Tong L, Mu XY, Wen J, Zhang ZX. 2020. Animal-mediated long-distance dispersals and migrations shaping the intercontinental disjunctions of *Celastrus* (Celastraceae) among five continents. *Journal of Systematics and Evolution* **58**: 945-957. DOI: <https://doi.org/10.1111/jse.12661>

Associate editor: Silvia Aguilar Rodríguez

Author contributions: ALHD, wrote manuscript and compilation of the database; SLGA; SRSCF, coordinated, designed the research, and revised manuscript.