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SISTEMÁTICA

ANÁLISIS FILOGENÉTICO DE UNA ESPECIE FÓSIL DE *SALACIA* L. (SALACIOIDEAE-CELASTRACEAE) Y SUS IMPLICACIONES BIOGEOGRÁFICAS EN EL ÁMBAR DE CHIAPAS, MÉXICO

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Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 0**8 de marzo de 2021** se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la estudiante **HERNÁNDEZ DAMIÁN ANA LILIA** con número de cuenta **303281072** con la tesis titulada **"ANÁLISIS FILOGENÉTICO DE UNA ESPECIE FÓSIL DE *SALACIA* L. (SALACIOIDEAE-CELASTRACEAE) Y SUS IMPLICACIONES BIOGEOGRÁFICAS EN EL ÁMBAR DE CHIAPAS, MÉXICO",** realizada bajo la dirección del **DR. SERGIO RAFAEL SILVESTRE CEVALLOS FERRIZ**, quedando integrado de la siguiente manera:

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Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
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CAPÍTULO II. UNA NUEVA PLANTA FÓSIL EN EL ÁMBAR DE CHIAPAS, MÉXICO

RESUMEN

Celastraceae *sensu lato* es una familia subcosmopolita constituida por alrededor de 98 géneros y 1211 especies, siendo más diversa en los trópicos y subtrópicos con pocas especies en zonas templadas. La familia está dividida en cuatro subfamilias, incluida Salacioideae; en esta se incluyen seis géneros: *Cheiloclinium* (13 especies de Centro y Sur América), *Peritassa* (19 especies de Centro y Sur América), *Salacighia* (2 especies de África), *Thyrosalacia* (4 especies de África), *Tontelea* (17 especies de Centro y Sur de América) y *Salacia* (200 especies trópicos del Viejo y Nuevo Mundo). En Salacioideae se ha reconocido una correspondencia entre el androceo y gineceo dímero en especies que actualmente crecen en el Paleotropico, y más recientemente en una especie extinta preservada en el ámbar del Mioceno de México: *Salacia lombardii*. Los depósitos de ámbar de Simojovel de Allende, Chiapas han sido poco estudiados en comparación con otros depósitos de ámbar que existen en el mundo. Hasta el momento, la evidencia paleobotánica de la zona es relativamente escasa, sin embargo, las angiospermas identificadas sugieren que existe una relación cercana entre los elementos florísticos que se desarrollaban hace ca. 23-15 Ma del sur de México con taxones actuales que crecen en esta misma zona, desafortunadamente estas hipótesis de relación no han sido evaluadas en un contexto filogenético. Debido a lo anteriormente expuesto, este trabajo explora la posición filogenética de *Salacia lombardii* usando una matriz combinada de datos moleculares y morfológicos generados previamente de 6 géneros y 28 especies de Salacioideae, mediante el criterio de parsimonia. La topología del árbol de consenso estricto recuperada aquí es consistente con la de análisis previos para Salacioideae al ser recuperado un clado Neotropical. La posición de *S. lombardii* en el árbol consenso es ambigua y causa una politomía entre las especies del Paleotrópico. Hay tres posiciones alternativas del fósil: 1) como hermana de Salacioideae, sustentada por pétalos orbiculares y estilo deltoide; 2) como hermana de *Thyrosalacia*, sustentada por la forma triangular de la antera y el plano de dehiscencia de la antera oblicua; y 3) como parte del clado de especies con dos estambres, sustentada por dos estambres más estaminoides, estigmas bilobados, un óvulo por lóculo. La hipótesis más parsimoniosa sustenta la idea de que la condición de dos estambres posiblemente tuvo un solo origen dentro Salacioideae. Finalmente, con base en la posición filogenética de *Salacia lombardii* se concluye que su presencia en el ámbar mexicano representa un elemento Paleotropical, sugiriendo que en el pasado los taxones

con dos estambres tenían una distribución circumtropical y, que debido a la disminución de la temperatura durante el Mioceno las plantas neotropicales se extinguieron en dicha región.

ABSTRACT

Celastraceae sensu lato is a subcosmopolitan family with around 98 genera and 1211 species, and it is more diverse in the tropics and subtropics than temperate zones. The family is divided into four subfamilies, including Salacioideae. It includes six genera: *Cheiloclinium* (13 species from Central and South America), *Peritassa* (19 species from Central and South America), *Salacighia* (2 species from Africa), *Thyrosalacia* (4 species from Africa), *Tontelea* (17 species from Central and South America) and *Salacia* (200 species from the Old and New World tropics). In Salacioideae, a correspondence between a dimerous androecium and gynoecium has been recognized in species that currently growing in the Paleotropic, and more recently in an extinct species preserved in the amber of the Miocene of Mexico: *Salacia lombardii*. The amber deposits of Simojovel de Allende, Chiapas have been little studied in comparison with other amber deposits that exist in the world. So far, the paleobotanical evidence for the area is relatively scarce, however, the angiosperms identified thus far suggest that there is a close relationship between the floristic elements that developed ca. 23-15 Ma from southern Mexico with current taxa growing in the area, unfortunately these relationship hypotheses have not been evaluated thought the phylogenetic context. Due to the above, this work explores the phylogenetic position of *Salacia lombardii* using a combined matrix of molecular and morphological data previously generated from 6 genera and 28 Salacioideae species, using the parsimony criterion. The strict consensus tree topology reported here is consistent with that of previous analyzes for Salacioideae because Neotropical clade was recovered. The position of *S. lombardii* in the consensus tree is ambiguous and causes polytomy among Paleotropic species. There are only three alternative positions of the fossil: 1) as sister to Salacioideae, supported by orbicular petals; 2) as sister to *Thyrosalacia*, supported by the triangular shape of the anther and the plane dehiscence of the oblique anther; and 3) as part of the clade of species with two stamens, supported by two stamen plus staminoids, bilobed stigmas, one ovule per loculum. The most parsimonious hypothesis supports the idea that the condition two stamens possibly had a single origin within Salacioideae. Finally, based on the phylogenetic position of *Salacia lombardii*, its presence in Mexican amber represents a Paleotropical element, suggesting that in the past the taxa with two stamens had a circumtropical distribution and, due to the decrease in temperature during Neotropical plants became extinct in this region in the Miocene.

I. INTRODUCCIÓN

I.I Antecedentes

Celastraceae R. Br.

Celastraceae *sensu lato* (s.l.) es una familia subcosmopolita constituida por alrededor de 98 géneros y 1211 especies, siendo más diversa en los trópicos y subtrópicos con pocas especies en zonas templadas (Simmons, 2004). Los miembros de Celastraceae exhiben una substancial variación en estambres, frutos y caracteres de la semilla, los cuales han sido usados tradicionalmente para subdividirla (Simmons & Hedin, 1999), pues históricamente existía discrepancia en el reconocimiento de Celastraceae y Hippocrateaceae como una sola familia (e.g., Bentham & Hooker, 1862; Baillon, 1880; Robson, 1965; Dahlgren, 1983; Takhtajan, 1997) o como dos familias separadas en los sistemas de clasificación tradicional (e.g., Candolle de, 1825; Miers, 1872; Hutchinson, 1967; Loesener, 1942; Cronquist, 1981), ésta última constituida típicamente por dos géneros: *Hippocratea* y *Salacia* (Miers, 1872; Peyritsch, 1878; Smith, 1940).

Los caracteres diagnósticos que han sido usados típicamente para distinguir a Hippocrateaceae de Celastraceae son: 3 estambres (raramente 2-5) vs 4 o 5 (raramente 10), filamentos insertos sobre el disco vs por debajo del margen del disco, filamentos connados y recurvados hacia la base vs libres y frecuentemente incurvados, así como semillas no albuminosas vs albuminosas (Cronquist, 1981).

La inclusión de Hippocrataceae dentro de Celastraceae se fundamenta formalmente por medio de un análisis filogenético usando caracteres morfológicos (Simmons & Hedin, 1999). Posteriormente, se propone la más reciente clasificación de la familia sustentada por subsecuentes análisis filogenéticos (e.g., Savolainen *et al.,* 1997; Simmons *et al.,* 2001a, b; Coughenour *et al.,* 2010, 2011), en la cual se reconocen tres subfamilias monofiléticas: Hippocrateoideae, Salacioideae y Stackhouioideae, diagnosticables morfológicamente y derivadas independientemente de Celastroideae que es parafilética (Simmons, 2004).

Celastraceae s.l. es un grupo bien soportado con base en su estructura floral, generalmente se presentan flores bisexuales, con un disco, 5 o menos estambres y un ovario más o menos inmerso, no obstante, este patrón general se ve modificado en el linaje [veáse:

http://www.mobot.org/mobot/research/apweb/]. Debido a que el número de partes de los verticilos florales o merismo, tiende a ser más o menos constante en algunos grupos de angiospermas (Kümpers, 2016), se ha considerado como un fenómeno llamativo en Celastraceae, la presencia de flores con un perianto pentámero y un androceo trímero, típico de Hippocrateoideae y Salacioideae (Ronse De Craene, 2010). Cuando existen cambios en el merismo, comúnmente se afectan a todos los órganos de la flor de la misma manera, aunque no siempre es así (Ronse De Craene 2013, 2016). Tal es el caso de Salacioideae, donde se mantiene la estructura pentámera del perianto, pero el número de estambres varía entre cinco, tres y dos (Hallé, 1986; Simmons, 2004; Matthews & Endress, 2005; Coughenour *et al.*, 2010).

Salacioideae

Salacioideae es una subfamilia originaria del Viejo Mundo que incluye alrededor de 255-265 especies clasificadas en seis géneros: *Cheiloclinium* Miers (13 especies de Centro y Sur América), *Peritassa* Miers (19 especies de Centro y Sur América), *Salacighia* Loes. (2 especies de África), *Thyrosalacia* Loes. (4 especies de África), *Tontelea* Aubl. (17 especies de Centro y Sur de América) y *Salacia* L. (200 especies trópicos del Viejo y Nuevo Mundo) (Coughenour *et al.*, 2010, 2011).

Coughenour *et al.* (2010) infieren la filogenia de Salacioideae usando datos morfológicos y moleculares (matK, trnL-F, ITS y 26S). Con base en este estudio se establecen como sinapormorfías del grupo la presencia de bayas con pulpa mucilaginosa interpretadas como un arilo, y como caracteres diagnósticos la presencia de flores bisexuales, perianto pentámero, disco extraestaminal y generalmente tres estambres. Este mismo estudio, es usado como marco de referencia para inferir el patrón evolutivo del número de estambres en el linaje, interpretando como un carácter ancestral la presencia de tres estambres y dos como el derivado, aunque dicho estudio prácticamente se encuentra sesgado a especies con tres estambres.

***Salacia* L.**

Salacia es un género heterogéneo con alrededor de 400 especies descritas (Hedin, 1999) y cerca de 200 aceptadas (Hedin, 1999; Simmons & Hedin; 1999; Coughenour *et al.*, 2010; Lombardi, 2014), las cuales se distribuyen en bosques húmedos, matorrales y pastizales del Paleo y Neotrópico (Simmons 2001a, 2004). El número de especies de *Salacia* es controversial (Ding Hou, 1962; Lombardi, 2009), debido a cambios nomenclaturales y al reporte de nuevas especies (e.g., Gosline & Cheek, 2014, Kanjiraparambil *et al.,* 2015). Ding Hou (1964) da un estimado de 29 especies para el Nuevo Mundo, 90 en África y 29 en Malasia, en una revisión de la base de datos de The Plant List (2013) y Catalogue of Life (Roskov *et al.*, 2015) existen alrededor de 134 especies aceptadas formalmente.

Salacia incluye lianas o trepadoras, raramente árboles o arbustos, glabros o glabarescentes. Hojas opuestas o subopuestas, raramente alternas; enteras, crenadas o serradas. Inflorescencia axilar o cauliflora, tirsoide, cimosa o fasciculada. Flores bisexuales, pentámeras; disco carnoso, anular, margen sobresaliente, entero o lobado, extraestaminal; androginóforo o ausente; estambres (2) 3; anteras longitudinales u oblicuas, dehiscencia transversal extrorsa o apical; ovario 2(3) lóculos; óvulos 2-9 por lóculo. Bayas esferoides, oblongas o fusiformes, coriáceas; semillas de 1-∞, oblongas, agudas. Exalbuminosa, rodeado por arilos mucilaginosos (Simmons, 2004; Lombardi, 2014).

El género *Salacia* fue descrito por Linneo (Mant. 159. 1767) basado en la especie tipo *S. chinesis* L. (Mant. 293. 1767). De acuerdo con la descripción original de *S. chinensis,* ésta se caracterizada por la presencia de hojas alternas, inflorescencias axilares y fasciculadas, flores con cinco sépalos y pétalos, así como tres estambres, sin embargo, estos caracteres son contrastantes con los diagnósticos del género (Smith, 1940).

Las especies de *Salacia* del Paleo y Neotrópico han sido tratadas por distintos autores (e.g., Loesener, 1910, 1942; Hallé, 1986, 1990; Wilczek, 1960; Ding Hou, 1964; Robson, 1966; Miers, 1872; Peyritsch, 1878; Smith, 1940, 1941; Dodson & Robyns, 1965; Lombardi 2007, 2009, 2014; Lombardi & Gonzalez, 2017). Dentro de los tratamientos taxonómicos para las especies de África destaca el trabajo de Loesener (1910) quien, divide al grupo en dos subgéneros: *Eusalacia* (dividido en 11 grupos) y *Dimerocarpium*. Posteriormente, Hallé (1986, 1990) reconoce diez grupos con base en los siguientes caracteres: la presencia/ausencia de resina (expresadas como hilos translúcidos), el ángulo y confluencia de las tecas de las anteras, estructura de las inflorescencias y el número de lóculos en el ovario. Éste mismo autor, sugiere que las especies de

Salacia que presentan flores de un tamaño considerable, perianto variable, anteras con líneas de dehiscencia cerca de la posición longitudinal y, elongación del tejido conectivo en las anteras podrían ser consideradas como especies ancestrales; mientras que las especies sin látex con flores pequeñas y con dos ciclos del perianto diferenciado y estables (e.g., *S. chinensis*).

El reconocimiento de *Salacia* en el Nuevo Mundo fue debatible (Miers, 1872), sin embargo, Peyritsch (1878) y Smith (1940) mantienen el nombre de *Salacia*. Smith (1940) incluye en el género a otros descritos para América por Miers (1872): *Raddisia, Raddia* y *Thermophila*, con base en la presencia de un disco anular-pulvinado, así como anteras con dehiscencia apical oblicua.

Para las especies de *Salacia* en América, Peyritsch (1878) y Smith (1940) proponen dividir a *Salacia* en secciones (6) y grupos (9) respectivamente. Posteriormente Hedin (1999) realiza un análisis filogenético de *Salacia* a través de un análisis de parsimonia con caracteres morfológicos, en dicho estudio soporta la monofília de 4 de los grupos propuestos por Smith (1940): Arboreae, Acreanae, Multiflorae, Crassifoliae.

Devipriya *et al.* (2015) usando datos moleculares (ITS) soportan la parafilia de *Salacia* y, señalan que la divergencia de *Salacia* en el Nuevo Mundo implicaría necesariamente hacer la separación del grupo a nivel genérico, como lo señalala Coughenour *et al.* (2010), ya que hasta el momento tampoco ha sido posible el reconocimiento de caracteres morfológicos que permitan separación de las especies del Paleo y Neotrópico.

De acuerdo con Villaseñor (2004) existen en México cuatro especies de *Salacia*, que se distribuyen en los Estados de Veracruz (Castillo-Campos & Medina-Abreo, 2005; Lombardi, 2014), Tabasco (West, 1966; Lombardi, 2014), Campeche (Dias *et al.,* 2011), Chiapas (Breedlove, 1986) y Oaxaca (Lombardi, 2014) aunque de manera formal sólo se reconoce a *Salacia cordata* (Miers) Mennega y *S. impresifolia* (Miers) A.C.Sm.

Ámbar de Chiapas, México

El término ámbar hace referencia a una gran variedad de resinas fosilizadas, sin embargo, su uso se restringe a una mezcla liposoluble de terpenoides o compuestos fenólicos, características que ayudan a distinguirlo de las gomas, mucílagos, aceites, látex y otros exudados de las plantas (Langenheim, 2003). Cuando la resina fue producida por la planta, su consistencia pegajosa le permitió funcionar como una matriz para fosilizar organismos completos o parte de ellos (Taylor *et al.*, 2009).

La formación del ámbar pasa por tres estados: el primero es la generación de resina pegajosa y viscosa, el segundo es su transformación a copal, el cual se caracteriza por ser relativamente suave, aromático, pero no flexible y, el tercero la formación del ámbar propiamente dicho. Existe confusión con relación a la diferencia entre el copal y el ámbar, marcar el límite entre ambos es complicado, aunque se presume que el ámbar es difícil de fundirse a temperaturas menores a los 250°C y es menos maleable que el copal (Poinar, 1998).

El origen botánico del ámbar de Simojovel de Allende fue determinado en un principio al comparar el espectro infrarrojo del ámbar con el de resinas de varias plantas actuales, concluyendo que el ámbar fue producido por plantas del género *Hymenaea* (Fabaceae) (Langenheim & Beck, 1965). Posteriormente, dos especies extintas se identificaron con base en estructuras aisladas como las productoras del ámbar en Chiapas; *H. mexicana* (Poinar & Brown, 2002) e *H. allendis* (Calvillo-Canadell *et al.*, 2010). La resina de estas plantas pudo acumularse en el suelo alrededor de la base del árbol en grandes cantidades, y desde ahí transportarse a un ambiente de depósito (Veiga-Crespo *et al.*, 2007).

El ámbar del área de Simojovel se encuentra en tres formaciones litoestratigráficas: Formación la Quinta o Simojovel, Esquisto Mazantico y Arenisca Balumtum (de base a techo), las cuales forman una secuencia compuesta principalmente de arenisca calcárea y limo con capas de lignita. Estas unidades están expuestas en la Sierra Madre del Sur en Chiapas, desde el margen norte de la depresión central (Totolapa) a Palenque, cerca de la Costa del Golfo de Tabasco, y fueron determinadas como parte proyectos de la Universidad de California (Licari, 1960; Allison, 1967). El nombre de Formación La Quinta fue propuesto en sustitución de Formación Simojovel, unidad que hace referencia a 884 m de una secuencia que se extiende al extremo suroeste del sinclinal La Esperanza y al suroeste del sinclinal de Simojovel. La Quinta es la unidad estratigráfica más característica del área y, está subdividida en tres miembros. El Miembro Camino Carretero es la parte inferior de la formación, y se caracteriza por intercalaciones de arenisca, arcilla y lutitas, de las cuales la mayoría son areniscas calcáreas que incluyen foraminíferos, corales escleractínidos, moluscos y equinoideos. El segundo, el Miembro Caliza Florida se distingue por tener limolitas y una alternancia heterogénea de estratos de areniscas que, en una parte son calcáreas y en otras arcillas y lutitas, así mismo se encuentran capas delgadas de lignitas. Y finalmente, el Miembro Finca Carmito que se compone por finos sedimentos clásticos terrígenos y cuarzos, así como estratos de caliza con equinoideos (Licari, 1960; Allison, 1967).

El esquema bioestratigráfico de la Formación La Quinta está basado en foraminíferos y polen. El primero, contempla un lapso temporal del Oligoceno tardío definido por las zonas de *Globigerina ciperoensis* y *Globorotalia kugleri* (Tomasini-Ortiz & Martínez-Hernández, 1984). Este estudio, es apoyado con datos palinológicos de la misma unidad, en donde se reconoce la biozona acme con la abundancia de *Pelliceria* sp. (Veiga-Crespo *et al.*, 2007). En los intervalos de las zonas N3 y N4 establecidos con foraminíferos usando nanoplacton se sugiere una edad numérica de 26-22.5 Ma (M. Benami, per. comm., 2004; Gómez-Bravo, 2005).

La bioestratigrafía de corales en la cima del Miembro Camino Carretero y la Finca, sugiere una edad de Mioceno temprano, sin embargo, este esquema no fue establecido explícitamente, resultando en una interpretación temporal de toda la Formación que va del Oligoceno tardío-Mioceno temprano (Frost & Langenheim, 1974). Recientemente, en el Miembro Finca Carmito se establecieron rangos bioestratigráficos usando nanoplacton. Con la presencia de *Sthenolithus disbelemnos* y *S. tintinnabalum* se reconoció la biozona N2, que sugiere una edad del Mioceno temprano, lo anterior es apoyado con la datación de conchas de gasterópodos usando 87Sr/86Sr sugiriendo una edad de 22. 8 Ma (Serrano-Sánchez *et al.*, 2015).

La Unidad Esquisto Mazantico fue definida con 310 m de arenisca masiva, que va de gris obscuro a negro, contiene restos de plantas, gasterópodos, bivalvos y crustáceos. El estudio bioestratigráfico de Esquisto Mazantico se estableció con foraminíferos bentónicos, identificando la biozona N8-N9 con Siphogenerina transversa que indica un lapso temporal que abarca del Mioceno medio a temprano, lo anterior es soportado con la datación de conchas de *Turbinella maya* con 87Sr/86Sr estableciendo una edad de 23 Ma (Vega-Vera *et al.*, 2009). El Esquisto Mazantico puede ser estratigráficamente correlacionado con el ámbar de República Dominicana, debido a la presencia de lechos de lignita, un similar registro fósil de insectos (40%) y un origen botánico similar por especies extintas de *Hymenaea*, estableciéndose una edad de 20-15 Ma (Solórzano-Kraemer, 2007).

La Arenisca Balumtum es la unidad más alta y ocasionalmente lleva ámbar. La unidad fue definida con un grosor aproximado de 760 m de arenisca gris masiva en donde se encuentran gasterópodos, bivalvos y crustáceos (Langenheim, 1995). Se ha señalado que Balumtum podría ser de la misma edad estratigráfica que el Esquisto Mazantico, sin embargo, no existe evidencia suficiente que apoye esta propuesta (Solórzano-Kraemer, 2010)

Tomando en cuenta lo anterior con respecto a la aproximación de la edad del ámbar interpretada como Mioceno medio-inferior, y para entender el medio en el que vivieron las comunidades antiguas fosilizadas es importante considerar estudios paleontológicos y geológicos en la zona. Por ejemplo, un estudio palinológico al norte de Chiapas con base en muestras de rocas del Mioceno inferior-medio, registra la abundancia de Junglandaceae, seguido de *Picea*, *Quercus*, *Pinus*, Melastomataceae y Cyatheaceae (Pteridophyta), sugiriendo que en el pasado debió prevalecer un clima fresco y muy húmedo en la zona (Palacios & Rzedowski, 1993). Otros estudios complementan esta información en rocas de la Formación la Quinta estableciendo que el polen más común es de *Rhizophora* seguido de *Phyllocladus*, *Pelliciera* y *Engelhardtia* (Langenheim *et al.*, 1967; Graham, 1999).

Los registros paleontológicos propios del ámbar de Simojovel están representados con más del 70% por reportes de animales y alrededor del 20% son plantas (Avendaño-Gil *et al.*, 2012). La fauna mejor representada en el ámbar es el grupo de los artrópodos (e.g., García-Villafuerte & Penney, 2003; Solórzano-Kraemer, 2007; Riquelme *et al.*, 2021), aunque muchos especímenes todavía requieren una descripción taxonómica formal, entre los cuales destacan Diptera e Hymenoptera. También se han reportado miriápodos y crustáceos, como cochinillas, anfípodos, ostrácodos, copépodos, tanaideos y cangrejos, los cuales sugieren un ambiente estuarino similar a las comunidades de manglares modernos (Serrano-Sánchez *et al.*, 2016). Otras inclusiones reportadas son de pequeños vertebrados como una lagartija (*Anolis electrum*) (Castañeda *et al.*, 2014).

Dentro del registro de plantas fósiles se encuentran representados distintos grupos tal es el caso de briofitas *Lejeunea paleomexicana* (Von Riclef, 1984), así como angiospermas identificadas a través de fragmentos de hojas como *Acacia* spp. (Miranda, 1963), así como de flores tal es el caso de *Tapirira durhamii* (Miranda, 1963), *Socrotea brownii* (Poinar, 2002), *Colpothrinax chiapensis* (Chambers *et al.*, 2012), *Swietenia miocenica* (Castañeda-Posadas & Cevallos-Ferriz, 2007) y *Gouania miocenica* (Hernández-Hernández & Castañeda-Posadas, 2018).

El registro fósil de plantas y animales del Mioceno en México sugiere que, durante este tiempo comienza a reconocerse una mayor similitud morfológica entre taxones fósiles y actuales (Cevallos-Ferriz & González-Torres, 2006; Cevallos-Ferriz *et al.*, 2012; Solorzano-Kraemer *et al.*, 2015). Es a partir de este momento que se puede establecer la pauta para debatir el inicio del establecimiento de las comunidades biológicas como actualmente las conocemos.

La correlación biogeográfica establecida entre los fósiles con sus representantes actuales sugiere una relación con el sur de América y el Caribe, como bien lo sugiere el registro de ostrácodos (Perrilliat *et al.*, 2010), insectos, vertebrados y plantas. Sin embargo, existen reportes paleontológicos que sugieren afinidad con el Paleotrópico como es el caso de *Hymenaea mexicana* (Poinar & Brown, 2002) y *Supella* (Vršanský *et al.*, 2011).

El clima durante el Mioceno en tierras bajas del sur de la antigua América se ha interpretado similar al actual, considerándolo en general como tropical (Jaramillo *et al.*, 2006). Aunque la configuración de los continentes para ese momento era muy parecida a la de hoy, se dieron cambios importantes donde aún separados América del Norte y del Sur, se llevaba a cabo el movimiento del Bloque Chortis en el margen suroeste de la costa del Pacífico de México, el cual se ha reconstruido como una paleopenínsula que paulatinamente se extendía hacia el sur con una intensa actividad volcánica y tectónica (Cevallos-Ferriz *et al.*, 2012).

En este escenario se considera que las corrientes de aire caliente con humedad llegaban al centro, debido a la ausencia del Itsmo de Panamá; dichas corrientes provenían principalmente del proto-Golfo de México. Entendida así la fisiografía de la paleopenínsula durante el Mioceno de México, puede postularse que la porción sur de la incipiente Faja Volcánica Transmexicana presentaba condiciones climáticas cálido-húmedas (tropicales) hacia el sur y hacia el norte cálido subhúmedas (subtropicales) (Caballero-Rodríguez *et al.*, 2016).

Durante este período ocurrieron otros eventos geológicos en México, incluyendo la extensión de grandes provincias magmáticas como la Sierra Madre Occidental, la cual se orienta de N-S a lo largo de la costa del Pacífico expandiéndose hasta el Mioceno Inferior; así como el surgimiento de la Faja Volcánica Transmexicana. Esta última tiene una orientación en dirección E-W y divide a México en dos regiones: una región subtropical y seca hacia el norte y una región tropical y húmeda hacia el sur. Así mismo, el margen del Pacífico sur de México ha demostrado que éste fue expuesto a un intenso proceso de intemperismo y erosión (Ferrari *et al.,* 1999). En este escenario se ha señalado que en México el material ígneo acumulado y las nuevas cadenas montañosas, fueron los agentes causantes de la variación en altitud, abriendo y cerrando cuencas, provocando cambios en la hidrología. Por otro lado, en el lado sur de la paleopenínsula comenzaba a formarse la Sierra Madre del Sur, posiblemente como una continuación de los plegamientos de la Sierra Madre Oriental, llegando actualmente hasta Chiapas, estos procesos muy posiblemente controlaron la magnitud de las barreras naturales y las fuerzas selectivas que influyeron en la distribución de las plantas (Gómez-Tuena *et al.,* 2005).

Alcances y límites en la exploración de la posición filogenética de los fósiles

Los fósiles constituyen la única fuente de información física y directa para conocer la vida del pasado; sin embargo, debido a su inherente naturaleza fragmentaria su estudio resulta altamente problemático en comparación al de taxones actuales (Wiley, 1981), ya que en los fósiles se encuentra restringido el acceso a caracteres moleculares y otras fuentes de información, siendo la morfología la única información disponible para su estudio con un enfoque sistemático (Cracraft, 1981).

A pesar de esta limitante, en los últimos años se ha reconocido el doble valor del registro fósil por ser informativo, o bien corroborativo, de una variedad de hipótesis basadas en estudios comparativos de taxones actuales (Crepet, 2008; Martínez-Millán *et al.,* 2009). Sin embargo, para maximizar el valor de los fósiles es fundamental el cuidado con el que se lleva a cabo su tratamiento sistemático (Gandolfo, 2008; Crepet, 2008; Martínez-Millán *et al.,* 2009).

Las flores fósiles suelen tener un alto valor sistemático, por lo que son usadas preferentemente para la identificación, ya que con frecuencia presentan caracteres diagnósticos, atributos que han permitido reconocerlas como el mejor indicador de familias en el registro fósil de angiospermas (Doyle, 2012), aunque existen registros que son cuestionables, tal es el caso de *Wuyunanthus hexapetalus* del Paleocene de China (Wang *et al.,* 2001), un miembro existinto de la familia Celastraceae que, aunque en apariencia general puede ubicarse dentro de la familia por ser una flor bisexual con un disco conspicuo, su inclusión dentro de la familia es cuestionable, debido a su merosidad o número de partes en los verticilios florales (6 vs 4-5; Friis *et al.*, 2011).

El requerimiento del estudio de fósiles con un enfoque filogenético ha sido señalado particularmente para la familia Celastraceae por Bacon *et al.* (2016). La mayor parte de los fósiles de la familia se encuentran representados por hojas, las cuales fueron descritas a finales de 1800 e inicios de 1900 (e.g., Göppert, 1853; Saporta, 1865; Berry, 1911; Knowlton, 1919), varios de estos con descripciones sin detalle, ausencia de caracteres diagnósticos, así como una pobre preservación haciendo controversial su asignación taxonómica (Bacon *et al.*, 2016).

El método filogenético constituye una técnica clara y repetible para la identificación de taxones fósiles (Crepet, 2008), a través de éste es posible analizar simultáneamente a los fósiles con sus potenciales parientes vivos más cercanos estableciendo hipótesis de relación entre ellos (Gandolfo *et al.,* 2004; Crepet, 2008; Sauquet *et al.*, 2012).

II. OBJETIVOS

Debido a lo anteriormente expuesto este trabajo tiene como objetivos 1) El reconocer y evaluar el registro fósil de Celastraceae, 2) Determinar una flor incluida en ámbar del Mioceno de Simojovel de Allende, Chiapas, 3) Explorar la utilidad de caracteres morfológicos en la postulación de hipótesis de relación entre una planta fósil de *Salacia* (Salacioidade-Celastraceae) del Mioceno del sur de México, y discutir sus implicaciones biogeográficas a través del contexto filogenético.

Los objetivos de la tesis son abordados en tres capítulos los cuales se presentan en formato de artículos de investigación separados, estos incluyen una introducción, metodología, resultados, discusión y conclusiones. Actualmente uno de los tres capítulos está publicado, un segundo esta aceptado y uno en preparación para ser sometido a publicación.

Capítulo I. Expone una revisión del estado del arte del registro fósil de Celastraceae, así como el establecimiento una lista de registros que permiten identificarlos como potenciales puntos de calibración para reloj molecular. Estos registros cumplen una serie de características como son: su relación con taxones actuales de la familia, el reconocimiento del carácter o de un conjunto de caracteres que permiten asignarlo y/o compararlo con el grupo, la edad geológica y su ubicación geográfica, así como datos de la institución de repositorio. Este trabajo permite reconocer y evaluar los alcances y límites del registro fósil de Celastraceae.

Capítulo II. En esta parte se presenta la determinación taxonómica de una especie extinta de *Salacia* Salacioideae (Celastraceae) identificada a través de una flor incluida en ámbar. Este registro se suma al registro taxonómico de plantas del ámbar de Chiapas, México el cual es relativamente escaso y poco estudiado. La identificación de esta planta extinta constituye un registro comparable cercanamente con especies de *Salacia* que actualmente se desarrollan en el Neotrópico y Paleotrópico.

Capítulo III. En capítulo se expone la exploración de la posición filogenética de *Salacia lombardii* (Salacioideae-Celastraceae) del Mioceno del sur de México con sus potenciales parientes vivos más cercanos. A través de un análisis filogenético se reconoce una relación cercana entre el fósil y especies de *Salacia* que actualmente crecen en el Paleotrópico. El contexto filogenético permite la discusión de las implicaciones biogeográficas en el ámbar de Simojovel de Allende, Chiapas.

III. METODOLOGÍA GENERAL

El método general de esta investigación para el estudio de una especie extinta de *Salacia* (Salacioideae-Celastraceae) y su implación biogeográfica en el ámbar de Simojovel de Allende, Chiapas, México se basó en tres ejes principales que se interrelacionan entre si: 1) Revisión bibliográfica y bases de datos, 2) Trabajo de laboratorio y 3) Acceso a colecciones biológicas y trabajo de gabinete.

1. Revisión bibliográfica y base de datos

Partiendo de una revisión bibliográfica exhaustiva de fósiles asignados y/o comparados a Celastraceae que incluyo la consulta especializada de revistas, libros y paleofloras, que se reflejó en la recopilación de protólogos e imágenes de los tipos examinados tanto en bases de datos. Del mismo modo se hizo la consulta de bases de datos como The PaleoBiology DataBase, GBIF-Infraestructura Mundial de Información en Biodiversidad, Biodiversity Heritage Library BHL, Palaeobotanical Repository@BSIP y TreeBase.

A través de la información compilada se llevó acabo la identificación y reconocimiento de los taxones fósiles de Celastraceae, permitiendo así el análisis morfológico comparativo de la flor fósil del Mioceno de Simojovel de Allende, Chiapas.

2. Acceso a Colecciones biológicas

La revisión bibliográfica permitió establecer el muestreo de material de comparación del fósil el cual fue obtenido en el Herbario Nacional de México (MEXU). Del mismo modo, el trabajo comparativo se sustentó a través de fotografías de alta resolución disponibles del JSTOR Global Plants.

3. Trabajo de laboratorio

Para el análisis del material fósil se llevó acabo la prepación en el Laboratorio de Paleobotánica del Instituto de Geología. En relación con el material fósil y actual colectado del Herbario Nacional de México (MEXU) se obervó y fotografió con el microscopio estereoscópico Olympus SZH (equipado con una cámara lúcida) y un microscopio óptico Olympus BH-2 iluminadas con luz blanca transmitida. Las fotografías fueron tomadas con un cámara Olympus DP11 con filtros polarizados.

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CAPÍTULO I. INTRODUCTORIO

Fossil record of Celastraceae: evaluation and potential use in molecular calibrations**.**

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Fossil record of Celastraceae: evaluation and potential use in molecular calibrations

Registro fósil de Celastraceae: evaluación y uso potencial en calibraciones moleculares

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Running title:

Fossils candidates of Celastraceae as calibration points

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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 1211 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, Crepet 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 Appendix 1).

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. Manchester *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 linage (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 Appendix 2). 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 strictly morphological criteria (Dilcher 1974). *Celastrophyllum* (Göppert 1853) 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 craspedodromus and semicraspedodromus 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 intervascular pits; and parenchyma variable in type and quantity, that sometimes can have scattered or even absent (Metcalf & 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 *Ailanthoxylon* (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 intervascular 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 intervascular pits, thin apotracheal bands of parenchyma, uniseriate homocellular rays, non-septate thick-walled fibers, and intercellular canals. *Lophopetalumoxylon* 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, intervascular 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 *Elaeondrendron* 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 endoaperturate 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, Ding Hou 1969, Lobreae-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 crosslinked 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. scabratus* (Hoeken-Klinkenberg 1964, Salard-Cheboldaeff 1974, 1978, 1979) have been related to *Campylostemon*; however, similar tetrads are common in other families (Copenhaver 2005). *Retitricoporites* 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 (Lobreau-Callen & Caratini 1973). Additionally, Ramanujam (1966) assigned tricolporate pollen grains with elongate ectoapertures to *Hippocrateaceaedites*, 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.

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 annettae* and *S. lebrunii*) (Ding 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 *Wuyunanthus 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 Appendix 2), 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 comparison 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, *Wuyunanthus* 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 (Ding 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 *Celastrophyllum*, 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.

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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**
Baasia armendarisense	wood	73.5*	Upper Cretaceous	McRae Formation, USA	Estrada-Ruiz *et al.* 2012	*Cassine*
Cathispermum pulchrum	fruit and seeds	33.9	Eocene	London Clay, England	Reid & Chandler 1933	*Catha edulis*
Celastrus comparabilis	leaves	33.9	middle Eocene	Kushtaka Formation, USA	Wolfe 1977	*Celastrus*
Elaeodendroxylon sp.	wood	33.9	Eocene	Braunkohlen-Tagebau, Germany	Gottwald 1992	*Elaeodendron*
Hippocrateaceaedi-tes sp.	pollen	33.9	Eocene	Laki Basin, India	Venkatachala & Kar 1969	*Loseneriella*
Lobocyclas anomala	flower	23-30*	middle Oligocene-lower Miocene	República Dominicana	Chase & Poinar 2016	*Prionostemma, Hippocratea*
Maytenoxylon perforatum	wood	5.3	Miocene	Ituzaingó Formation, Argentina	Franco 2018	*Maytenus*
Salacia lombardii	flower	23-15*	middle-early Miocene	Simojovel de Allende, Mexico	Hernández-Damián *et al.* 2018	*Salacia*
Wuyunanthus hexapetalus	flower	66.0-61.6*	lower Paleocene	Wuyun, China	Wang *et al.* 2001	*Euonymus, Celastrus*

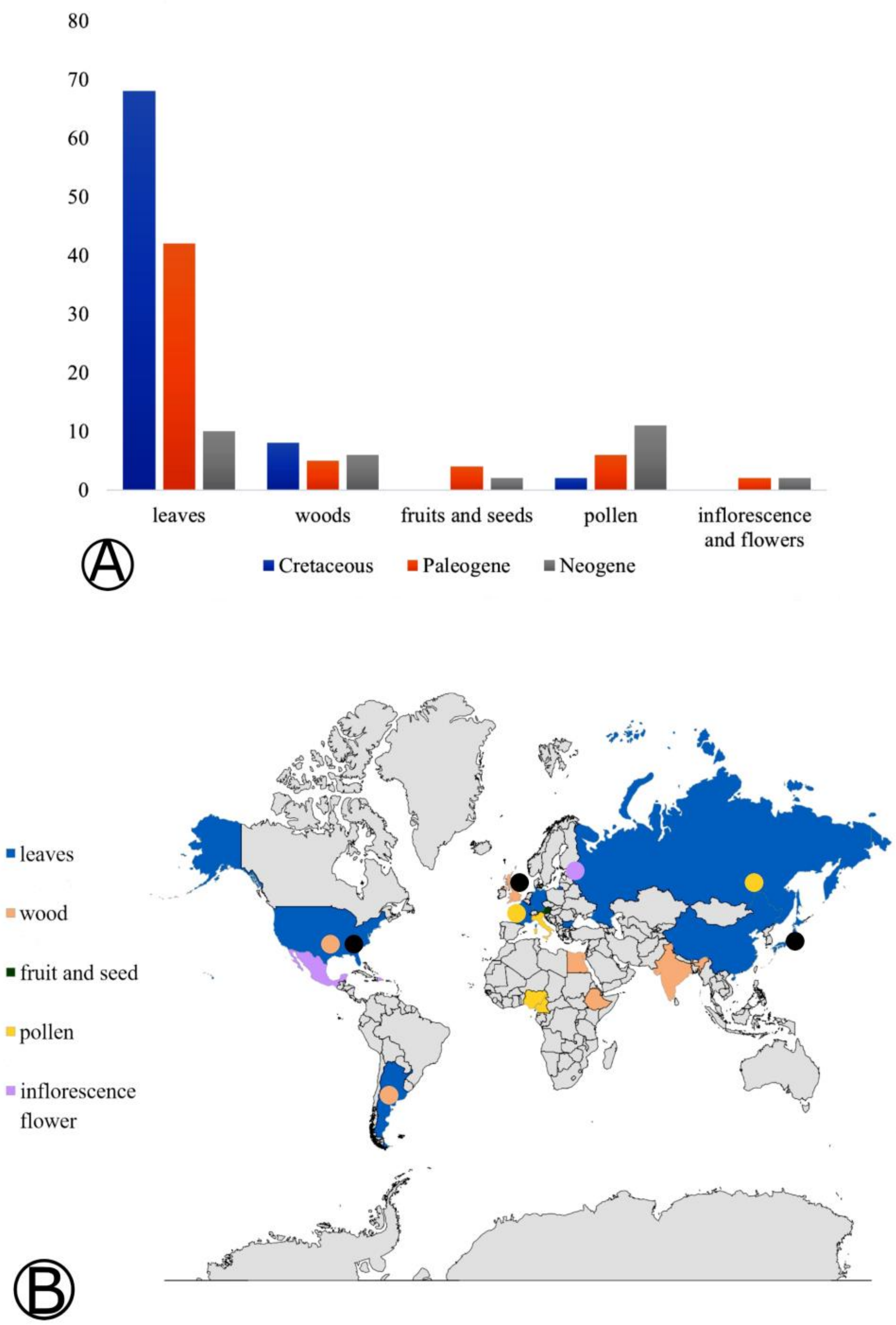
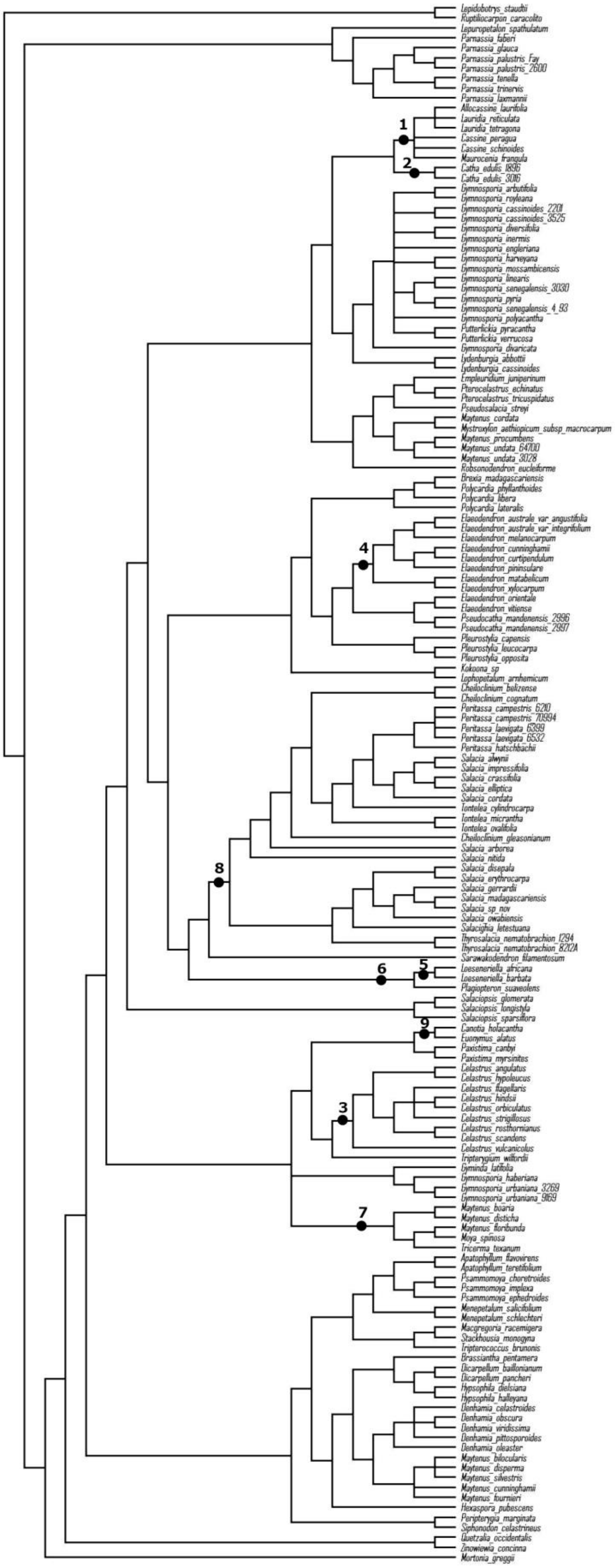


Figure 1. A. Abundance of leaves, woods, fruit-seeds, pollen, inflorescences, and flowers fossils assigned to Celastraceae by geologic time. B. Map showing the distribution of fossilized organs of plants identified as a member of Celastraceae.


Lepidobotrys_staudtii
Ruptiliocarpon_caracolito
Lepuropetalon_spathulatum
Parnassia_faberi
Parnassia_glauca
Parnassia_palustris_Fay
Parnassia_palustris_2600
Parnassia_tenella
Parnassia_trinervis
Parnassia_laxmannii
1
Allocassine_laurifolia
Lauridia_reticulata
Lauridia_tetragona
Cassine_peragua
Cassine_schinoides
Maurocenia_frangula
2
Catha_edulis_1896
Catha_edulis_3016
Gymnosporia_arbutifolia
Gymnosporia_royleana
Gymnosporia_cassinoides_2201
Gymnosporia_cassinoides_3525
Gymnosporia_diversifolia
Gymnosporia_inermis
Gymnosporia_engleriana
Gymnosporia_harveyana
Gymnosporia_mossambicensis
Gymnosporia_linearis
Gymnosporia_senegalensis_3030
Gymnosporia_pyria
Gymnosporia_senegalensis_4_93
Gymnosporia_polyacantha
Putterlickia_pyracantha
Putterlickia_verrucosa
Gymnosporia_divaricata
Lydenburgia_abbottii
Lydenburgia_cassinoides
Empleuridium_juniperinum
Pterocelastrus_echinatus
Pterocelastrus_tricuspidatus
Pseudosalacia_streyi
Maytenus_cordata
Mystroxylon_aethiopicum_subsp_macrocarpum
Maytenus_procumbens
Maytenus_undata_64700
Maytenus_undata_3028
Robsonodendron_eucleiforme
Brexia_madagascariensis
Polycardia_phyllanthoides
Polycardia_libera
Polycardia_lateralis
Elaeodendron_australe_var_angustifolia
Elaeodendron_australe_var_integrifolium
Elaeodendron_melanocarpum
4
Elaeodendron_cunninghamii
Elaeodendron_curtipendulum
Elaeodendron_pininsulare
Elaeodendron_matabelicum
Elaeodendron_xylocarpum
Elaeodendron_orientale
Elaeodendron_vitiense
Pseudocatha_mandenensis_2996
Pseudocatha_mandenensis_2997
Pleurostylia_capensis
Pleurostylia_leucocarpa
Pleurostylia_opposita
Kokoona_sp
Lophopetalum_arnhemicum
Cheiloclinium_belizense
Cheiloclinium_cognatum
Peritassa_campestris_6210
Peritassa_campestris_70994
Peritassa_laevigata_6399
Peritassa_laevigata_6532
Peritassa_hatschbachii
Salacia_alwynii
Salacia_impressifolia
Salacia_crassifolia
Salacia_elliptica
Salacia_cordata
Tontelea_cylindrocarpa
Tontelea_micrantha
Tontelea_ovalifolia
Cheiloclinium_gleasonianum
Salacia_arborea
Salacia_nitida
8
Salacia_disepala
Salacia_erythrocarpa
Salacia_gerrardii
Salacia_madagascariensis
Salacia_sp_nov
Salacia_owabiensis
Salacighia_letestuana
Thyrosalacia_nematobrachion_1294
Thyrosalacia_nematobrachion_8212A
Sarawakodendron_filamentosum
6
5
Loeseneriella_africana
Loeseneriella_barbata
Plagiopteron_suaveolens
Salaciopsis_glomerata
Salaciopsis_longistyla
Salaciopsis_sparsiflora
9
Canotia_holacantha
Euonymus_alatus
Paxistima_canbyi
Paxistima_myrsinites
Celastrus_angulatus
Celastrus_hypoleucus
Celastrus_flagellaris
Celastrus_hindsii
3
Celastrus_orbiculatus
Celastrus_strigillosus
Celastrus_rosthornianus
Celastrus_scandens
Celastrus_vulcanicolus
Tripterygium_wilfordii
Gyminda_latifolia
Gymnosporia_haberiana
Gymnosporia_urbaniana_3269
Gymnosporia_urbaniana_9169
Maytenus_boaria
7
Maytenus_disticha
Maytenus_floribunda
Moya_spinosa
Tricerma_texanum
Apatophyllum_flavovirens
Apatophyllum_teretifolium
Psammomoya_choretroides
Psammomoya_implexa
Psammomoya_ephedroides
Menepetalum_salicifolium
Menepetalum_schlechteri
Macgregoria_racemigera
Stackhousia_monogyna
Tripterococcus_brunonis
Brassiantha_pentamera
Dicarpellum_baillonianum
Dicarpellum_pancheri
Hypsophila_dielsiana
Hypsophila_halleyana
Denhamia_celastroides
Denhamia_obscura
Denhamia_viridissima
Denhamia_pittosporoides
Denhamia_oleaster
Maytenus_bilocularis
Maytenus_disperma
Maytenus_silvestris
Maytenus_cunninghamii
Maytenus_fournieri
Hexaspora_pubescens
Peripterygia_marginata
Siphonodon_celastrineus
Quetzalia_occidentalis
Zinowiewia_concinna
Mortonia_greggii

)

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

Appendix 1. List of fossils assigned and/or compared to Celastraceae. A) leaves.

Fossil name	**Age**	**Country**	**Province**	**Reference**
Celastrophyllum aff. *hunteri*	Cretaceous (Albian)	Siberia	Toptanskaja suite	Samylina AA. 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
Celastrinites alatus	Late Cretaceous	USA	Laramie Formation	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
Celastrinites ambiguus	Eocene	USA	Denver: Golden	Lesquereux L. 1874. *Contributions to the fossil flora of the western territories, Part II*. USA, Washington: Government Printing Office. Bulletin of the United States Geological and Geographical Survey of the Territories.
Celastrinites artocarpidioides	Eocene	USA	Denver: Golden	Lesquereux L. 1874. *Contributions to the fossil flora of the western territories, Part II*. USA, Washington: Government Printing Office. Bulletin of the United States Geological and Geographical Survey of the Territories.
Celastrinites cowanensis	Late Cretaceous	USA	Laramie Formation	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.
Celastrinites elegans	Miocene	USA	Florissant Formation	Lesquereux L. 1878. *Contributions to the fossil flora of the western territories, Part III.* USA, Washington: Government Printing Office. Bulletin of the United States Geological and Geographical Survey of the Territories.
Celastrinites eriensis	Late Cretaceous	USA	Laramie Formation	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.
Celastrinites laevigatus	Late Cretaceous	USA	Laramie	Lesquereux L. 1878. *Contributions to the fossil flora of the western territories, Part III.* USA, Washington: Government Printing Office. Bulletin of the United States Geological and Geographical Survey of the Territories.

Celastrinites populifolius	Eocene	USA	Denver: Golden	Knowlton FH. 1930. The Flora of the Denver and associated Formations of Colorado. *United States Geological Survey Professional Paper* **155**:1-141
Celastrinites venulosus	Paleogene	France	?	Saporta G de. 1865. Etudes sur la végétation du Sud-Est de la France à l'époque tertiaire, 2e partie, III. Flore d' Armissan et de Peyriac, dans le bassin de Narbonne (Aude). *Annales des Sciences Naturelles* **4**: 5-264
Celastrophyllum acutidens	Cretaceous	USA	Patapsco Formation	Fontaine WM. 1890. The Potomac or younger Mesozoic Flora. *United States Geological Survey, Monographs* **15**: 1-377.
Celastrophyllum alabamensis	Cretaceous	USA	?	Berry EW. 1919. Upper Cretaceous floras of the eastern Gulf region in Tenessee, Mississippi, Alabama, and Georgia. *United States Geological Survey Professional Paper* **112:**1-177.
Celastrophyllum albadomus	Cretaceous	USA	?	Ward LF, Fontaine WM, Bibbins A, Wieland GR. 1905. *Status of the Mesozoic floras of the United States.* Second paper. USA, Washington, Government Printing Office.
Celastrophyllum angustifolium	Cretaceous	USA	?	Newberry JS. 1895. The Flora of the Amboy Clays. *United States Geological Survey, Monographs* **26**:1-260.
Celastrophyllum arcinerve	Cretaceous	USA	Patapsco Formation	Fontaine WM. 1890. The Potomac or younger Mesozoic Flora. *United States Geological Survey, Monographs* **15**: 1-377.
Celastrophyllum attenuatum	Paleogene	Java	?	Göppert HR. 1853. Über die Tertiär-Flora Java's.*Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde*. 433-436.
Celastrophyllum australe	Eocene	New Zealand	Grey River	Ettingshausen von C. 1887. Beitraege zur Kenntnis der Fossilen Flora Neuseelands. *Denkschriften der Akademie der Wissenschaften, Wien* **53**:143-194.
Celastrophyllum brittonianum	Late Cretaceous	USA	Redmond Formation	Newberry JS. 1895. The Flora of the Amboy Clays. *United States Geological Survey, Monographs* **26**: 1-260.
Celastrophyllum carolinensis	Late Cretaceous	USA	Ripley Formation	Berry EW. 1925. The flora of the Ripley Formation. U*nited States Geological Survey Professional Paper* **129**: 199-226.
Celastrophyllum carolinensis	Cretaceous	USA	Dakota Formation	Berry EW. 1914. The Upper Cretaceous and Eocene floras of South Carolina and Georgia. *United States Geological Survey Professional*

				Paper **84**: 1-200.
Celastrophyllum columbianum	middle Eocene	USA	Yegua Formation	Berry EW. 1924.The Middle and Upper Eocene floras of south eastern America. *United States Geological Survey Professional Paper* **92**:1-206.
Celastrophyllum crassipes	Cretaceous	USA	Dakota Formation	Lesquereux L.1891. Flora of the Dakota Group. *United States Geological Survey, Monographs* **17:**1-400.
Celastrophyllum crenatum	Late Cretaceous	USA	Raritan Formation	Berry EW. 1911. The Flora of the Raritan Formation. *The Geology of New Jersey, Bull* **3**:1-233.
Celastrophyllum cretaceum	Cretaceous	USA	Dakota Formation	Lesquereux L.1891. Flora of the Dakota Group. *United States Geological Survey, Monographs* **17**:1-400.
Celastrophyllum cunninghamii	Eocene	Australia	Dalton	Ettingshausen von C. 1883. Beiträge zur Kenntniss der Tertiärflora Australiens. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematische-naturwissenschaftliche*. **47**: 1-48.
Celastrophyllum decurrens	Late Cretaceous	USA	Raritan Formation	Berry EW. 1911. The Flora of the Raritan Formation. *The Geology of New Jersey Bulletin* **3**: 1-233.
Celastrophyllum denticulatum	Cretaceous	USA	Patapsco Formation	Fontaine WM. 1890. The Potomac or younger Mesozoic Flora. *United States Geological Survey, Monographs* **15**:1-377.
Celastrophyllum elaeodendriforme	Eocene	Argentina	Rio Pichileufu	Berry EW. 1938. Tertiary Flora from the Rio Pichileufu, Argentina. *Geological Society of America Special Papers* **12**:1-149.
Celastrophyllum elegans	Cretaceous	USA	Montawan Formation	Berry, E. W.1903. The flora of the Montawan Formation. *Bulletin of the New York Botanical Garden* **3**:45-103.
Celastrophyllum ensifolium	Eocene	USA	Dakota Group	Lesquereux L.1878. Contribution of the fossil flora of the Western Territories II. The tertiary flora. *United States Geological Survey of the Territories, Monographs* **7**:1-382.
Celastrophyllum fraunhoferifolium	Eocene	Argentina	Rio Pichileufu	Berry EW. 1938. Tertiary Flora from the Rio Pichileufu, Argentina. *Geological Society of America Special Papers* **12**:1-149.
Celastrophyllum grandifolium	Late Cretaceous	USA	Raritan Formation	Berry EW. 1911. The Flora of the Raritan Formation. *The Geology of New Jersey, Bulletin* **3**: 1-233.

Celastrophyllum gymindoides	middle Eocene	USA	Lisbon Formation	Berry EW. 1924.The Middle and Upper Eocene floras of south eastern America. *United States Geological Survey Professional Paper* **92**:1-206.
Celastrophyllum hunteri	Cretaceous	USA	Potomac Formation	Ward LF. 1895. The Potomac Formation. *United States Geological Survey Bulletin* **37**: 1-115.
Celastrophyllum hymnoides	Eocene	USA	Cleinborn	Berry EW. 1924.The Middle and Upper Eocene floras of south eastern America. *United States Geological Survey Professional Paper* **92**:1-206.
Celastrophyllum integrifolium	Eocene	USA	Dakota Group	Lesquereux L.1878. Contribution of the fossil flora of the Western Territories II. The tertiary flora. *United States Geological Survey of the Territories, Monographs* **7**:1-382.
Celastrophyllum japonicum	Late Cretaceous	Japan	Kotsuki, Sasu-mura, Shimogata-gun, Tsushima Province	Tataiwa I. 1933. Cretaceous Flora of Tsushima Japan. *Japanese journal of geology and geography* **11**:185-211
Celastrophyllum kazachstanense	Cretaceous	Russia	Chushkakul Mountains, Western Kazachstan.	Vakhrameevv A. 1952. The stratigraphy and the fossil flora of the Cretaceous deposits of western Kazakhstan. Russia: Moscow, Regional stratigraphy the USSR.
Celastrophyllum kryshtofovichii	Late Cretaceous	Russia	Tap river, left tributary of Viliga river, Magadan region	Samylina VA. 1984. Pozdnemelovaja flora Tap (Severnoe Priokhot'je). *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva* **27**:236-246
Celastrophyllum lanceolatum	Eocene	USA	Dakota Group	Lesquereux L.1878. Contribution of the fossil flora of the Western Territories II. The tertiary flora. *United States Geological Survey of the Territories, Monographs* **7**:1-382.
Celastrophyllum latifolium	Cretaceous	USA	Patapsco Formation	Fontaine WM. 1890. The Potomac or younger Mesozoic Flora. U*nited States Geological Survey, Monographs* **15**: 1-377.
Celastrophyllum maytenoides	Miocene	Hungary	Bánhorváti locality	Kovács É. 1957. Összehasonlító flóra- és vegetációtanulmányok Bánhorváti és környékének szarmata növénymaradványai alapján. *Földtani közlöny* **87**: 425-446
Celastrophyllum	Late	USA	Raritan	Berry EW. 1911. The Flora of the Raritan

minus	Cretaceous		Formation	Formation. *The Geology of New Jersey, Bulletin* **3**:1-233.
Celastrophyllum myrsinoides	Cretaceous	USA	Dakota Formation	Lesquereux L.1891. Flora of the Dakota Group. *United States Geological Survey, Monographs* **17**:1-400.
Celastrophyllum newberryanum	Late Cretaceous	USA	Raritan Formation	Berry EW. 1911. The Flora of the Raritan Formation. *The Geology of New Jersey Bulletin* **3**:1-233.
Celastrophyllum obliquum	Cretaceous	USA	Dakota Formation	Lesquereux L.1891. Flora of the Dakota Group. *United States Geological Survey, Monographs* **17**:1-400.
Celastrophyllum obtusum	Eocene	USA	Dakota	Lesquereux L.1878. Contribution of the fossil flora of the Western Territories II. The tertiary flora.*United States Geological Survey of the Territories, Monographs* **7**:1-382.
Celastrophyllum obtusum	Cretaceous	Greenland	Atane Formation	Heer von O. 1882. Flora Fossilis Arctica. Flora Fossilis Greenlandica. Vol. 6, Zurich.
Celastrophyllum parvifolium	Late Cretaceous	USA	Raritan Formation	Berry EW. 1911. The Flora of the Raritan Formation. *The Geology of New Jersey Bulletin* **3**:1-233.
Celastrophyllum praecrassipes	Cretaceous	USA	?	Berry EW.1919. Upper Cretaceous floras of the eastern Gulf region in Tenessee, Mississippi, Alabama, and Georgia. *United States Geological Survey Professional Paper* **112**:1-177.
Celastrophyllum retinerve	Late Cretaceous	Russia	Konglomeratovyj cape, North-Western Kamchatka territory	Herman AB. 1987. Novye pokrytosemennye iz turona Severo-Zapadnoj Kamchatki. *Paleontologicheskii Zhurnal* **4**:96-106
Celastrophyllum robustum	Late Cretaceous	USA	Redmond Formation	Newberry JS. 1895. The Flora of the Amboy Clays. *United States Geological Survey, Monographs* **26**:1-260.
Celastrophyllum salicifolium	Late Cretaceous	Russia	Viljuj river, Lena river basin	Budantsev LY. 1968. Pozdnemelovaja flora Viljujskoj vpadiny. *Botanicheskij Zhurnal* **53**:3-16.
Celastrophyllum serrulatue	Cretaceous	Siberia	Toptanskaja suite	Samylina AA. 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
Celastrophyllum spatulatum	Late Cretaceous	USA	Raritan Formation	Berry EW. 1911. The Flora of the Raritan Formation. *The Geology of New Jersey Bulletin* **3**:1-233.
Celastrophyllum subundulatum	Late Cretaceous	Russia	Siljap river, Kolyma river basin, Yakutia (Saha) republi	Kryshtofovich AN. 1938. Cretaceous plants of Kolyma: contributions to the Knowledge of the Kolima-Indigirka Land. Ser 2. *Geology and geomorphology* **15**:1-26.
Celastrophyllum yokoyamae	Late Cretaceous	Russia	Mgachi, Aleksandrovsk-Sakhalinsky district, Sakhalin region	Kryshtofovich AN. 1918. On the Cretaceous flora of Russian Sakhalin. *Journal of the College of Science, Imperial University of Tokyo* **40**:1-73.
Celastrus comparabilis	middle Eocene	USA	Kushtaka Formation	Wolfe JA. 1977. Paleogene floras from the Gulf of Alaska region. U*nited States Geological Survey, Professional Paper* **997**: 1-108.
Celastrus borealis	Eoceno	USA	Kenai: Nenana coal field, Tanana region, Coal Creek	Hollick A. 1936. The Tertiary floras of Alaska. *United States Geological Survey, Professional Paper* **182**: 1-171.
Celastrus bruckmannifolia	Eocene	USA	Wilcox (Rockdale Formation)	Berry EW. 1916. The Lower Eocene floras of Southeastern North America. *United States Geological Survey Professional Paper* 91:1-481.
Celastrus bruckmannii	Miocene	USA	Virginia coastal	Berry EW. 1909. Miocene flora from the Virginia coastal Plain. *The Journal of Geology* **17**:19-30.
Celastrus caducidentatus	middle Miocene	China	Dajie Formation	Liang, X.-Q., Ferguson DK, Jacques FMB, Sua T, Wang L., Zhou Z.-K.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
Celastrus confluens	middle Eocene	USA	John Day Basin	Knowlton FH. 1902. Fossil Flora of the John Day Basin, Oregon. *United States Geological Survey Bulletin* **204**: 1-153.
Celastrus culveri	Paleocene	USA	Yellowstone River	Knowlton FH. 1899. Fossil flora of the Yellowstone national Park. *United States Geological Survey of the Territories, Monographs* **32**:651-882.
Celastrus culveri	Eocene	USA	Fort Union: Elk Creek, Yellowstone National Park	Knowlton FH.1919. A catalogue of the Mesozoic and Cenozoic plants of North America. *United States Geological Survey Bulletin* **696:**1-815.
Celastrus curvinervis	Eocene	USA	Fort Union: Elk Creek, Yellowstone National Park	Knowlton FH.1919. A catalogue of the Mesozoic and Cenozoic plants of North America. *United States Geological Survey Bulletin* **696**:1-815.
Celastrus dignatus	Miocene	USA	Mascall: Van Horn's ranch, John Day Basin	Knowlton FH. 1902. Fossil Flora of the John Day Basin, Oregon. *United States Geological Survey Bulletin* **204**:1-153.
Celastrus ellipticus	Eocene	USA	Fort Union: Elk Creek, Yellowstone National Park	Knowlton FH.1919. A catalogue of the Mesozoic and Cenozoic plants of North America. *United States Geological Survey Bulletin* **696:**1-815.
Celastrus eolignitica	Eocene	USA	Wilcox (Rockdale Formation)	Berry EW. 1916. The Lower Eocene floras of Southeastern North America. *United States Geological Survey Professional Paper* **91**:1-481.
Celastrus ferquisti	middle Miocene	USA	Latah Formation	Berry EW. 1929. A revision of the flora of the Latah Formation. *United States Geological Survey Professional Paper* **154:**225-267.
Celastrus ferrugineus	Eocene	USA	Fort Union: Burns's ranch and Iron Bluff, near Glendive and Bull	Knowlton FH.1919. A catalogue of the Mesozoic and Cenozoic plants of North America. *United States Geological Survey Bulletin* **696:**1-815.

			Mountains, Mont.	
Celastrus fraxinifolius	Miocene	USA	Florissant, Colorado	Lesquereux L.1883. Contributions to the Miocene flora of Alaska. *Proceedings of the United States National Museum* **5**:443-449.
Celastrus gaudini	Eoceno	USA	Denver: Golden	Knowlton FH. 1930. The Flora of the Denver and associated Formations of Colorado. *United States Geological Survey Professional Paper* **155**:1-139
Celastrus grewiopsis	Eocene	USA	Fort Union: Burns's ranch, Glendive, Mont.	Knowlton FH.1919. A catalogue of the Mesozoic and Cenozoic plants of North America. *United States Geological Survey Bulletin* **696**:1-815.
Celastrus haddeni	Late Cretaceous	USA	Vermejo Formation	Lee TW, Knowlton FH. 1917. Raton Mesa and other regions in Colorado and New Mexico. *United States Geological Survey Professional Paper* **101**:1-561.
Celastrus herendeenensis	Late Cretaceous (Santonian)	USA	Coal Bluff, Herendeen Bay, Yukon River region	Hollick A.1930. The Upper Cretaceous Floras of Alaska. U*nited States Geological Survey Professional Paper* **159**:1-185.
Celastrus hesperius	Late Cretaceous	USA	Vermejo Formation	Knowlton FH.1919. A catalogue of the Mesozoic and Cenozoic plants of North America. *United States Geological Survey Bulletin* **696:**1-815.
Celastrus inaequalis	Eocene	USA	Fort Union: Elk Creek, Yellowstone National Park.	Knowlton FH.1919. A catalogue of the Mesozoic and Cenozoic plants of North America. *United States Geological Survey Bulletin* **696**:1-815.
Celastrus lacoei	middle Miocene	USA	Latah Formation	Berry EW. 1929. A revision of the flora of the Latah Formation. *United States Geological Survey Professional Paper* **154**:225-267.
Celastrus lanceolatus	Paleocene	Germany	Eisleben	Walther H. 1995. *MAI, D. H., Tertiäre Vegetationsgeschichte Europas. Methoden und Ergebnisse.* New York., USA: Gustav Fischer Verlag, Jena, Stuttgart. ISBN: 3-334-60456-X
Celastrus laurinensis	Eocene	USA	Wilcox (Rockdale Formation)	Berry EW. 1916. The Lower Eocene floras of Southeastern North America. *United States Geological Survey Professional Paper* **91**:1-481.
Celastrus lindgreni	Eocene	USA	Payette:	Knowlton FH.1919. A catalogue of the

			Idaho City, Idaho	Mesozoic and Cenozoic plants of North America. *United States Geological Survey Bulletin* **696**:1-815.
Celastrus minor	Eocene	USA	Wilcox (Rockdale Formation)	Berry EW. 1916. The Lower Eocene floras of Southeastern North America. *United States Geological Survey Professional Paper* **91**:1-481.
Celastrus minor	Eocene	USA	Wilcox (Rockdale Formation)	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.
Celastrus minutus	early Oligocene (52-49 My)	Bulgaria	Satovcha Graben	Bozukov V. 2000. Miocene macroflora of the Satocha Graben (Western Rhodopes). I. Sytematics.5. Magnoliophyta: Araliaceae, Aquifoliaceae, Celastraceae,Rhamnaceae,Vitaceae,Apocynaceae,Caprifoliaceae, Convolvulaceae, Smilacaceae,Cyperaceae,Sparganiaceae,Typhaceae. *Phytologia Balcanica* **6**:15-30
Celastrus mioangulata	Miocene (17-15 Ma)	China	Shanwang Formation	Hu HH, Chaney RW. 1940. *A Miocene Flora from Shantung Province, China. Part I. Introduction and Systematic Considerations.*USA Washington, D.C.: Carnegie Institution of Washington.
Celastrus oeningensis	late Oligocene-early Miocene	Bulgaria	Valche Pole Molasse Formation	Bozukov V, Palamare PA. 2008. The fossil macroflora of the Vulche Pole Molasse Formation (SE Bulgaria). *Phytologia Balcan* **14**: 173-184.
Celastrus pseudocurvinervis	Late Cretaceous (Santonian)	USA	Coal Bluff, Herendeen Bay, Yukon River region	Hollick A.1930. The Upper Cretaceous Floras of Alaska. *United States Geological Survey Professional Paper* **159**:1-185.
Celastrus pterospermoides	Eocene	USA	?	Ward LF. 1885. Flora of the Laramie Group. *United States Geological Survey Annual Report* **6**:399-570.
Celastrus serratus	Eocene	USA	Raton: Primero and Woolton.	Knowlton FH.1919. A catalogue of the Mesozoic and Cenozoic plants of North America. *United States Geological Survey Bulletin* **696**:1-815.
Celastrus sp.	Late Cretaceous	USA	Mesaverde Formation	Knowlton FH.1919. A catalogue of the Mesozoic and Cenozoic plants of North America. *United States Geological Survey Bulletin* **696**:1-815.

Celastrus sp.	Eocene	Japan	Yubari, Hokkaido, Japan	Huzioka K.1961. A new Palaeogene species of the genus *Eucommia* from Hokkaido, Japan. *Transactions and Proceedings of Palaeontological Society of Japan, New Series* **41**: 9-12
Celastrus spokanensis	middle Miocene	USA	Latah Formation	Berry EW. 1929. A revision of the flora of the Latah Formation. *United States Geological Survey Professional Paper* **154**:225-267.
Celastrus taurinensis	Eocene	USA	Wilcox (Rockdale Formation)	Berry EW. 1916. The Lower Eocene floras of Southeastern North America. *United States Geological Survey Professional Paper* **91**:1-481.
Celastrus taurinensis	Eocene	USA	Fort Union: Bull Mountains and Burns's ranch, near Glendive, Mont.	Knowlton FH.1919. A catalogue of the Mesozoic and Cenozoic plants of North America. *United States Geological Survey Bulletin* **696**:1-815.
Celastrus typica	Oligocene	USA	Florissant Formation	MacGinitie HD. 1953. *Fossil Plants of the Florissant Beds, Colorado*. USA Washington, D.C.Carnegie Institution of Washington.
Celastrus veatchi	Eocene	USA	Wilcox	Knowlton FH.1919. A catalogue of the Mesozoic and Cenozoic plants of North America. *United States Geological Survey Bulletin* **696**:1-815.
Celastrus veatchi	Eocene	USA	Wilcox (Rockdale Formation)	Berry EW. 1916. The Lower Eocene floras of Southeastern North America. *United States Geological Survey Professional Paper* **91**:1-481.
Celastrus veatchi	Eocene	USA	Wilcox (Rockdale Formation)	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.
Celastrus wardii	Eocene	USA	Big Horn County, Wyo.	Knowlton FH.1919. A catalogue of the Mesozoic and Cenozoic plants of North America. *United States Geological Survey Bulletin* **696**:1-815.
Cellastrophyllum elaeodendriforme	early Eocene/late Miocene	Argentina	?	Berry EW. 1938. Tertiary Flora from the Rio Pichileufu, Argentina. *Geological Society of America Special Papers* **12**: 1-149.

Cellastrophyllum fraunhoferifolium	early Eocene/late Miocene	Argentina	?	Berry EW. 1938. Tertiary Flora from the Rio Pichileufu, Argentina. *Geological Society of America Special Papers* **12**: 1-149.
Cetrastrophyllum cassinoides	Late Cretaceous	USA	Ripley Formation	Berry EW. 1925. The flora of the Ripley Formation. *United States Geological Survey Professional Paper* **129**: 199-226.
Cetrastrophyllum minimum	Late Cretaceous	USA	Ripley Formation	Berry EW. 1925. The flora of the Ripley Formation. *United States Geological Survey Professional Paper* **129**: 199-226.
Cetrastrophyllum perryi	Late Cretaceous	USA	Ripley Formation	Berry EW. 1925. The flora of the Ripley Formation. *United States Geological Survey Professional Paper* **129**: 199-226.
Cetrastrophyllum ripleyanum	Late Cretaceous	USA	Ripley Formation	Berry EW. 1925. The flora of the Ripley Formation. *United States Geological Survey Professional Paper* **129**: 199-226.
Cetrastrophyllum variabilis	Late Cretaceous	USA	Ripley Formation	Berry EW. 1925. The flora of the Ripley Formation. *United States Geological Survey Professional Paper* **129**: 199-226.
Euonymus glanduliferus	late Paleocene-early Eocene	USA	Elgin Standard (Rockdale Formation)	Irving RS, Stuessy TF. 1971. A New paratropical Angiosperm Florule in the Eocene Rockdale Formation of Bastrop County Texas. *The Southwestern Naturalist* **16**:111-116.
Euonymus knowlton	middle Miocene	USA	Latah Formation	Berry EW. 1929. A revision of the flora of the Latah Formation. *United States Geological Survey Professional Paper* **154**:225-267.
Euonymus pacificus	Miocene 21.3-12.1	USA	Latah Formation	Brown RW.1937. Additions to Some Fossil Floras of the Western United States. *United States Geological Survey Professional Paper* **186***:*163-207
Euonymus protobungeana	Miocene (17-15 Ma)	China	Shanwang Formation	Hu HH, Chaney RW. 1940. A Miocene Flora from Shantung Province, China.Part I. Introduction and Systematic Considerations. USA Washington, D.C.: Carnegie Institution of Washington.
Euonymus santotomaserisis	middle Eocene	USA	Mount Selman Formation	Berry EW. 1924.The Middle and Upper Eocene floras of south eastern America. *United States Geological Survey Professional Paper* **92**: 1-206.
Euonymus splendes	Eocene	USA	Wilcox (Rockdale Formation)	Berry EW. 1916. The Lower Eocene floras of Southeastern North America. *United States Geological Survey Professional Paper* **91**:1-481.
Maytenoides	middle	Germany	Geiseltal	Rüffle L,Litke R. 2008. Ergänzungen zur

papillosa	Eocene			Eozän-Flora des Geistales, Deutschland, und einigir weiterer Eozän-Fundstätten. *Feddes Repertorium* **111**:449-463
Maytenus ellipticus	Eocene	Argentina	Rio Pichileufu	Berry EW. 1938. Tertiary Flora from the Rio Pichileufu, Argentina. *Geological Society of America Special Papers* **12**: 1-149.
Maytenus latifolioides	Eocene	Argentina	Rio Pichileufu	Berry EW. 1938. Tertiary Flora from the Rio Pichileufu, Argentina. *Geological Society of America Special Papers* **12**: 1-149.
Paxistima deweyensis	Eocene 50–43	USA	Thunder Mountain caldera	Axelrod DI.1998. The Eocene Thunder Mountain Flora of Central Idaho. *University of California Publications in Geological Sciences* **143**:1-160.
Salacia floribundifolia	early Eocene/late Miocene	Argentina	Pichileufu	Berry EW. 1938. Tertiary Flora from the Rio Pichileufu, Argentina. *Geological Society of America Special Papers* **12**: 1-149.

Appendix 1. List of fossils assigned and/or compared to Celastraceae. B) woods.

Fossil name	**Age**	**Country**	**Province**	**Reference**
Baasia armendarisense	Late Cretaceous	USA	McRae	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
Celastrinoxylon celastroides	Late Cretaceous	Egypt	Hefhuf Formation	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
Celastrinoxylon celastroides	Late Cretaceous	Egypt	Hefhuf Formation	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
Celastrinoxylon celastroides	Late Cretaceous	Egypt	Hefhuf Formation	Kräusel R. 1939. Der Bayerischen Akademie der Wissenschaften Ergebnisse der Forschungsreisen Prof. E. Stromers. A*bhandlungen der Bayerischen Akademie der Wissenschaften Mathematisch-naturwissenschaftliche Abteilung* **47**: 1-140.
Celastrinoxylon celastroides	Eocene	Ethiopia	Harar	Beauchamp J, Lemoigne Y. 1973. Description d'une paléoflore du Crétacé terminal-Éocène dans le Massif du Chercher (province d'Harar, Éthiopie). *Documents des laboratoires de géologie de la Faculté desSciences de Lyon* **56**:167–179.
Celastrinoxylon meyeri	Eocene	Egypt	?	Schönfeld E. 1955. Die Kieselhölzer aus der Braunkohle von Böhle bei Leipzig. *Palaeontographica Abteilung B* **99**:1-83.

Celastrinoxylon ramunculiformis	late Eocene	United Kingdom	London Clay	Poole I, Wilkinson HP. 1999. A celastraceous twigs from the Eocene London Clay of south-east England. *Botanical Journal of the Linnean Society* **129**:165-176. DOI: 10.1111/j.1095-8339.1999.tb00498.x.
Celastrinoxylon sp.	lower Miocene-late Pliocene	Sumatra	?	Kramer K. 1974. Die Tertiären Hölzer Südost-Asiens (Unter Ausschluss Der Dipterocarpaceae). 2. Teil. *Palaeontographica Abteilung B* **145**: 1-150.
Elaeodendroxylon polymorphum	Miocene	USA	Yellowstone National Park	Platen P. 1907. Untersuchungen fossiler Hblzer aus dem Westen der Vereinigten Staaten von Noordamerika. *Naturforschende Gesellschaft Lkptlg Sitzusber* **34**: 1-173
Elaeodendroxylon sp.	late Eocene	Germany	Braunkohlen-Tagebau	Gottwald H.1992. Hölzer aus marinen Sanden des oberen Eozän von Helmstedt (Niedersachsen). *Palaeontographica Abteilung B* **225**:27-103.
Gondwanoxylon ghiarii	Late Cretaceous	India	Kathotia village	Saksena SD. 1962. On two fossil dycotyledonous woods from South Rewa, Central India. *The Palaebonist* **11**: 30-37.
Gondwanoxylon kathotiai	Late Cretaceous	India	Ghiar village	Saksena SD. 1962. On two fossil dycotyledonous woods from South Rewa, Central India. *The Palaebonist* **11**: 30-37.
Gymnosporioxylon paleoemarginatum	late Miocene	India	?	Lalitha C, Prakash U.1984. *Gymnosporia*, a new addition to the fossil record. *In*: Sharma AK, Mitra GC, Banerjee M. eds. *Proc. Symp. Evolutionary Botany and Biostratigraphy (A.K. Ghosh Commem. Vol.).* Print.and Publ., New Delhi, pp. 121-127
Hippocrateoxylon javanicum	Paleogene	Europa	?	Hoffmann H. 1884. Untersuchngen über fossile Hölzer. *Zeitschrift für Naturwissenschaften* **57**:156-195
Lophopetalumoxylon	early Pliocene	India	Subansiri Formation	Srivastava G, Mehrotra RC, Srikarni C. 2018. Fossil wood flora from the Siwalik Group of Arunachal Pradesh, India and its climatic and

				phytogeographic significance. *Journal of Earth System Science* **127**: 2. DOI: 10.1007/s12040-017-0903-2
Lophopetalumoxylon indicum	Late Cretaceous	India	Deccan Intertrappean Beds	Mehrotra RC, Prakash U, Bande MB. 1983. Fossil woods of *Lophopetalum* and *Artocarpus* from the Deccan Intertrappean beds of Mandla District, Madhya Pradesh, India. *Palaeobotanist* **32**: 310-320.
Maytenoxylon perforatum	late Miocene	Argentina	Ituzaingó Formation	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:10.1080/08912963.2017.1313840
Perrottetioxylon mahurzari	Cretaceous	India	Mahurzari	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.

Appendix 1. List of fossils assigned and/or compared to Celastraceae. C) pollen.

Fossil name	**Age**	**Country**	**Province**	**Reference**
Celastrus capellinii	late Miocene	Italy	Sarzana basin	Federici PR. 1973. La tettonica recente dell'Appenino. I. II bacino Villafranchiano di Sarzana e il suo significato nel quadro dei movimenti distensivi a nord-ovest delle Alpi Apuane. *Bollettino della Società geologica italiana* **92**:287-301.
Euonymoipites	Miocene-Pliocene	China	Donghai	Song Z. 1985. Cenozoic-Mesozoic Palaeontology and Stratigraphy of east China (Series 1). *In A Research on Cenozoic Palynology of the Longjing Structural Area in the Shelf Basin of the East China Sea (Donghai) Region*. China: Anhui Science and Technology Publishing House.
Hippocrateaceaedites leizhouensis	Pliocene (1.806 My)	China	Wanglugang Formation	Song Z.-C., Wang WM, Fei H. 2004. Fossil pollen records of extant angiosperms in China. *Botanical Review* **70**: 425-458.
Hippocrateaceaedites sp.	Miocene	Cameroon	Kwa-Kwa	Salard-Cheboldaeff, M., 1974. Pollens Tertiaires du Cameroun rapportées a la famille des Hippocrateacees. *Pollen et Spores* **16**:499-506.
Hippocrateaceaedites sp.	Eocene	India	Laki basin	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.
Hippocrateaceaedites sp.	lower Eocene	India	Naredi Formation	Kar RK. 1978. Palynostratigraphy of the Naredi (Lower Eocene) and the Narudi (Middle Eocene) Formations in the District of Kutch, India. *The Palaeobotanist* **25**:161- 178.
Hippocrateaceaedites sp.	Middle Eocene	USA	New Madrid	Frederiksen NO, Bybell LM, Christopher RA, Crone AJ, Edwards LE, Gibson TG, Hazel JE, Repetski JE, Russ DP, Smith CC, Ward LW. 1982. Biostratigraphy and paleoecology of Lower Paleozoic, Upper Cretaceous and Lower Tertiary rocks in U.S. Geological Survey New Madrid test wells, southeastern Missouri. T*ulane Studies in Geology and Paleontology* **2**: 23-45.
Hippocrateaceaedites sp.	Ypresian-Eocene	India	?	Kar RK. 1985. The fossil floras of Kachchh. IV. Tertiary palynostratigraphy. *The Palaeobotanist* **34**: 1-279.
Hippocrateaceaedites sp.	middle-Miocene	India	?	Varma YNR, Ramanujam CGK, Patil RS. 1986. Palynoflora of Tertiary sediments of

				Tonakkal area, Kerala. *Journal of Palynology* **22**: 39-53
Hippocrateaceaedites van compoae	Miocene	India	Neyveli	Ramanujam CGK. 1966. Palynology of the Miocene Lignite from south Arcot District, Madras, India. *Pollen et Spores* **8**: 149- 203.
Microtropis	lower Oligocene	France	Aquitaine	Lobreau-Callen D, Caratini C. 1973. Pollens de "Celastraceae" à l'Oligocène en Gironde (France). *Bulletin de la Société Linnéenne de Bordeaux* **3**: 227-231.
Microtropis fokienensis	Pliocene	France	?	Suc JP. 1976. Quelques taxons-guides dans l' étude paléoclimatique du Pliocbne et du Pleistocéne infrieur du Languedoc (France). *Revue de Micropaléontologie* **18**: 246-255.
Peritassa	lower Oligocene	France	Aquitaine	Lobreau-Callen, D. and C. Caratini. 1973. Pollens de "Celastraceae" a l'Oligocene en Gironde (France). *Bulletin de la Société Linnéenne de Bordea* **3**: 227-231.
Polyadopollenites macroreticulatus	Miocene	Cameroon	Kwa-Kwa	Salard-Cheboldaeff M. 1974. Pollens Tertiaires du Cameroun rapportes a la famille des Hippocrateacees. *Pollen et Spores* **16**: 499-506.
Polyadopollenites microreticulatus	Miocene	Cameroon	Kwa-Kwa	Salard-Cheboldaeff, M. 1974. Pollens Tertiaires du Cameroun rapportes a la famille des Hippocrateacees. *Pollen et Spores* **16**: 499-506.
Retitricoporites sp.	Miocene	Cameroon	Kwa-Kwa	Salard-Cheboldaeff, M., 1974. Pollens Tertiaires du Cameroun rapportes a la famille des Hippocrateacees. *Pollen et Spores* **16**: 499-506.
Triporotetradites campylostemonoides	Miocene	Cameroon	Kwa-Kwa	Salard-Cheboldaeff, M. 1974. Pollens Tertiaires du Cameroun rapportes a la famille des Hippocrateacees. *Pollen et Spores* **16**: 499-506.
Triporotetradites scabratus	Cretaceous	Nigeria	Borehole	Hoeken-Klinkenberg PMJ Van. 1964. A palynological investigation of some Upper Cretaceous sediments in Nigeria. *Pollen et Spores* **6**: 209-331.
Triporotetradites sp.	Cretaceous	Nigeria	?	Van der Hammen Th, Garcia de Mutis C. 1964. A palynological investigation of some Upper Cretaceous sediments in Nigeria. *Pollen et Spores* **6**:209-231.

Appendix 1. List of fossils assigned and/or compared to Celastraceae. D) fruits and/or seeds.

Fossil name	Age	Country	Province	Reference
Canthicarpum celastroides	Eocene (52-49 My)	England	London Clay	Reid EM, Chandler MEJ. 1933. *The London Clay Flora*. United Kingdom, London. The British Museum.
Cathispermum pulchrum	Eocene (52-49 My)	England	London Clay	Reid EM, Chandler MEJ. 1933. *The London Clay Flora*. United Kingdom, London. The British Museum.
Celastrocarpus eocenicus	Eocene	USA	Wilcox (Rockdale Formation)	Berry EW. 1930. Revision of the Lower Eocene Wilcox flora of the southern United States. *United States Geological Survey Professional Paper* **156**:1-189.
Euonymus	Eocene	USA	Wilcox (Rockdale Formation)	Berry EW. 1930. Revision of the Lower Eocene Wilcox flora of the southern United States. *United States Geological Survey Professional Paper* **156**:1-189
Euonymus moskenbergensis	Miocene	Austria	Styria	Ettingshausen C. von. 1869. Beiträge zur Kenntniss der Tertiärflora Steiermarks. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften* **60**: 17-100.
Tripterygium kabutoiwanum	Pliocene (3.4 ± 0.2 My)	Japan	Kabutoiwa Formation	Ozaki K. 1991. Late Miocene and Pliocene floras in central Honshu, Japan. *Bulletin of Kanagawa Prefectural Museum.* Natural Science Special Issue, Yokohama. **1**: 1-188.

Appendix 1. List of fossils assigned and/or compared to Celastraceae. E) inflorescence and/or flower.

Fossil name	**Age**	**Country**	**Province**	**Reference**
Celastrinanthium hauchecornei	early Paleogene	Prusia	Russia	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.
Lobocyclas anomala	middle Oligocene-lower Miocene	Dominican Republic	Dominican amber	Chambers KL, Poinar Jr GO. 2016. *Lobocyclas anomala*, a new genus and species of Celastraceae subfamily Hippocrateoideae in Dominican amber. J*ournal of the Botanical Research Institute of Texas* **10**: 137-140.
Salacia lombardii	early-middle Miocene	Mexico	Simojovel de Allende	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. R*eview of Palaeobotany and Palynology* **252**:1-9. DOI: https://doi.org/10.1016/j.revpalbo.2018.02.003
Wuyunanthus hexapetalus	Paleocene Danian 66.0-61.6 My)	China	Wuyun	Wang Y-F, Li Fls C-S, Li Z-Y, D-Z Fu. 2001. Wuyununthus gen. nov., a flower of Celastraceae from the Palaeocene 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.

Appendix 2. Details of fossil records proposed as calibration points in molecular clock according to criteria of Martínez-Millán (2010).

Fossil name	**Discussion of key characters**	**Character or set characters supports identification**	**Description and diagnosis of fossil**	**Photographs of the specimen**	**Drawings, diagrams, and reconstructions of the fossils**	**Safeguard institution collection number, holotype designation**
Baasia armendarisense	present	solitary vessels; scalariform perforation plates.	present	8	absent	TXSTATE 1200. Texas State University, San Marcos.
Cathispermum pulchrum	present	wing-like arils; testa seed	present	6	absent	V. 22576.Natural History Museum, London
Celastrus comparabilis	present	serrate margins; camptodrome secondary veins; intercostal tertiary veins	present	5	absent	USNM 38744, 43356, 43357, 245728 National Museum of Natural History, Washington
Elaeodendroxylon sp.	present	scalariform perforation plates	present	4	absent	Die Geologisch-Paläontologische Sammlung der Universität Leipzig
Hippocrateaceaedites sp.	present	pollen grains subtriangular; tricolporate.	present	1	absent	Birbal Sahni Institute of Palaeobotany, Lucknow.
Lobocyclas anomala	present	nectarial disk; matured into the kind of trilobed capsular fruit	present	3	absent	Cat. No. Sd-9-62, Poinar amber collection, Oregon State University

Maytenoxylon perforatum	present	Diffuse porous, simple perforation plates, fibers dimorphic, band of thin-walled septate fibers resembling parenchyma, homo and heterocellular, uni and multiseriate rays and perfored ray cells	present	24	absent	CIDPALBO-MEG 94, CIDPALBO-MIC 1133. Colección de Paleobotánica del Laboratorio de Paleobotánica, CICYTTP-CONICET', Argentina.
Salacia lombardii	present	bisexual flower; pentamerous periant; nectarial disk	present	5	absent	GMPB-1351 Colección Nacional de Paleontología, Museo Ma. Carmen Perrilliat M., del Instituto de Geología, Mexico.
Wuyunanthus hexapetalus	present	bisexual flower, nectarial disk	present	3	present	wy-92-101a&b National Museum of Plant History of Institute of Botany. Chinese Academy of Sciences, Xiangshan, Beijing, P. R. China.

CAPÍTULO II. UNA NUEVA PLANTA FÓSIL EN EL ÁMBAR DE CHIAPAS, MÉXICO

Fossil flower of *Salacia lombardii* sp. nov. (Salacioideae-Celastraceae) preserved in amber from Simojovel de Allende, Mexico

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Fossil flower of *Salacia lombardii* sp. nov. (Salacioideae-Celastraceae) preserved in amber from Simojovel de Allende, Mexico

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ABSTRACT

A new fossil flower preserved in amber from Miocene sediments of Simojovel de Allende, Mexico, is described and recognized as a new member of Celastraceae. This fossil flower is bisexual, with a 5-merous perianth and extrastaminal disk, furthermore the presence of two stamens inserted in the inside surface of a pentagonal disk and ovoid pistil constitute characters that allows its inclusion in *Salacia* (Salacioideae). This is a new extinct taxon and represents a *Salacia* species with a mosaic of characters today present in different extant species distributed along the Paleo and Neotropic. The presence of *Salacia* ca. 23–15 My in southern Mexico can be explained through the Boreotropical Flora Hypothesis, a proposal supported by the Paleogene fossil record of Celastraceae in high latitude North America. The neobotanical data suggest that the Salacioideae was derived from an independent Old World Celastraceae lineage, and subsequently diversified in the New World. Fossil and extant plant evidence support the importance of fossil plants collected in low latitude North America and highlight the relevance of paleobotanical studies in challenging biogeographical hypothesis.

1. Introduction

Celastraceae is a sub-cosmopolitan family that includes about 98 genera and 1211 species. It is more diverse in the tropics and subtropics, with only few species in temperate zones (Simmons, 2004). Simmons (2004) proposed the most recent classification of the family based on different phylogenetic analyses (Savolainen et al., 1997; Simmons and Hedin, 1999; Simmons et al., 2001a, 2001b), and recognized three monophyletic subfamilies: Hippocrateoideae, Stackhousioideae and Salacioideae. These subfamilies are morphologically diagnosable and independently derived from Celastroideae, which is paraphyletic (Simmons, 2004).

The circumscription of Celastraceae has been controversial (Simmons and Hedin, 1999). Sometimes Celastraceae and Hippocrateaceae are treated as a single family (e.g. Bentham and Hooker, 1862; Baillon, 1872; Hou, 1962; Robson, 1965; Dahlgren, 1983; Thorne, 1992; Takhtajan, 1997), but recognition of two separate groups is also common (e.g. de Candolle, 1825; Miers, 1872; Hutchinson, 1967; Loesener, 1942; Cronquist, 1981; Simmons and Hedin, 1999).

Traditionally, the number of organs within floral whorls or merism (Ronse De Craene, 2010) is used as a diagnostic character to differentiate Hippocrateaceae from Celastraceae (anisomerous vs isomerous; e.g. Miers, 1872; Loesener, 1942). The most recent proposal for familial organization suggest that the presence of bisexual flowers with a 5-merous perianth, an extrastaminal disk and three stamens constitute diagnostic characters of the subfamilies Hippocrateoideae and Salacioideae (Coughenour et al., 2010, 2011), which are differentiated by dehiscent vs indehiscent nature of their fruit (Hallé, 1986; Simmons and Hedin, 1999; Coughenour et al., 2010, 2011; Lombardi, 2014).

The reproductive organs have been used traditionally to recognize extant members of Celastraceae (Simmons and Hedin, 1999); however, the extinct taxa of this linage have been identified mainly through vegetative organs, like leaves. Most fossil organs related to Celastraceae consist of leaves, and only few reproductive organs are known (Bacon et al., 2016). The use of the putative celastraceous fossils in other biological areas is weakened since they are in need of critical re-examination, due to their poor preservation and descriptions, as well as lack of diagnostic characters, thus, the identifications are controversial (Bacon et al., 2016). *Wuyunanthus hexapetalus* Y.F. Wang, C.S. Li, Z.Y. Li, et D.Z. Fu, from the Paleocene of China (Wang et al., 2001) was considered as the only accepted fossil of Celastraceae and is based on a flower. Recently *Lobocyclas anomala* Chambers et Poinar (Hippocrateoideae) preserved in amber from Dominican Republic has joined this status (Chambers and Poinar, 2016). Although the general appearance of these fossil flowers seems similar to that of Celastraceae flowers, especially in that

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0034-6667/

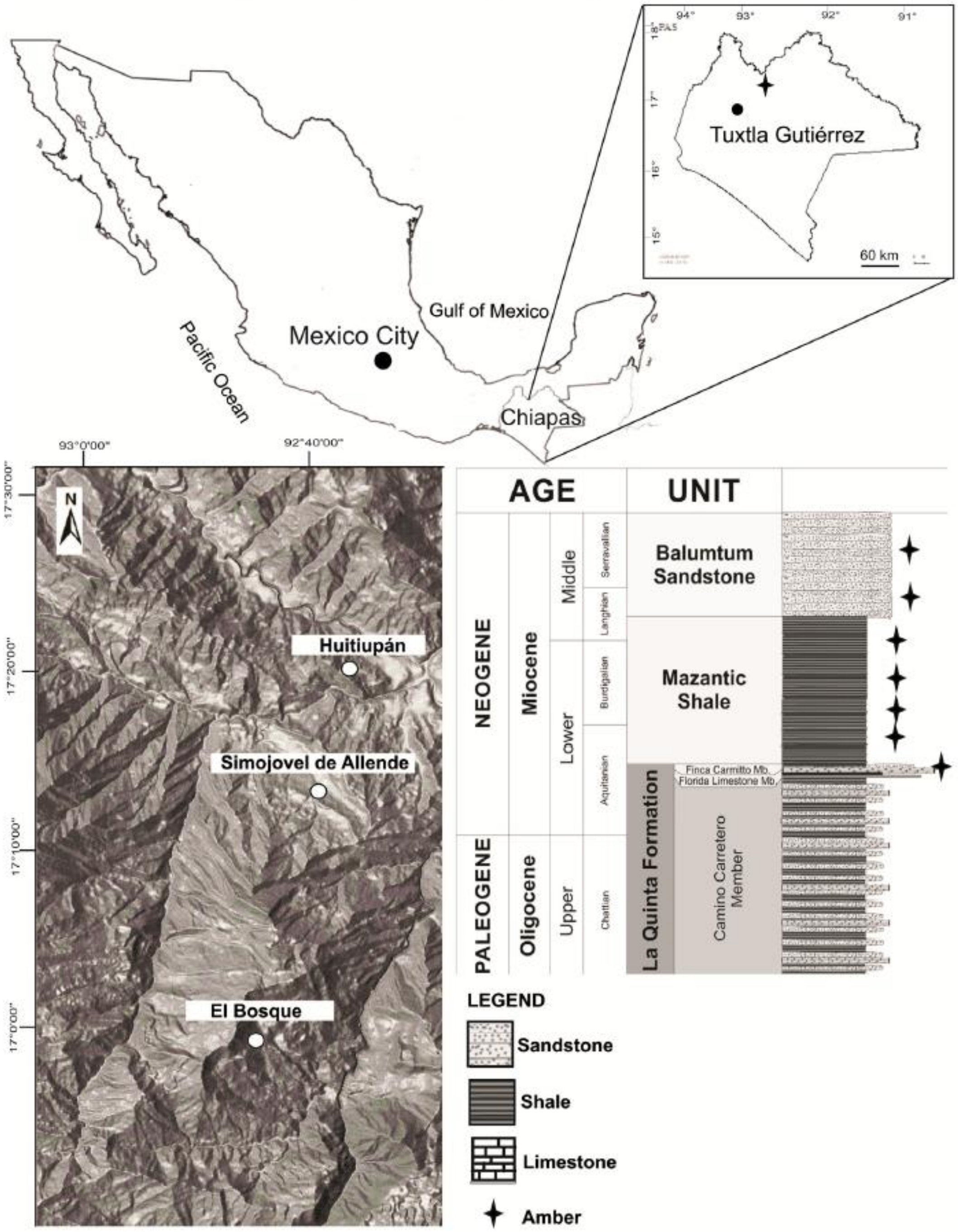

Fig. 1. Geographic location of amber outcrops in Simojovel de Allende, Chiapas, Mexico.
(Taken and modified from Serrano-Sánchez et al., 2016)

Plate I. *Salacia lombardii* Hernández-Damián et al. sp. nov. IGMPB 1351.

Fig. 1. Longitudinal section of complete flower arrows show pedicel (bottom) and 5-merous perianth (top). Bar = 1.0 mm.

Fig. 2. Perianth differentiated, calyx with five orbicular and puberulent sepals (arrow right) and corolla with five sub-orbicular petals (arrow left). Bar = 2.0 mm.

Fig. 3. Annular-pulviniform, pentagonal and extrastaminal disk (middle arrow), two opposite stamens (bottom and top arrows) and triangular, basifixed and bilocular anthers (right arrow). Bar = 0.2 mm.

Fig. 4. Two stamens (bottom and top arrows), and superior ovary partially immersed in the disk and ovoid style (middle arrow). Bar = 0.2 mm.

Fig. 5. Ovoid style and bifid stigma (left and right arrows). Bar = 0.2 mm.

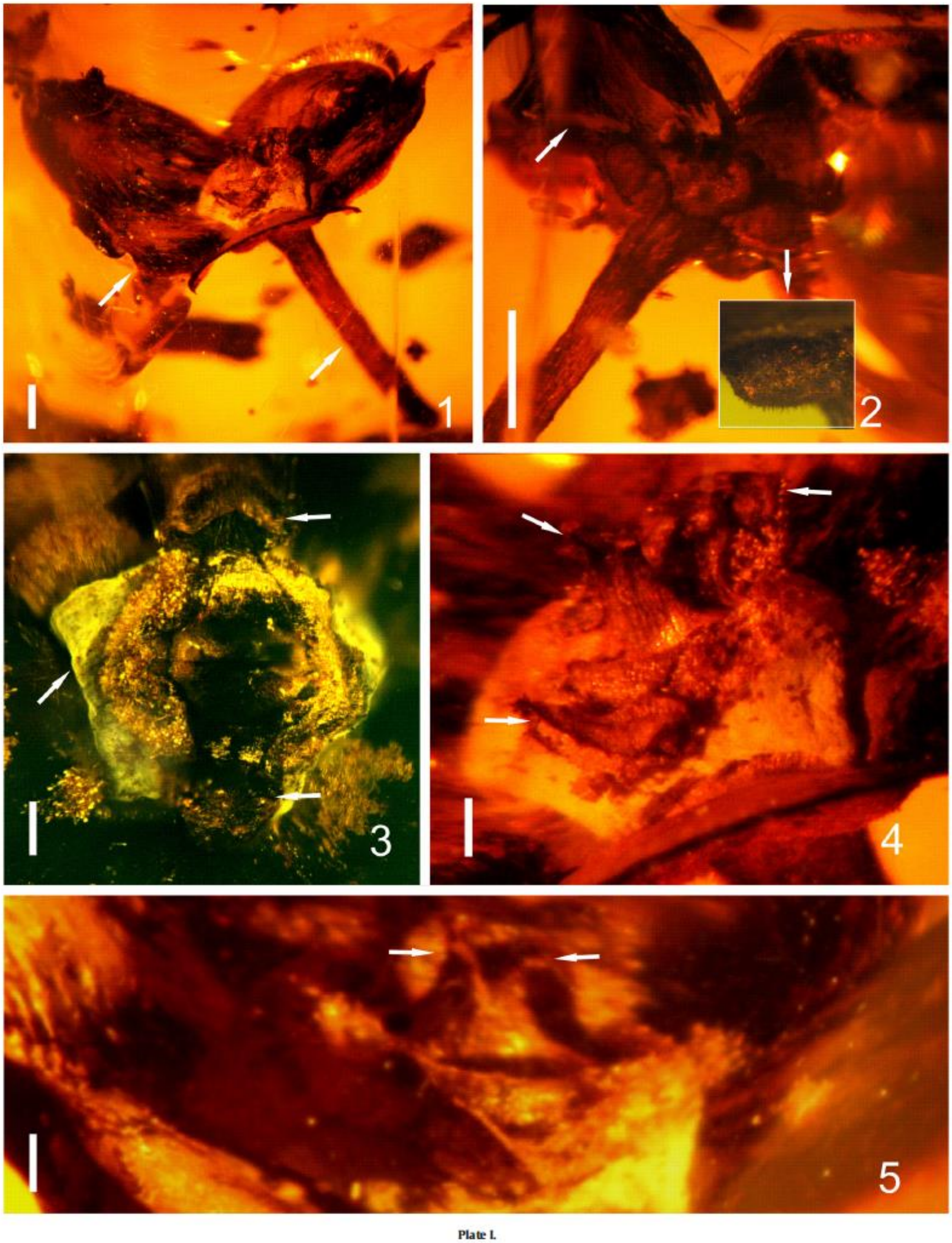

Plate I.

Plate II. *Semialarium mexicanum* (Hippocrateoideae) and *Salacia impresifolia* (Salacioideae).
Fig. 1. *Semialarium mexicanum* complete flower 5-merus perianth. Bar = 2.0 mm.
Fig. 2. *S. mexicanum* oblong petals (right arrow) and annular disk-pulvinate (left arrow). Bar = 1.0.
Fig. 3. *Salacia impresifolia* complete flower, sepals with ciliate margin. Bar = 2.0 mm.
Fig. 4. *S. impresifolia* circular and patelliform disk (left arrow) and glabrous petals. Bar = 1.0 mm.

Table 1
Morphologic comparison between *Salacia lombardii* Hernández-Damián et al. sp. nov. and flowers of extant Neotropical *Salacia* species (Smith, 1940; Hedin, 1999; Lombardi, 2014).

	Salacia lombardii sp. nov.	*S. panamensis*	*S. impresifolia*	*S. miqueliana*
Sepal shape	Orbicular	Triangular	Triangular	Elliptic
Indument sepals	Puberulent	Glabrous	Glabrous	Glabrous
Petals shape	Suborbicular	Elliptic	Obovate	Elliptic
Indument petals	Glabrous	Glabrous	Glabrous	Glabrous
Disk shape	Annular-pulvinate	Patelliform	Annular-pulvinate	Patelliform-pulvininate
Number of stamens	2	3	3	3
Anther shape	Triangular	Rhombic-triangular	Reniform	Triangular-oblong
Number of locules in anthers	2	2	2	2
Appendicular anthers	Absent	Present	Present	Present

they have a conspicuous disk, their inclusion within the family is still questionable due to their merosity, especially that of *Wuyunanthus* (6 vs 4–5; Matthews and Endress, 2005; Friis et al., 2011).

Here we expand the fossil record of Celastraceae by describing and identifying a new fossil flower included in amber from Miocene of Simojovel de Allende, Mexico. This fossil flower is important because it represents both a new extinct member of Salacioideae, as well as the first fossil record for the family in Mexico. Additionally, in this paper we highlight the mosaic of androecium and gynoecium features found in living and extinct members of the family, and discuss the relevance of the new fossil in the context of the current distribution of Celastraceae.

2. Material and method

2.1. Locality and age

The fossil flower was collected in Miocene sediments from Simojovel de Allende, Chiapas, Mexico, at 17° 08′ 19″ N, 92° 42′ 00″ W, at 600 m, approximately 50 km from the city of Tuxtla Gutierrez, Chiapas. The area is limited to the north by Huitiupán municipality, and to the south by El Bosque municipality (Wichard et al., 2006; Fig. 1).

Typically the amber of the Simojovel area is found in three lithostratigraphic units: La Quinta or Simojovel Formation, Mazantic Shale and Balumtum Sandstone (from base to top). They form a sequence composed mainly of calcareous sandstone and silt with layers of lignite (Licari, 1960; Allison, 1967). These units are exposed in the Sierra Madre del Sur, Chiapas; from the northern margin of the Central Depression (Totolapa) to Palenque, near the Gulf Coast of Tabasco. They were described by Licari (1960) and Allison (1967), but for further information on this topic see Solórzano-Kraemer (2007, 2010) and Serrano-Sánchez et al. (2015).

La Quinta or Simojovel Formation is the most characteristic litostratigraphic unit in the area and is subdivided into three members. The "Camino Carretero" is the lower most member of this formation, and is composed of calcareous sandstone, clay and shale intercalations, and contains foraminifera, scleractinid corals, molluscs and equinoids. The second member, "Limestone Florida", is composed of limolites and a heterogeneous alternation of calcareous sandstones, clays and shales, as well as thin lignite layers. The upper most member, "Finca Carmitto", is composed of fine terrigenous clasts, quartz, and limestone containing equinoids (Tomasini-Ortíz and Martínez-Hernández, 1984).

The biostratigraphic scheme of the La Quinta formation is based on foraminifera that suggest a late Oligocene age, as defined by the *Globigerina ciperoensis* Bolli and *Globerotalia kugleri* Bolli zones (Frost and Langenheim, 1974; Veiga-Crespo et al., 2007). These zones correspond with intervals Nn3 and Nn4 of the nanoplacton stratigraphic sequence, suggesting an age of 26–22.5 My (M. Benami, per comm. 2004; Gómez-Bravo, 2005).

Coral biostratigraphy at top of 'Camino Carretero' and the 'Finca Carmitto' members suggest an early Miocene age; however, this scheme was not explicitly established, but its inclusion would result in a late Oligocene to early Miocene temporal interpretation of the entire formation (Frost and Langenheim, 1974). Recently, the biostratigraphic rank of the 'Finca Carmitto' member, was established using nanoplacton. The presence of *Sphenolithus disbelemnos* Fornaciari & Rio and *Sphenolithus tintinnabalum* Maiorano & Monechi suggest the presence of Nn2 biozone, which corresponds with the early Miocene (Solórzano-Kraemer, 2007; Serrano-Sánchez et al., 2015). From this same member Serrano-Sánchez et al. (2015) dated gastropod shells using 87Sr/86Sr assigning an age of 22.88 My (Aquitanian) for the carrying sediments.

Moving up stratigraphically, the Mazantic Shale unit is composed of dark gray to black massive sandstone containing plant remains, gastropods, bivalves and crustaceans (Vega et al., 2009). It was dated with benthic foraminifera like *Siphogenerina transversa* Cushman, which correspond to early-middle Miocene, especially the zones N8-N9 (Solórzano-Kraemer, 2007). Later Vega et al. (2009) using well-preserved gastropod shell collected at Los Pocitos mine (lower Mazantic Shale) made 87Sr/86Sr isotopic measurements and suggested an absolute age of 23 My for this unit (Aquitanian). This unit has been correlated with the amber containing sediments of the Dominican Republic based on the similar botanical origin of the amber, as well as the presence of lignite beds, and comparable insect fossil record (40%). Thus its age is suggested as 20–15 My (Burdigalian-Langhian) (Solórzano-Kraemer, 2007).

The Balumtum Sandstone, the upper most united in the Simojovel de Allende amber area, has been compared with the Mazantic Shale; however, there is insufficient evidence to support their correlation (Solórzano-Kraemer, 2010). The unit consists of ca. 760 m of gray sandstone containing gastropods, bivalves and crustaceans (Frost and Langenheim, 1974). In the area of Simojovel, it rests uncomfortably on the top La Quinta Formation and the Mazantic Shale produces most of the commercial Chiapas amber, due to its abundance and facility to extract (Serrano-Sánchez et al., 2015). The material studied here was collected in this unit.

In summary, the age of the amber carrying sediments varies depending on the unit being considered (Serrano-Sánchez et al., 2015). According to Vega et al. (2009), and some other authors, amber was deposited from the late Oligocene to the early Miocene (Langenheim, 1966; Tomasini-Ortíz and Martínez-Hernández, 1984; Santiago-Blay and Poinar, 1993; Bousfield and Poinar, 1994; Poinar and Brown, 2002; Poinar, 2003; Castañeda-Posadas and Cevallos-Ferriz, 2007). However, other interpretations indicate that the stratigraphic units carrying the amber have middle-early Miocene age (Meneses-Rocha, 2001; Perrilliat et al., 2010; Solórzano-Kraemer, 2007).

2.2. Specimens

The studied material consists of a flower preserved in Miocene sediments of Simojovel de Allende, Mexico. An Olympus SZH stereoscopic microscope (equipped with a camera lucida) and an Olympus BH-2 optical microscope illuminated with transmitted white light were used for morphological observations. The photographs were taken with an Olympus DP11 camera using polarizing filters. The comparison of the fossil material with extant taxa was performed using literature like

Table 2
Morphological comparison between *Salacia lombardii* Hernández-Damián et al. sp. nov. and flowers of extant Paleotropic *Salacia* species (Hallé, 1986, 1990).

	Salacia lombardii sp. nov.	*S. howesii*	*S. annettae*	*S. lebrunii*
Sepal shape	Orbicular	Ovate	Semiorbicular	Semiorbicular
Indument sepals	Puberulent	Puberulent	Glabrous	Glabrous
Petal shape	Suborbicular	Ovate	Oblong	Oblong
Indument petals	Glabrous	Puberulent	Glabrous	Glabrous
Disk shape	Annular-pulvinate	Subcylindrical	Globular	Subglobular
Number of stamens	2	3	2	2
Anther shape	Triangular	Reniform	Reniform	Reniform
Number of locules	2	2	2	2
Appendicular anthers	Absent	Present	Absent	Absent

Cronquist (1981); electronic keys such a Neotropikey-Interactive key, and information resources for flowering plants like Neotropics (Milliken et al., 2010); FAMEX: Key to families of flowering plants Magnoliophyta Mexico (Murguía and Villaseñor, 1993); The Families of Flowering Plants: descriptions, illustrations, identification and information retrieval (Watson and Dallwitz, 1992), and Kevin Nixon's Families of Dicotyledons (Plantsystematics, 2012). The results from Cronquist (1981) and electronic keys suggested that members of Celastraceae have flowers morphologically similar to the fossil material. Subsequently we consulted specialized literature of Celastraceae to compare the fossil material with extant members of the family (e.g. Hallé, 1986, 1990; Hedin, 1999; Simmons and Hedin, 1999; Lombardi, 2014). Finally, the fossil flower was compared with material from MEXU herbarium.

3. Systematic description

Family: Celastraceae R. Brown

Subfamily: Salacioideae N. Hallé ex Thorne et Reveal

Genus: ***Salacia*** L.

Species: *Salacia lombardii* Hernández-Damián, Gómez-Acevedo et Cevallos-Ferriz sp. nov. (Pl. I, 1–5)

Holotype: IGMPB (Colección Nacional de Paleontología, Museo Ma. Carmen Perrilliat M., del Instituto de Geología, de la Universidad Nacional Autónoma de México) 1351.

Age: Middle-Early Miocene

Locality: Simojovel de Allende, Chiapas, Mexico.

Repository: Colección Nacional de Paleontología, Museo Ma. Carmen Perrilliat M., del Instituto de Geología, de la Universidad Nacional Autónoma de México (IGMPB).

Etymology: The specific epithet honors Dr. Julio Antonio Lombardi, botanist and specialist of *Salacia*.

Number of examined specimens: One

Diagnosis: Small, bisexual, actinomorphic flower; puberulent pedicel; five orbicular, puberulent sepals; five sub-orbicular petals; annular-pulviniform, pentagonal, extrastaminal disk; two opposites stamens inserted on the inner margin of the disk; triangular, basifixed anthers, bilocular, locules confluent at an acute angle; superior ovary, partially immersed in the disk, ovoid style and bifid stigma.

Description: Small, bisexual, actinomorphic flower, 7.5 mm long × 3.0 mm wide; with a square puberulent pedicel, 6.0 mm long × 0.65 mm wide (Pl. I, 1).

The perianth is well-differentiated into calyx and corolla. The calyx is persistent and has five orbicular sepals that are adaxially puberulent. They are similar in form and size, ca. 0.75 mm long × 1.0 mm wide (Pl. I, 2).

The corolla is persistent too, although with five, sub-orbicular petals that are glabrous. They are similar in form and size, 2.0 mm long × 1.4 mm wide, and they are partially fused towards their proximal zone.

The extrastaminal disk is prominent, annular-pulvinate and pentagonal. The androecium has two opposites stamens with ligulate filaments inserted in the inner margin of the disk, ca. 4.0 mm long × 2.0 mm wide. The anthers are triangular, basifixed, bilocular anthers, with confluent locules at an acute angle (Pl. I, 3–4).

The gynoecium is superior. The ovary is partially immersed in the disk, the style is ovoid and the stigma bifid, ca. 2.0 mm long × 0.5 mm wide (Pl. I, 4, 5).

4. Discussion

According to Matthews and Endress (2005) Celastraceae is a well-supported group based on its floral architecture. It has bisexual flowers, a conspicuous disk, five or fewer stamens and a semi-immersed ovary (Stevens, onwards). All of these characters states are present in the new flower preserved in amber from Simojovel de Allende, Mexico.

A striking phenomenon of Celastraceaea is the presence of a 3-merous androecium in flowers with a 5-merous perianth, wich is typical of Hippocrateoideae and Salacioideae (Pl. II) (Matthews and Endress, 2005; Coughenour et al., 2010; Ronse De Craene, 2010, 2016). According to Chambers and Poinar (2016) the gynoecium is a critical feature to support a fossil flower as a member of Hippocrateoideae or Salacioideae (deeply lobed vs subterete or trigonous). The new fossil material has two stamens inserted in the inner margin of the disk with an ovoid pistil, a condition that allows its recognition as a member of Salacioideae, with special resemblance to *Salacia* L.

Salacia is a heterogeneous genus with ca. 400 described species (Hedin, 1999), but about 200 accepted ones (Hedin, 1999; Simmons and Hedin, 1999; Coughenour et al., 2010; Lombardi, 2014). This genus includes lianas, rarely trees or shrubs, and is distributed along the Paleo- and Neotropics (Simmons et al., 2001a; Simmons, 2004). Although the flowers have high structural (shape and texture) variation in sepals, petals and disk (Smith, 1940; Hallé, 1986, 1990), these same morphological characteristics have been considered important in the taxonomic studies of the group (Smith, 1940; Hedin, 1999). The floral organization depicted in the new fossil flower of *Salacia* is closer to species with circular and pentagonal disk distributed in both the Neo- and Paleotropics (Tables 1, 2).

For example, the fossil flower is similar to *Salacia impresifolia* (Miers) A.C. Smith. in that they share glabrous petals; however, the shape of the disk and anthers (annular-pulvinate and triangular vs patelliform and rhombic-triangular) distinguish them (Pl. II, 3–4). Likewise, the fossil resembles *Salacia panamensis* Lombardi in the presence of suborbicular petals, though they differ in the shape of the sepals (orbicular vs triangular) and anthers (triangular vs reniform). The fossil flower is also similar to *Salacia miqueliana* Loes.; both have triangular anthers, but the presence vs absence of connective tissue distinguishes them. Finally, *Salacia howesii* Hutchinson et M.B. Moss has flowers similar to the fossil specimen; both have puberulent sepals, although the indumentum of the outer surface of petals and stamens (glabrous vs puberulent) and the disk shape (annular-pulvinate vs subcylindrical) differ between them (Pl. III, 1–2).

Most of the species of *Salacia* have three stamens; however, exceptional cases with just two opposites stamens are found in species from Africa (*Salacia annettae* N. Hallé, *Salacia lebrunii* R. Wilczek) (Pl. III, 3–4), Australia (*Salacia disepala* (C.T. White) Ding Hou, *Salacia erythrocarpa* K. Schumann) and Indonesia *Salacia forsteniana* Miquel (Hallé, 1990; Coughenour et al., 2010; Hou, 1962). These can be fused with the gynoecium, forming an androgynophore (Pl. III, 3–4; Hallé, 1986, 1990). In the fossil flower this condition has not been observed (Pl. I.). While flowers with androgynophore tend to elongate, its presence does not necessarily imply elongation of the floral axis (e.g. *Salacighia* and some species of *Salacia*; Hallé, 1986, 1990; Matthews and Endress, 2005).

This comparison supports the recognition of a new member of *Salacia* in the amber from Miocene sediments of Mexico, and highlights the mosaic of characters found in the flower of the new plant. Its mixture of characters states are found individually in several extant species

Plate III. *Salacia lombardii* Hernández-Damián et al. sp. nov. IGMPB 1351, *Salacia howesii* and *Salacia annettae*.

Fig. 1. *Salacia lombardii* complete flower, stamen (right arrow) and ovoid pistil (left arrow). Bar = 1.0 mm.

Fig. 2. *S. lombardii* two opposite stamens (bottom and top arrows). Bar = 2.0 mm.

Fig. 3. *S. howesii* complete flower, pubescent sepals (right arrow) and subcylindrical disk (left arrow) (Taken and modified from Hallé, 1986, 1990). Bar = 1.0 mm.

Fig. 4. *S. howesii* appendicular and reniform anthers (right arrow) (Taken and modified from Hallé, 1986, 1990). Bar = 1.0 mm.

Fig. 5. *S. annettae* complete flower, androgynophore (left arrow) (Taken and modified from Hallé, 1986, 1990). Bar = 1.0 mm.

Fig. 6. *S. annettae* two opposite stamens (bottom and top arrows) and disk pentagonal (left right). Bar = 1.0 mm.(Taken and modified from Hallé, (1986, 1990)

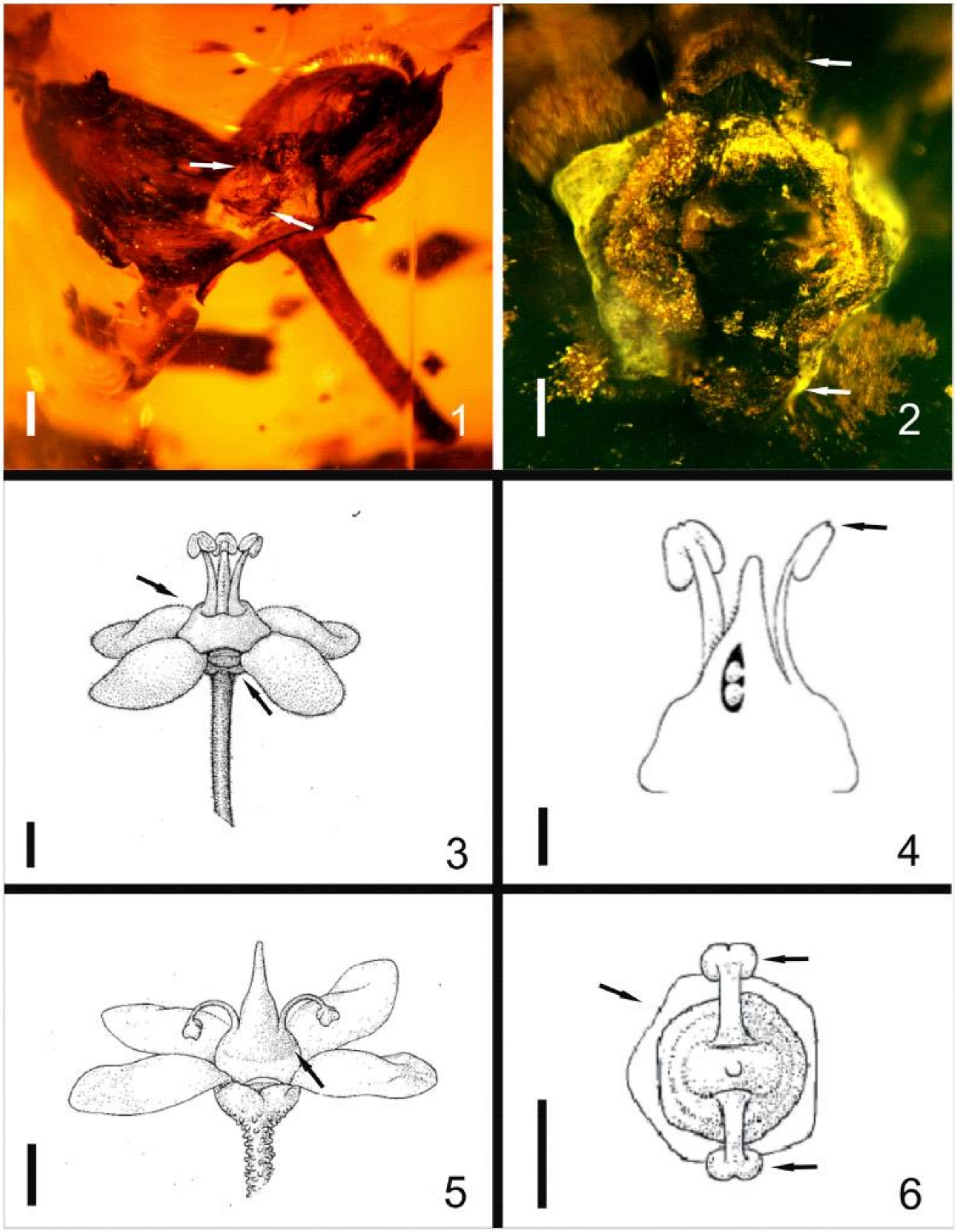

Plate III.

of *Salacia* that grow along in the Paleo and Neotropic regions. They support its identification as a new extinct species, *Salacia lombardii* Hernández-Damián, Gómez-Acevedo et Cevallos-Ferriz sp. nov., that represents the first Celastraceae fossil plant reported from Mexico.

While *Salacia lombardii* Hernández-Damián et al. sp. nov. also has a great morphological resemblance with species that currently grow in South America (e.g., *Salacia impresifolia*), the mosaic of characters present in the fossil material (Tables 1, 2) weakens any resemblance and taxonomic relationships. The morphological similarity of the fossil flower with those of plants from different geographic regions highlights the complex morphological or phylogenetic relationships within the subfamily (Hedin, 1999).

In Mexico two species of *Salacia* grow naturally, *Salacia cordata* (Miers) Mennega and *Salacia impresifolia*. They are distributed in the states of Veracruz (Castillo-Campos and Medina-Abreo, 2005; Lombardi, 2014), Tabasco (West, 1966; Pérez et al., 2005; Lombardi, 2014), Campeche (Dias et al., 2011), Oaxaca (Lombardi, 2014) and Chiapas (Breedlove, 1986). It is intriguing that the new species seems morphologically more similar to the Paleotropic species than to the ones growing naturally in Mexico. However, Smith (1940) pointed out that some species from Africa have a substantial resemblance to species of America.

The presence of *Salacia lombardii* et al. sp. nov. in southern Mexico suggests a history of at least ca. 23–15 My for the lineage in low latitude of North America. Its presence in the area coincides with a period in which increased morphological similarity between fossils and extant taxa has been documented. This was a time period of floristic "modernization" that prompted the establishment of current vegetation of Mexico (Cevallos-Ferriz et al., 2012). *Salacia lombardii* et al. sp. nov. is a good example of a Paleotropic plant that by that time was present in low latitude North America, and whose inclusion in phylogenetic or biogeographic studies will most probably become important in the generation of a better-sustained hypothesis.

The Boreotropical Flora Hypothesis (Wolfe, 1975) represents a great alternative to explain how the lineage extended its distribution to southern Mexico. Coughenour et al. (2010) and Bacon et al. (2016) suggest that Salacioideae was originated from a lineage of the Old World, where the greatest diversity of *Salacia* is currently documented. It concentrates more than 60 species, mainly in the tropical forest of Cameron and Gabon (Hallé, 1986, 1990).

Although the fossil record of Celastraceae at high latitude North America needs a critical review (Bacon et al., 2016), the available information supports its introduction to the Americas as part of the Boreotropical Flora. If Celastraceae arrived to the Americas from the Old World (Africa to Asia) their biogeographical expansion might have occur during the Cretaceous or Paleogene through intercontinental bridges formed by islands. Later, its arrival to Mexico and South America should have occurred during the Neogene, as suggests by the presence of *Salacia lombardii* Hernández-Damián et al. sp. nov. This biogeographical proposition is supported by the presence of *Baasia armendarisense* Estrada-Ruiz, Upchurch, Wheeler et Mack, a plant represented by its wood, from the Cretaceous of South-Central New Mexico, USA (Estrada-Ruiz et al., 2012), and leaves of *Celastrus comparabilis* Hollick from the Eocene the Gulf of Alaska Region (Wolfe, 1977). Other fossil reports are in needed of re-examination before being included in this history, like leaves of *Salacia miocenica* and *Salacia floribundifolia* Berry from the Miocene of India (Srivastava and Mehrotra, 2014) and Argentina (Berry, 1938) respectively; as well as the pollen reported from the Marshall Islands (Leopold, 1969).

The presence of *Salacia lombardii* Hernández-Damián et al. sp. nov. also improves the paleoenvironmental reconstruction for the depositional area. The plant that produced the fossil flower probably grew in the lowlands, where mangroves and a rain forest dominated by *Hymenaea* L. flanked streams and rivers of a deltaic system (Langenheim, 1966; Langenheim et al., 1967; Solórzano-Kraemer, 2007). In the rain forests of the Neotropics most *Salacia* species are lianas (Gentry, 1991), and grow in association with *Hymenaea*, as in El Cerrado, in southern Brazil; however, *Salacia* also forms part of gallery forests, especially where the savanna and rain forest come in contact (Felfili et al., 2000). A similar scenario can be depicted for the Simojovel de Allende, Chiapas, region during the time of amber deposition.

5. Conclusion

Salacia lombardii sp. nov. (Salacioideae-Celastraceae) is the first fossil record of the family reported in low latitudes of North America. This new Miocene fossil flower amber from Mexico has a mosaic of morphological characters comparable with extant species of the Paleo and Neotropics. The presence of *Salacia* in southern Mexico confirms the importance of the Boreotropical Flora Hypothesis to understand the origin of extant Mexican vegetation, and highlights that it is fundamental to incorporate paleo and neobotanical data to the discussion.

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CAPÍTULO III. EXPLORANDO LA RELACIÓN FILOGENÉTICA DE UNA ESPECIE EXTINTA DE *SALACIA*

Phylogenetic position of a Miocene species of *Salacia* from Mexican amber and its biogeographical implications.

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Abstract

Amber deposits from Chiapas, Mexico, provide evidence of a tropical forest in low latitude of America during the Miocene. Unfortunately, they have a scarce fossil record of plants, and the most part of them have been related to extant taxa of the Neotropical region. Here, we analyzed the phylogenetic position of *Salacia lombardii* (Salacioideae-Celastraceae), a Miocene flower with two stamens. The floral structural pattern of Salacioideae (Celastraceae) is uncommon because its pentamerous perianth and typically trimerous androecium. To evaluate the relationship between *S. lombardii* with their potential near relatives we used a combined matrix previously generated of molecular data combined with morphological characters from 6 genera and 28 species of Salacioideae through of the parsimony criterion. The topology of the strict consensus tree reported here is consistent with that of previous analyses for Salacioideae and we recovered a Neotropical clade. *Salacia lombardii* has an ambiguous position causing a polytomy among the Paleotropical species in the consensus tree. Nevertheless, there are only three alternative positions. Among them, we propose that *S. lombardii* is sister to *S. erythorcarpa*, due to is consistent with previous studies forming a small clade of species with two stamens. Furthermore, the close relationship between *S. lombardii* and the Paleotropical species suggests that taxa with two stamens had a circumtropical distribution in the past. We believe that Neotropical taxa with two stamens went extinct during the Miocene due to a decrease in temperature in the area.

Key words: disjunct pattern, Salacioideae, Mexican amber, Miocene, Neotropical flora.

1. Introduction

Amber deposits from Chiapas, Mexico, are unique in the world due to their age and geographic location (Solórzano-Kraemer, 2010). Particularly, their paleobotanical evidence is relevant because provides information to understand biodiversity in low latitude North America complementing the Neotropical flora concept (Castañeda-Posadas and Cevallos-Ferriz, 2007).

Unfortunately, the records of plant inclusions in the zone are relatively scarce in comparison to other biological groups (Avendaño-Gil et al., 2012, Hernández-Hernández et al., 2020). Most of them suggest an affinity with taxa that currently grow in the area due to the morphological similarity recognized between them (Solórzano-Kraemer, 2007; Cevallos-Ferriz and González-Torres 2006; Cevallos-Ferriz et al., 2012; Solórzano-Kraemer, 2015). However, this relationship hypothesis between extinct and extant plants has not been evaluated through a phylogenetic context.

Until recently, a flower of *Salacia lombardii* was identified in the Mexican amber (Hernández-Damian et al., 2018). It has a dimerous androecium comparable with species currently growing in Africa (Salacia annettae and S. lebrunii), Australia (*S. erythrocarpa* and *S. disepala*), and Indonesia (*S. forsteniana*) (Ding Hou, 1962; Hedin, 1999; Coughenour et al., 2010). The description of S. lombardii suggested a paramount question, since previous phylogenetic studies (Simmons et al., 2001a,b; Coughenour et al., 2010, 2011) have shown that *Salacia* has a clade of Neotropical species with three stamens, while the two-stamen species form part of a Paleotropical lineage (Coughenour et al., 2010). Therefore, the inclusion of the fossil of Salacia lombardii in the phylogenetic framework can address the question of whether the two stamens condition in the genus originated independently twice (once in the Neotropics and another time in the Paleotropics) or the two stamens from the Neotropics represents an ancestral extension of the geographic distribution for the clade that is nowadays restricted to the Paleotropics.

Hence, the objectives of this paper are to infer the phylogenetic position of the extinct Neotropical two-stamen fossil of Salacia, and to discuss its implications on the historical geographic distribution.

2. Material and method

2.1 Data collection of paleontological material

Salacia lombardii is included in a single amber piece (holotype 1351 IGMPB). The type locality is Simojovel, Chiapas, and the age is middle-early Miocene (Hernández-Damián et al., 2018) (Fig. 1).

2.2 Cladistics analysis

To evaluate the phylogenetic position of the fossil, we used a combined matrix of morphological and molecular characters previously published by Coughenour et al. (2010). This matrix was submitted to TreeBase and can be located under study number S10157. Two phylogenetic analyses were performed to assess the relationship between *Salacia lombardii* and extant members of Salacioideae.

2.3 Taxonomic sampling (outgroup and ingroup)

According to Nixon and Carpenter (1993) the outgroup should include taxa with more inclusive synapomorphies in comparison with the study group. This group can be recognized through previous phylogenetic studies. Simmons and Hedin (1999) and Simmons et al. (2001b) in a phylogenetic analysis based on morphological and molecular characters recognized Lophopetalum and Kookona as the sister group of Salacioideae, while in another study Coughenour et al. (2010, 2011) suggested *Sarawakodendron* as the sister group. Here we included these three taxa as the outgroup.

For sampling within the subfamily, we subsampled the Salacioideae matrix of Coughenour et al. (2010) to include 28 terminals that represent all genera in the subfamily: *Salacia, Peritassa, Tontelea, Cheiloclinium*, *Thyrosalacia,* and *Salacighia.*

2.4 Morphological characters

The morphological dataset published by Coughenour et al. (2010) was used here as the starting point, which in turn is based on Simmons and Hedin (1999), Simmons et al. (2001a, b) and Islam et al. (2006). To be able to include the fossil flower of *Salacia* in the combined analysis, a synthesis of morphological characters of Salacioideae with emphasis on the flower was generated through a review of the work of Simmons and Hedin (1999), Hedin (1999) and Coughenour et al. (2010) (Appendix A). The final matrix included 35 discrete characters coded as binary (19) and multistate (16), of which (22) correspond to those of Simmons and Hedin (1999), (27) to Hedin (1999) and (18) to Coughenour et al. (2010) (Appendix B). To minimize a priori assumptions about the relative value of the characters, all of them were unweighted and the multistate characters were treated as unordered (Jud et al., 2018).

2.5 Molecular characters

We used the alignment published by Coughenour et al. (2010), which includes plastid (matK, trnL-F) and nuclear (ITS and 26S rDNA) genes. All molecular data were coded as missing (?) for the fossil.

2.6 Cladistics analyses

Fusion of molecular and morphological matrices was performed using the program WinClada version 1.00.08 (Nixon, 2015); the combined matrix includes 31 morphological characters and the aligned sequence data from Coughenour et al. (2010), of which 421 characters are potentially informative (Appendix B).

2.7 Parsimony analyses

Parsimony analyses were performed with NONA (Goloboff, 1999) using the traditional search option and following the standard strategy suggested by Nixon (2015) for matrices with less than 120 terminals: searches using the TRB algorithm on Wagner trees constructed with random sequence addition, with 10000 repetitions in groups of 100, retaining 50 trees on each of them. Ambiguously supported branches were collapsed on the most parsimonious trees (MPTs), and identical and suboptimal trees were removed before the calculation of the consensus tree. To calculate the level of stability or robustness of the clades (Holmes, 2003) a bootstrap analysis (Felsenstein, 1985) was carried out also in NONA, using 1000 repetitions and saving the consensus tree on each of them.

Character mapping was performed using the ‘‘unambig’’ option in WinClada (unless otherwise stated), which only has character transformations (polarity and node) that do not change depending on the different optimization criteria (e.g., both DELTRAN and ACCTRAN). Using this optimization avoids misleading character changes that might be interpreted as synapomorphies when in fact other equally parsimonious interpretations are possible.

3. Results

The cladistics analysis yielded 36 equally parsimonious trees of 1268 steps (L), consistency index (CI) of 0.54, and retention index (IR) of 0.69. The strict consensus tree (Fig.1A) was L=1808, CI=0.59, and RI= 0.61, with a Neotropical clade including several species of Salacia, Cheiloclinium, Peritassa and Tontelea. This major clade is part of a larger polytomy with the paleotropical species of Salacia, the two-stamen species (including the fossil), and species of Thyrosalacia. This polytomy is the result of the ambiguous position of the fossil, which involves three equally parsimonious alternative solutions: 1) as sister to the entire subfamily, supported by orbicular petals (character 13/character state 3), and deltoid style (28/0); 2) as sister to Thyrosalacia, supported by triangular shape of the anther (20/1; acctran) and oblique anther dehiscence plane (23/1); and 3) as part of the two-stamen clade, supported by two stamens plus staminoids (19/2; acctran), bilobate stigmas (29/1; acctran), one ovule per locule (30/0; acctran), and more precisely within this clade, as sister to S. erythrocarpa by regular calix symmetry (10/0).

4. Discussion

Our hypothesis was constructed with the aim of establishing the phylogenetic position of an extinct species of *Salacia* recognized through its flower. Since the characters coded for the fossil were restricted to floral morphology (18 characters), its phylogenetic position is inherently unstable (Hermsen et al., 2006). However, the consensus tree in our analysis is mainly congruent with the one presented by Coughenour et al. (2010). One of the differences is the position of Salacighia letestuana as part of the Paleotropical polytomy instead of as the sister to the Paleotropical clade (Coughenour et al., 2010). This together with the unstable position of S. nitida, results in the more inclusive polytomy, partly affected by the fossil position. Despite the little number of characters coded for the fossil, the main polytomy produced by the inclusion of the fossil is resolved with only three alternatively equally parsimonious solutions (Fig. 1B-D).

In the consensus tree obtained from 3 MPT’s Salacia lombardii support value is low (35). This low value constitutes an indirect measure of the characters that support the topology (Holmes, 2003), and is influenced by the fact that the information of the new fossils is mainly restricted to morphology. Cobbett et al. (2007) suggests an objective way to evaluate the influence of fossils on tree stability through bootstrap analysis and the low support of *S. lombardii* could be interpreted as sending an equivocal signal. However, it has been noted that fossils commonly have low bootstrap values compared to extant taxa (e.g., Martínez-Millán & Crepet 2014; Toledo et al., 2018; Díaz-Cruz et al., 2019) as is the case of *S. lombardii*.

An increase in taxonomic sampling may has a positive effect on the accuracy of phylogenetic inference (e.g., Hillis et al., 2003). This is reaffirmed when terminals are considered as species with a "key" position (Wang et al., 2016). In our case, key species include Salacia with two stamens, however few molecular data are available for Salacioideae and their use can reduce robustness in the analysis (e.g., Hillis, 1998). Therefore, we suggest to continue with the research of the intergeneric relationships in the subfamily.

The Neotropical region is a hotspot of extant angiosperms; however, the origin of its biodiversity is still a topic highly debatable. To address this problem, the fossil record provides relevant insights about the history of its integration (Burnham and Graham, 1999; Bardon et al., 2013). The deposits of amber from Chiapas, Mexico, are among the most important resources for the reconstruction of former terrestrial environments, especially in tropical and subtropical regions of the Neotropics (Solórzano-Kraemer et al., 2015). The fossil plants reported in the Mexican amber have been related with extant taxa that currently grow in the Pacific coast (Solórzano-Karemer, 2007; Cevallos-Ferriz & González-Torres, 2006; Cevallos-Ferriz *et al.*, 2012; Solórzano-Kraemer et al., 2015). However, it is not the case of *Salacia lombardii* according to its phylogenetic position.

All hypotheses generated in this study support the biogeographic affinity of *Salacia lombardii* with extant Paleotropic species. According to Coughenour et al. (2010) Salacioideae had its origin in the Old World followed by a radiation event in the New World. Bacon et al. (2016)

support this hypothesis though a biogeographical study of Malagasy species of Celastraceae and suggest an age of divergence of Neotropical clade ca. 41-38 Ma ago, during the Eocene-Oligocene. There are various hypothesis to explain the historic distribution of linages with disjunctive distribution (Peris et al. 2015). The Boreotropical Flora Hypothesis (Wolfe, 1975) represents a viable explication about the presence of Celastraceae in Neotropical region, based on its fossil record in America (e.g. Wolfe, 1977; Estrada-Ruiz et al., 2012; Franco, 2018); however, for Salacioideae the only fossil record that supports this idea is Salacia lombardii from the Mexican amber (Hernández-Damián et al., 2018).

This disjunct distribution pattern recognized in *Salacia* is comparable with other linages reported in the Mexican amber, such is the case of *Hymeneae* (Fabaceae). It has been identified through isolated structures as two species: Hymeneae mexicana (Poinar and Brown, 2002) and *H. allendis* (Calvillo-Canadell et al., 2010). Nowadays, *Hymenaea* has an amphi-Atlantic distribution (Langenheim and Lee, 1974; Langenheim, 2003). In the Paleotropic it is represented by Hymenaea verrucosa, that is found in East Africa and Madagascar and is considered the most primitive species of the genus (Lee and Langenheim, 1975; Langenheim, 2003; Fougère-Danezan et al., 2010).

Other examples of disjunct biogeographic pattern have been reported in members of the Mexican amber entomofauna (Solórzano-Kraemer, 2007; Vršanský et al., 2011). A nice example includes *Mastotermes*, a termite that is currently growing in Australia and New Zealand (Solórzano-Kraemer, 2007), as well as cockroaches of the genus *Supella* and *Allacta* (Vršanský et al., 2011) with the same disjunction. Even more, abundant presence of *Cenocephalus* and *Hymenaea* is comparable to nowadays relationship insect-plant between *Mitosoma* and *Hymeneae verrucose* from Paleotropic region (Peris et al., 2015).

In the tropical region the change in vegetation during the Miocene has been poorly studied and requires of further documentation (e.g., Becerra, 2005; Sosa et al., 2018). Nevertheless, the loss of taxa with wide distribution during the Miocene of southern Mexico is possibly due to the development of a period of cooling in the oceans during the Seravaliiano (13.65-11.61 Ma), which in the continent led to a period of drought (Becerra, 2005; Solórzano-Kraemer, 2007;

Vršanský et al., 2011). This idea is supported by the ecological tolerances and habitat preferences of mangrove vegetation that have remained similar since the Miocene (Plaziat et al., 2001).

The new observations further improve fossil evidence allowing for deeper insights into morphological changes through time and supporting the establishment and diversification of lineages (Heinrichs et al., 2014). At the subfamily level, a modification of the ancestral condition of three stamens, to two stamens, as in *Salacia annetae, S. lebrunnii, S. disepala, S. erythrocarpa, S. forsteniana* and *S. lombardii* (Ding Hou, 1962; Hallé, 1986, 1990; Coungheour et al., 2010, Hernández-Damián et al., 2018) has been documented. Our analysis suggests two possibilities about the meristic androecium reduction in Salacioideae. The first is supported by the position of S. lombardii as sister to Salacioideae or as sister to *Thyrosalaci*a (Fig. 1B, C), which would imply at least two independent reductions, and the second is based on the phylogenetic position of *S. lombardii* within the two-stamen clade, as sister to *S. erythrocarpa*, which would imply a single reduction event.

The first two alternative positions of the fossil in our analysis (Fig. 1B, C) would conflict with the conclusion of Coughenour et al. (2010), who, based on living species suggested a single origin for the two stamens condition within the subfamily. Nevertheless, there is still a parsimonious solution for the position of the fossil that corroborates this hypothesis (Fig. 1D, E). However, this situation may change drastically as more in-depth morphological studies are integrated into a phylogenetic context as well as the taxonomic sample is expanded.

5. Conclusions

The close relationship between *S. lombardii* and extant Paleotropic species enhances the biogeographic history of the linage in the Neotropical region, as a persistent element of a circumtropical group that collapsed after the Miocene cool period. In the same way, the position of *S. lombardii* as part of two-stamens clade is consistent and congruent with previous analysis of Salacioideae supporting the idea that the dimerous condition of androecium had a single origin in Salacioideae; however, this last idea requires the integration of neo and paleobotanical evidence of linage.

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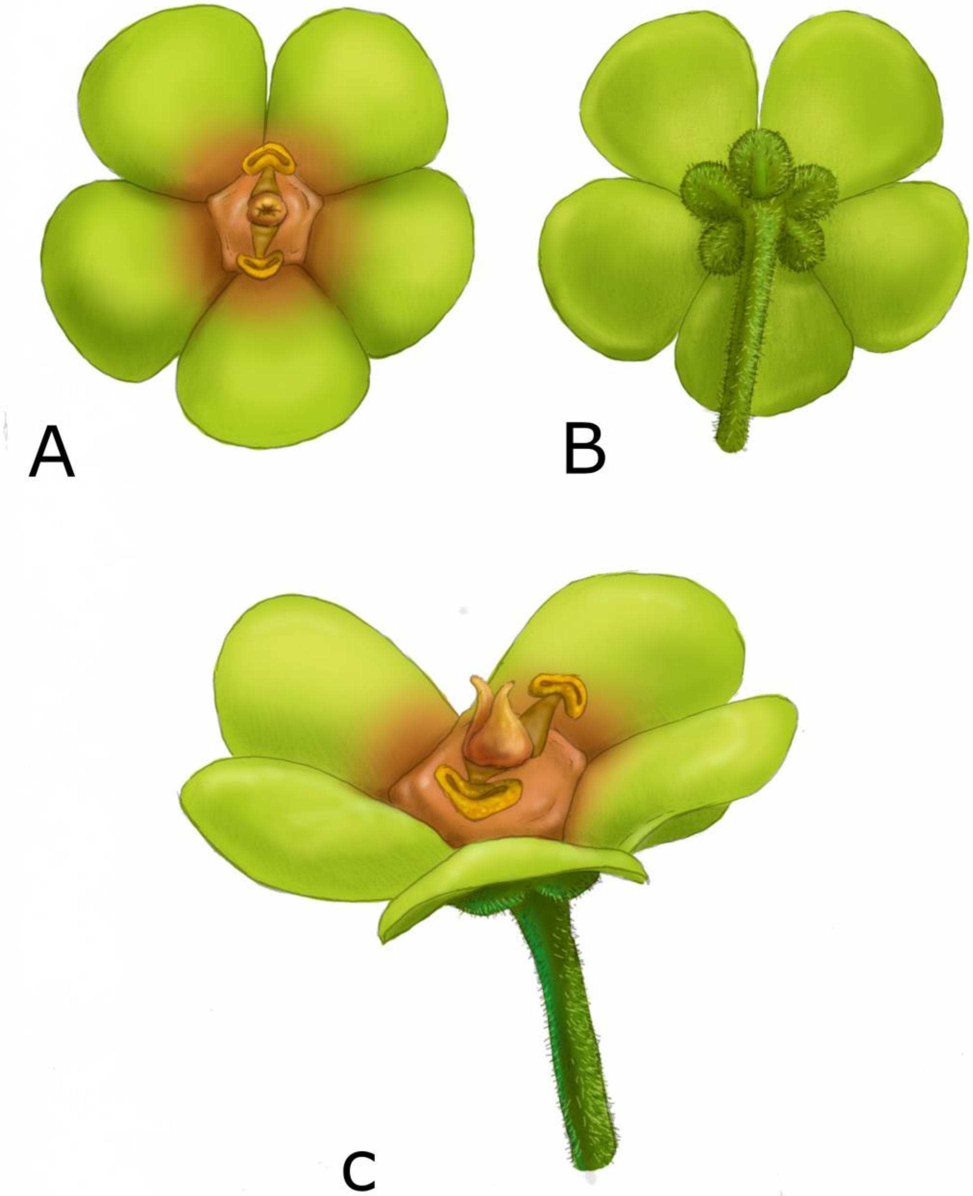
A
B
C

Fig.1. Reconstruction of *Salacia lombardii*. A. Flower top view, opposite two stamens and nectarial disk. B. Flower bottom view, pentamerous perianth. C. General view, Bisexual flower, pentamerous perianth, nectarial disk and dimerous androecium. The colouring was chosen here for artistic reasons.

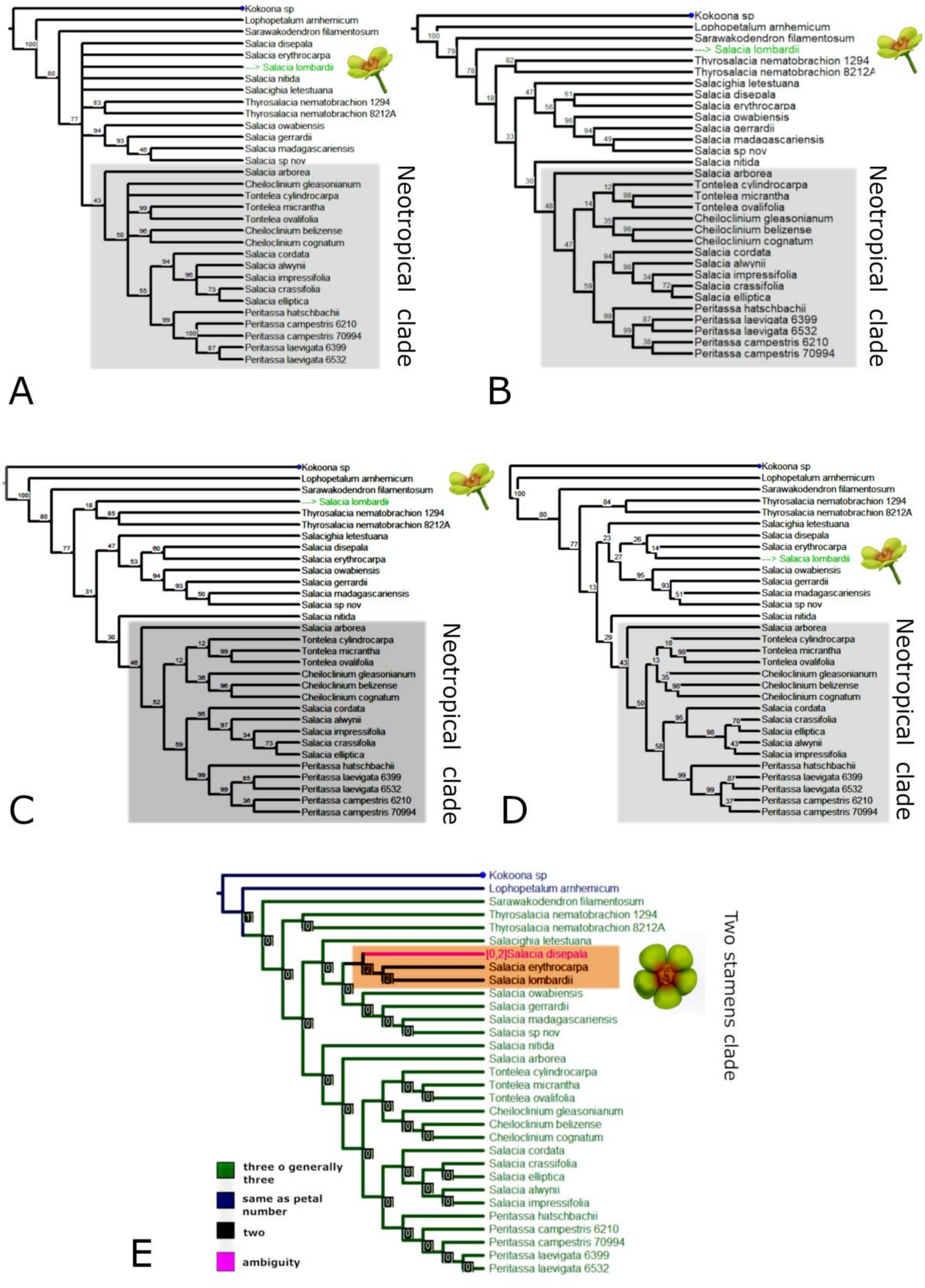
A
Kokoona sp
Lophopetalum arnhemicum
Sarawakodendron filamentosum
Salacia disepala
Salacia erythrocarpa
---> Salacia lombardii
Salacia nitida
Salacighia letestuana
Thyrosalacia nematobrachion 1294
Thyrosalacia nematobrachion 8212A
Salacia owabiensis
Salacia gerrardii
Salacia madagascariensis
Salacia sp nov
Salacia arborea
Cheiloclinium gleasonianum
Tontelea cylindrocarpa
Tontelea micrantha
Tontelea ovalifolia
Cheiloclinium belizense
Cheiloclinium cognatum
Salacia cordata
Salacia alwynii
Salacia impressifolia
Salacia crassifolia
Salacia elliptica
Peritassa hatschbachii
Peritassa campestris 6210
Peritassa campestris 70994
Peritassa laevigata 6399
Peritassa laevigata 6532
Neotropical clade
B
Neotropical clade
C
Neotropical clade
D
Neotropical clade
E
[0,2]Salacia disepala
Two stamens clade
three o generally three
same as petal number
two
ambiguity

Fig. 2. Phylogenetic positions of *Salacia lombardii* between members of Salacioideae with bootstrap values. In green Salacia lombardii. Purple box, Neotropical clade. (A) strict consensus tree *S. lombardii* is part of a polytomy (B) *S. lombardii* as sister group of Salacioideae. (C) S. lombardii as sister group *Thyrosalacia*. (D) *S. lombardii* as sister group of *S. erythrocarpa*. (E) Mapping of stamen plus staminode number (character 19). Number in the node is the character state. Green, three o generally three (character state 0). Blue, same as petals number (character state 1). Black, two (character state 2). Pink (ambiguity). Orange box, Two stamens clade.

Appendix A. Rejected characters in the cladistic analysis of Simmons & Hedin (1999), Hedin (1999) and Coughenour et al. (2010).

1. Rejected characters for cladistic analysis from Simmons & Hedin (1999). Reason(s) for rejection. “1”=inapplicable, “2”=invariant, "3" = unknow information from literature, “4”=lack independence from other character(s)

Character	Reason for rejection
1. Tendril presence	1
2. Thorn presence	1
3. Stem apices	1
4. Presence of glands on stems	1
6. Phyllotaxy on plants with alternate leaves	3,4
7. Leaf form	2
8. Leaf pubescence	1
9. Leaf venation	2
10. Leaf position	1
11. Domatia in axils of midrib and secondary veins	1
12. Distinct-crossbar tertiary leaf veins	1
13. Upper petiole angle	1
14. Stipule morphology on opposite leaves	1,3
17. Flower sexuality	2
18. Unisexual-flowered plants	1
19. Perianth merosity	2
20. Sepal gland presence	1
22. Corolla symmetry	3
23. Petal fleshiness	1
24. Petal conation	3
28. Disk pubescence	1
31. Fertile stamen length	1
32. Staminode presence in the same flower with functional stamens	1
33. Stamen-petal arrangement	2
34. Numerous stamen arrangement	1
35. Filament insertion relative to disk	2
41. Ovary pubescence	1
42. Apical hollow in ovary center	1
43. Style connation	3
45. Ovary septa walls	3
47. Placentation	3
48. Axile ovule attachment	3
49. Obturator presence	1
52. Fruit wing form	1
54. Mericarp connation	1
53. Capsular fruit shape	2

55. Capsular fruit dehiscence	1
56. Aril presence	1,4
57. Aril position seed	2
59. Fleshy aril form	1
60. Basal seed wing form	1
61.Rapha branching	1
62. Endosperm presence	2
63.Exotemic palisade of lignified malpighian cells present on seed	1
64. Seed tegmen composition	2,3
65. Seed germination type	2,3
66. Seedling growth	2,3
67.Mucilaginous leaf epidermal	3
69.Crystal type	3
70.Vascular strand trough petiole in cross section	2
72. Ray width	2.3
73.Unlignified ray cells on the growth ring border presence	2
74.Perforation plate type	2
75.Parenchyma-like bands of thin-walled septate wood fibers presence	2
76. Pollen aggregation	2,3
78.Base chromosome number	2,3
79. Haploid chromosome number of plants with base chromosome number of 14.	2,3

2. Rejected characters for cladistic analysis from Hedin (1999). Reason(s) for rejection. “1”=inapplicable, “2”=invariant, "3" = unknow information from literature, “4”=lack independence from other character(s)

Character	Reason for rejection
3. Leaf blades monochromatic when dry	1
5. Leaf blade edge	3
6. Venation forming bullates	3
7. Leaf blade Surface	3
10. Inflorescence internodes	4
13. Flower color	3
14. Flowers turning black when dried	3
18.Petal aestivation	3
19.Nectary	2
25.Disk covering petal bases	2
26.Disk with horizontal groove around lateral edge	2
28.Stemen position at anthesis	3
36.Ovule position	2
39.Fruit color	3
41.Fruit with 3 ridges	3
42.Fruit lenticellate	3
43.Seed shape	3
44.Seed funicle	2,3
46.Aril color	3
47.Amount of seed enveloped by aril	3
48.Endosperm	2

3. Rejected characters for cladistic analysis from Coughenour et al. (2010). Reason(s) for rejection. “1”=inapplicable, “2”=invariant, "3" = unknow information from literature, “4”=lack independence from other character(s)

Character	Reason for rejection
1. Thorn presence	1
2. Stem apices	1
3. Presence of glands on stems	1
5. Phyllotaxy on plants with alternate leaves	3,4
7. Leaf form	2
8. Presence of upper pulvinus	2
9. Leaf pubescence	2
10. Leaf venation	2
11. Leaf position	2
14. Flower sexuality	2
15. Unisexual-flowered plants	1
16. Perianth merosity	2
18. Petal connation	3
19. Disk presence	2
22. Disk pubescence	2
23. Androgynophore presence	2
25. Fertile stamen length	2
26. Staminode presence in same flower with functional stamens	2
27. Numerous stamen arrangement	1,2
28. Numerous stamen number	1
29. Filament insertion relative to disk	2
34. Pollen aggregation	2
36. Ovary pubescence	2
37. Shape of ovary apex	2
38. Style position on fruit	2
39. Carpel number	2
40. Ovary septal walls	2
42. Placentation	3
43. Axile ovule attachment	3
46. Fruit wing form	2
47. Capsular fruit dehiscence	1
48. Mericarp connation	1
50. Aril presence	1,4
51. Aril position on seed	2
53. Non-arillate basal seed wing presence	1
54. Basal non-arillate seed wing form	1
55.Raphe branching	1
56.Endosperm presence	2

Appendix B. combined matrix based on Coughenour et al. (2010)

```
TABLE 1. Characters 0 - 45
                                  0    5    10   15   20   25   30   35
40   45
                                  |    |    |    |    |    |    |    |
|    |
Kokoona sp                        20*$0111?00000000113100111 01$20--
3021122023121
Lophopetalum arnhemicum           20*00101?0003001101?0?011100020--
3121322023121
Sarawakodendron filamentosum      210000-120103001100301210?00220--
0021103021021
Cheiloclinium belizense           011$011020$0011---
03012?0?1?21101212110302102 1
Cheiloclinium cognatum            *01101002002001---
030121001?21111212110302102 1
Cheiloclinium gleasonianum        00100100?0$3011---
03012???00211$?2????????????
Peritassa campestris 6210
$0*10101?1$12$0001011?000000211112121103021031
Peritassa campestris 70994
$0*10101?1$12$0001011?0000002111121???????????
Peritassa hatschbachii
00100110?00221000000011100?01$110121??????????
Peritassa laevigata 6399
*0110101?211$10001011 0000?0021100212110302103 1
Peritassa laevigata 6532
*0110101?211$10001011 0000?0021100212110302103 1
Salacia alwynii                   $01000-
??2$00000110301???01?2???2121103121021
Salacia arborea
$1*1011020002101100011210001021002121103021021
Salacia cordata
*01021101011$101010310210?000110*2121103021031
Salacia crassifolia               $00000-
020$2000000111?10?0021101212110302102 0
Salacia disepala                  10**00-
?12$?0?001?$????1??0*??10?2121303021021
Salacia elliptica                 *01000-
010000000*00011?10?002210?2121103021020
Salacia erythrocarpa              $01$00-
??010100?102?002?????1010?2121303021021
Salacia gerrardii                 00*200-
?1120310110011 1?1??01?110?2101303021021
Salacia impressifolia             *0*000-
0201000001001112100000210121211031 21021
Salacia lombardii                 ?????????00030011021011 1??001??????-----
------
Salacia madagascariensis          $1*200-
011101001000110$1??010110121??????????
Salacia nitida
00*$01012123000101001021000121120212110302 1021
```

```
Salacia owabiensis                011$00-
02210?10001011001??00021002101303021021
Salacia sp nov
??*?010???$???0?0?0?*?11??0??11??2?01303021021
Salacighia letestuana             000010-
11220$201110101210?01011002?21303021021
Thyrosalacia nematobrachion 1294
101001012200$$0110010111??01211102?23103001021
Thyrosalacia nematobrachion 8212A
101001012200$00110010111??01211102?23103001021
Tontelea cylindrocarpa
00102001?110200000030?210?00021012121103021021
Tontelea micrantha
$01$0101?1$20$0000000?210?00211012121103021321
Tontelea ovalifolia
0010011??01?$1000*0?0?210?00211??21???????????


TABLE 2. Characters 46 - 91
                                  46   51   56   61   66   71   76   81
86   91
                                  |    |    |    |    |    |    |    |
|    |
Kokoona sp
1132311330031022322222212021310313130000323320
Lophopetalum arnhemicum
1132310330031022302222212021310313130000323320
Sarawakodendron filamentosum      ----311320013232120302$---
21110313330030322300
Cheiloclinium belizense           ???????????????????????----
1110313330130322300
Cheiloclinium cognatum            31$233122001323210030--
12121110313330030322300
Cheiloclinium gleasonianum
??????????????????????????????????????????????
Peritassa campestris 6210         33$233122-11323312030--
12123111313330031322100
Peritassa campestris 70994
??????????????????????????????????????????????
Peritassa hatschbachii
??????????????????????????????????????????????
Peritassa laevigata 6399          133233022-
113233120302212123111313330031322100
Peritassa laevigata 6532          333233122-
113233120300012123111313330031322100
Salacia alwynii                   1133330220-
13232120302212121130303330030322302
Salacia arborea
1132331220013232130302212121110313330130322300
Salacia cordata
???????????????????????12121110313330030322300
Salacia crassifolia
1133330220013232120302212121130303330030322302
```

```
Salacia disepala                  ----
331220013232120302232121110313330130322300
Salacia elliptica
$133330220013232120 30$$12121130303330030322302
Salacia erythrocarpa              $13233122001323212030--
32121110313330030322300
Salacia gerrardii                 --32130220013232120 30--
12121110313320030322300
Salacia impressifolia             113333022001323212 0?0$$------
303033300 30322302
Salacia lombardii                 ----------------------------------------
------
Salacia madagascariensis          ???????????????????????---
21110313320030322300
Salacia nitida                    ---
2331220013232120302212121110313330030322300
Salacia owabiensis                31321312200132321 2030--
12121110313330030322300
Salacia sp nov
11321312200132321203000121211103133200 30322300
Salacighia letestuana             ???????????????????????-----------------
------
Thyrosalacia nematobrachion 1294  31$23312220132321 2030--
10131110211332030202300
Thyrosalacia nematobrachion 8212A 11$23312220132321 2030--
10131110211332030202300
Tontelea cylindrocarpa            ???????????????????????-----------------
------
Tontelea micrantha                $1021312200132321 2030--
12121110313330030322300
Tontelea ovalifolia
??????????????????????????????????????????????


TABLE 3. Characters 92 - 137
                                  92   97   102  107  112  117  122  127
132  137
                                  |    |    |    |    |    |    |    |
|    |
Kokoona sp                        0101331212332330201--------
1320010312320001001
Lophopetalum arnhemicum
0101331212322330201210002011120010332320003203
Sarawakodendron filamentosum
110231123013323022121000201???????????????????
Cheiloclinium belizense           130211133013323022101020001-----
30123133123103
Cheiloclinium cognatum
1302311330133230221010200011120030123123103103
Cheiloclinium gleasonianum
??????????????????????????????????????????????
Peritassa campestris 6210
1302111330133220221110220031320032323132001330
```

```
Peritassa campestris 70994
??????????????????????????????????????????????
Peritassa hatschbachii
???????????????????????????1320032123312001130
Peritassa laevigata 6399
1302111330133220221110220031320032123132001330
Peritassa laevigata 6532
13021113301332 2$2211102200313200323231320013 30
```

```
Peritassa campestris 70994
??????????????????????????????????????????????
Peritassa hatschbachii
???????????????????????????1320032123312001130
Peritassa laevigata 6399
1302111330133220221110220031320032123132001330
Peritassa laevigata 6532
130211133013322$221110220031320032323132001330
Salacia alwynii
1302311330133230221010200011300030123332001310
Salacia arborea                   130231133013323022101020001----
010123333001103
Salacia cordata                   13023113301332302210-------
3100030123132001330
Salacia crassifolia
1302311330133230221010200011300030123312001310
Salacia disepala
1302313330133210220010200011320012103333001113
Salacia elliptica
1302311330133230221010200011300030123332001310
Salacia erythrocarpa
1302313330133230220010200011320032102333021113
Salacia gerrardii                 1302311332123230221031200011 32-
232123332001113
Salacia impressifolia
130231133013323022101020001???????????????????
Salacia lombardii                 ----------------------------------------
------
Salacia madagascariensis
130231133212323$2210312002113202321233332001113
Salacia nitida
1102111330133230221010200011320010123332001103
Salacia owabiensis                130211133013323022103020001---
0232123332001113
Salacia sp nov
130231133212323$2210312002113202321233332001113
Salacighia letestuana             --------------
3222101020001???????????????????
Thyrosalacia nematobrachion 1294
1112311330123230321010200011322032123320001101
Thyrosalacia nematobrachion 8212A 11123113301332303210-------
1322032123320001101
Tontelea cylindrocarpa            --------------
32221010200013320030323332001101
Tontelea micrantha
1302111330133230221010200011320030123312001101
Tontelea ovalifolia
??????????????????????????????????????????????


TABLE 4. Characters 138 - 183
                                  138  143  148  153  158  163  168  173
178  183
```

```
                                  |    |    |    |    |    |    |    |
|    |
Kokoona sp                        312222021011312313212112002331-2220----
13213--
Lophopetalum arnhemicum           2122210012131223112321120023111222 0----
21223--
Sarawakodendron filamentosum
??????????????????????????????????????????????
Cheiloclinium belizense
3120222212131131110101323321110222110033212231
Cheiloclinium cognatum
3120222232131131110001323321110222110023212231
Cheiloclinium gleasonianum
??????????????????????????????????????????????
Peritassa campestris 6210         1312022223123332311 3233---3211-
122232233213231
Peritassa campestris 70994
??????????????????????????????????????????????
Peritassa hatschbachii            13120322211031111123233---3211-
112232231212211
Peritassa laevigata 6399          13120222231233323113233---3211-
122212233213231
Peritassa laevigata 6532          13120222231233323113233---3211-
122232233213231
Salacia alwynii                   131202222032313111032132332111-
222130233212231
Salacia arborea                   312020221213313111012132332111-
022132233232231
Salacia cordata                   13120222223231311121233---2111-
022130233233233
Salacia crassifolia               131202222032313111012332332111-
222130233012231
Salacia disepala                  120212212221333110232132312111-
022130231232211
Salacia elliptica                 131202222030313111012332332133-
222130223012231
Salacia erythrocarpa              120212212213113111012132312111-
02213023$232211
Salacia gerrardii                 120232212213311312010130312113-
020130231232213
Salacia impressifolia
??????????????????????????????????????????????
Salacia lombardii                 ----------------------------------------
------
Salacia madagascariensis          120232212213311312010132312113-
220130231232211
Salacia nitida                    312022221211313111002132332111-
222110233232231
Salacia owabiensis                120232212213321311010132312111-
020132231232211
Salacia sp nov                    120232212213311312010130012113-
020130231232211
```

```
Salacighia letestuana
??????????????????????????????????????????????
Thyrosalacia nematobrachion 1294  31202222121111311121213233221 1-
022130233222230
Thyrosalacia nematobrachion 8212A 312022221211113111212132332211-
022130233222230
Tontelea cylindrocarpa            322022221213033111012132132111-
002132233212231
Tontelea micrantha
3120202212131131110121323321111012332231232231
Tontelea ovalifolia
??????????????????????????????????????????????
```

TABLE 5. Characters 184 - 229

```
                                  184  189  194  199  204  209  214  219
224  229
                                  |    |    |    |    |    |    |    |
|    |
Kokoona sp                        31110-20121213211200032231 1200-2-
31232311--211
Lophopetalum arnhemicum           11112-1302121321120003021 1120--003----
??131211
Sarawakodendron filamentosum
??????????????????????????????????????????????
Cheiloclinium belizense           00111113--32312302030100112020-2-
2012313312332
Cheiloclinium cognatum            00111-121332112312120000112020-2-
2012313312112
Cheiloclinium gleasonianum
??????????????????????????????????????????????
Peritassa campestris 6210         002320111312112312100000113022-2-
0012303322312
Peritassa campestris 70994
??????????????????????????????????????????????
Peritassa hatschbachii            102132111312113312120000111322-
000212313312312
Peritassa laevigata 6399          002320111312112312100000113022-2-
2012303322312
Peritassa laevigata 6532          002320111312112312100000113022-2-
2012303322312
Salacia alwynii
0013201113323133321300001320020020212313332312
Salacia arborea                   001120111312112312120000112020-2-
0012313312312
Salacia cordata                   001100131332112312110000031320--
020212313332312
Salacia crassifolia
0011201113023133321100001320002020212313332312
Salacia disepala                  201102112303113312130102111020-2-
0010313032312
Salacia elliptica
0011201113323133321300001320000020212313332332
```

```
Salacia erythrocarpa              201122102303110332130022111022-2-
0012313032312
Salacia gerrardii                 201102112303111312320002111020-2-
0012313032312
Salacia impressifolia
??????????????????????????????????????????????
Salacia lombardii                 ----------------------------------------
------
Salacia madagascariensis          2011021123031113123$0002111020-2-
0012313032312
Salacia nitida                    021100111332111310120000110020-2-
0032113331312
Salacia owabiensis                201102312303113312300002111020-2-
0012313032312
Salacia sp nov                    201101112303111312320002111020-2-
0012313032312
Salacighia letestuana
??????????????????????????????????????????????
Thyrosalacia nematobrachion 1294  00310-311332312310102002110020-2-
0012313331312
Thyrosalacia nematobrachion 8212A 00310-311332312310102002110020-2-
0012313331312
Tontelea cylindrocarpa            00131-031302132332120000113020-2-
2212313332313
Tontelea micrantha                00112311113211231212000011200220--
123211312312
Tontelea ovalifolia
??????????????????????????????????????????????
```

TABLE 6. Characters 230 - 275

```
                                  230  235  240  245  250  255  260  265
270  275
                                  |    |    |    |    |    |    |    |
|    |
Kokoona sp
012322220322323103332033?210311211031113121110
Lophopetalum arnhemicum           0121202203233031203020332-
11231213131113101111
Sarawakodendron filamentosum
??????????????????????????????????????????????
Cheiloclinium belizense           010012202121303-1313201100130112310001-
3103111
Cheiloclinium cognatum            010012222121303-
131320110013211231031011133101
Cheiloclinium gleasonianum
??????????????????????????????????????????????
Peritassa campestris 6210
2120322033233031103320112230211231031131101011
Peritassa campestris 70994
??????????????????????????????????????????????
Peritassa hatschbachii
2120222032213031103320112231211230123113101-11
```

```
Peritassa laevigata 6399          21203220332330311033201122302112310321-
3101011
Peritassa laevigata 6532          21203220332330311033201122300112310321-
3101011
Salacia alwynii
2320222033213031330322112020211231031133101*11
Salacia arborea
012202201323301131332011021021123103113311-110
Salacia cordata                   232022201321303133332211221021103100121-
--112-
Salacia crassifolia
2120022022313031330322112020211031031133101111
Salacia disepala
3122012210210330033320112011230211231131311113
Salacia elliptica
2120222013213031130322112020231031031133101111
Salacia erythrocarpa
31220122102102300333201120132302112311313-----
Salacia gerrardii
3122013233213030133300112210232210123113131101
Salacia impressifolia
??????????????????????????????????????????????
Salacia lombardii                 ----------------------------------------
------
Salacia madagascariensis
3122013233213030133320112210230210123113131101
Salacia nitida
0120222011213031133020110230211233031131321-11
Salacia owabiensis
3122012233213030133320112210232210123113133101
Salacia sp nov
3122013233213030133320112210232210103113131101
Salacighia letestuana
??????????????????????????????????????????????
Thyrosalacia nematobrachion 1294
0120322013223031133310110030211211001133120111
Thyrosalacia nematobrachion 8212A
0120322013223031133310110030211211001133320101
Tontelea cylindrocarpa
0120022013213031133320112230211031333033101111
Tontelea micrantha                012022223231331133332011223021101103112-
-03-11
Tontelea ovalifolia
??????????????????????????????????????????????
```

TABLE 7. Characters 276 - 321

```
                                  276  281  286  291  296  301  306  311
316  321
                                  |    |    |    |    |    |    |    |
|    |
Kokoona sp                        3-13-1----
32022001200021320331311202132313321-
```

```
Lophopetalum arnhemicum           3-13-1----
13020201003201300330311232132313321-
Sarawakodendron filamentosum
??????????????????????????????????????????????
Cheiloclinium belizense           3-31-
01011301220002221333303310212123002313101
Cheiloclinium cognatum            111----01132-
220002221313303310212123002311101
Cheiloclinium gleasonianum
??????????????????????????????????????????????
Peritassa campestris 6210         --1213----
012200210312213323330212003002311101
Peritassa campestris 70994
??????????????????????????????????????????????
Peritassa hatschbachii            --1112----
022200210312033323110112203102311101
Peritassa laevigata 6399          --1213----
01222021$31221332333021200300231 1101
Peritassa laevigata 6532          --1213----
0120202103122133233$0212003002311101
Salacia alwynii                   --1323----
000200210332033303120001123002313123
Salacia arborea                   --03-1----
10022200210023330331021212300011131-
Salacia cordata                   ---113----
002322210312033303311202123002313121
Salacia crassifolia               --1321----
002200210332033301320001123002311121
Salacia disepala                  1-11-2---
0222200210312012303312232121002301121
Salacia elliptica                 --1321----
002200212332033301320001123002311121
Salacia erythrocarpa              -------------------
312012303312032121002301121
Salacia gerrardii                 1131-
21322222200210312012303312032121002111003
Salacia impressifolia
??????????????????????????????????????????????
Salacia lombardii                 ----------------------------------------
------
Salacia madagascariensis          1311-2---
0222200210312012303312032121002311001
Salacia nitida                    --1113----
00220021031201332331023212100011121-
Salacia owabiensis                1331-2---
0222200210312012303312032121002111021
Salacia sp nov                    1313-2---
0222200210312012303312032121002311001
Salacighia letestuana
??????????????????????????????????????????????
Thyrosalacia nematobrachion 1294  --11-
13130022300210312013323330332121002313121
```

```
Thyrosalacia nematobrachion 8212A --11-
1313002230021031201332333033212100231312 1
```

```
Tontelea cylindrocarpa            ----------
232000210312003003310222123002311121
Tontelea micrantha                ----------
202200210312033303310212123002311103
Tontelea ovalifolia
??????????????????????????????????????????????
```

TABLE 8. Characters 322 - 367

```
                                  322  327  332  337  342  347  352  357
362  367
                                  |    |    |    |    |    |    |    |
|    |
Kokoona sp                        310201322121032-
2212100232110022220221020201111
Lophopetalum arnhemicum           010201320120032-
221213022210013022021212120111
Sarawakodendron filamentosum
??????????????????????????????????????????????
Cheiloclinium belizense
0322033001012131201212021212000222202300222111
Cheiloclinium cognatum
0322013201012131201212021211000222202302222111
Cheiloclinium gleasonianum
??????????????????????????????????????????????
Peritassa campestris 6210         032200303323213020121002021300022220-
020022131
Peritassa campestris 70994
??????????????????????????????????????????????
Peritassa hatschbachii            032200300123113120131202121222-022220-
022022111
Peritassa laevigata 6399          032200303323213020121002021300022220-
020022131
Peritassa laevigata 6532          032200303323213020121002021300022220-
020022131
Salacia alwynii                   0122233021032133201212031 21??-?22220-
002022111
Salacia arborea                   210301302303213120121202121100222200-
000022111
Salacia cordata                   012223303103213120121202121000222220-
002022111
Salacia crassifolia               012223302103213320323220101??-?22220-
002022111
Salacia disepala
0102230323032131201211221222222102200030020113
Salacia elliptica                 012023302103213320321203101??-?22220-
002022111
Salacia erythrocarpa
0102230023032131201231201222222102200030022113
Salacia gerrardii                 01222100330321310013112212222210210----
0202011
```

```
Salacia impressifolia
??????????????????????????????????????????????
Salacia lombardii                 ----------------------------------------
------
Salacia madagascariensis          01222100330321310013112212222210210----
0202011
Salacia nitida                    2202013023012131201212021211002222 00-
010020111
Salacia owabiensis                03222100230321310013112212222210210----
0202011
Salacia sp nov                    01202100330321310013112212222210210----
0202011
Salacighia letestuana
??????????????????????????????????????????????
Thyrosalacia nematobrachion 1294
0301013031212131203212021221022222021302020111
Thyrosalacia nematobrachion 8212A
0301013031212131203212021221022222021302020111
Tontelea cylindrocarpa            032201000103213120121202121102222220-
300222111
Tontelea micrantha                012001302321213120121202101032222220-
002222121
Tontelea ovalifolia
??????????????????????????????????????????????


TABLE 9. Characters 368 - 413
                                  368  373  378  383  388  393  398  403
408  413
                                  |    |    |    |    |    |    |    |
|    |
Kokoona sp                        201-2313110010-
2302013231012212311011123203131
Lophopetalum arnhemicum           201-2313110020---
022132112322123110111 23202131
Sarawakodendron filamentosum
??????????????0212201123123223011101112120 1131
Cheiloclinium belizense           2212313111003----
0201301101223031103112 1223131
Cheiloclinium cognatum            22123131110030---
0201301101223031103112 1223131
Cheiloclinium gleasonianum        ??????????????-
2102013231212230311031121223131
Peritassa campestris 6210         2212313131001----
0233301303223031103110 1223131
Peritassa campestris 70994        ??????????????-
2102333013032230311031101223131
Peritassa hatschbachii
2212313131023000102333013032230311033101223131
Peritassa laevigata 6399          22123131310010---
0233301303223031103110 1223131
Peritassa laevigata 6532          2212313131001-
02102333013032230311031101223131
```

```
Salacia alwynii                   0012313131201-
00102033031232032131231120123333
Salacia arborea                   221231333103---
0102033031232223031103112122313 1
Salacia cordata
021231313122100210201321123222323112311201 23133
Salacia crassifolia               0212313133203------
0330312320321312311201 23333
Salacia disepala                  20312333312202-
2101033231232223031103112122311 1
Salacia elliptica                 021231310320--
00102033031232032131231120123333
Salacia erythrocarpa              2031233331220--
2101033231032230311031121223111
Salacia gerrardii                 2013233331220----
21033231032230111031321223111
Salacia impressifolia             ??????????????-
0102033031230032131231120123333
Salacia lombardii                 ----------------------------------------
------
Salacia madagascariensis
2013233331220222121033231032230311031321223111
Salacia nitida                    2112313331022--
2102033231232223031103112122313 1
Salacia owabiensis                2010233331220----
21033231032230311031321223111
Salacia sp nov                    2013233331220-
221210332310322303110313212231 11
Salacighia letestuana
??????????????02103031231032230311033121223111
Thyrosalacia nematobrachion 1294
1000313333021000102033031033230313031101221131
Thyrosalacia nematobrachion 8212A 101-231331021-
00102033031033230313031101221131
Tontelea cylindrocarpa            03123131312------
02033011232223231103112122313 1
Tontelea micrantha
0212313101301000302013011212030311031121223111
Tontelea ovalifolia
??????????????00302013011212030311031121223111
```

TABLE 10. Characters 414 - 455

```
                                  414  419  424  429  434  439  444  449
454
                                  |    |    |    |    |    |    |    |
|
Kokoona sp                        0011033310021133231-2031311??3111----
11310
Lophopetalum arnhemicum           301101131002123 10-1120313110210111---
11311
Sarawakodendron filamentosum      10111123202212101131220131102111 11---
21111
```

```
Cheiloclinium belizense          30113301202212113310200113302121111--
21111
Cheiloclinium cognatum           30113301202212113310200113302121112--
21111
Cheiloclinium gleasonianum       30113101202212113331000113103101112--
21111
Peritassa campestris 6210
131133012022121133312021133021011122321131
Peritassa campestris 70994       1313330120221211333120211---------------
--
Peritassa hatschbachii           10111101202212113311202113322103132--
21111
Peritassa laevigata 6399
131333012022121131312021133021011110221131
Peritassa laevigata 6532
131333012022121131312021133021011102321131
Salacia alwynii
300103312222131033320021333023011111123111
Salacia arborea                  3011130120221211333100013310230111---
121111
Salacia cordata
301131312022121133310021333021013111221111
Salacia crassifolia              30010331222213303331002131302301110--
23111
Salacia disepala
001113012022123131112021331231010111121111
Salacia elliptica                30010331222213103331302133302301132--
23111
Salacia erythrocarpa
001113012022123131112021331231010110121111
Salacia gerrardii
001113012022123131112021331021010111121111
Salacia impressifolia            3001033122221310333100213330230111$--
23111
Salacia lombardii                ----------------------------------------
--
Salacia madagascariensis
001113012022123131112021331021010111121111
Salacia nitida                   3011130120221231313120213310210111---
21111
Salacia owabiensis
001113012022123131112021331021010111121111
Salacia sp nov
001113012022123131112021331021010111121111
Salacighia letestuana            3011330120221231313120213310213113---
21111
Thyrosalacia nematobrachion 1294  30113321202232313331220113102101110--
21313
Thyrosalacia nematobrachion 8212A 30113321202232313331220113102101110--
21313
Tontelea cylindrocarpa           3011330120221211113100013330210311---
21111
```

```
Tontelea micrantha
301111012020121131312003133021111111121111
Tontelea ovalifolia
301111012020121131312003133021111111121111



SUMMARY PERCENTAGES

MISSING (?): 2189 cells, 15 percent of matrix.
DASHES (-): 1027 cells, 7 percent of matrix.
TOTAL POLYMORPHISM ($ , *): 83 cells, 0 percent of matrix.
TOTAL FULL AMBIGUITY (? , -): 3216 cells, 22 percent of matrix.
TOTAL FULL + PARTIAL AMBIGUITY (? , -, *, $): 3299 cells, 23 percent of
matrix.
STATE (0): 2556 cells, 18 percent of matrix.
   STATE (0) EMBEDDED IN POLYMORPHISM: 67 cells, 0 percent of matrix.
STATE (1): 3350 cells, 23 percent of matrix.
   STATE (1) EMBEDDED IN POLYMORPHISM: 55 cells, 0 percent of matrix.
STATE (2): 2622 cells, 18 percent of matrix.
   STATE (2) EMBEDDED IN POLYMORPHISM: 42 cells, 0 percent of matrix.
STATE (3): 2309 cells, 16 percent of matrix.
   STATE (3) EMBEDDED IN POLYMORPHISM: 9 cells, 0 percent of matrix.


CHARACTER LIST (only named characters listed!)

0. PLANT HABIT:  liana = 0; shurb = 1; tree = 2. [nonadditive].
1. LATEX:  absent = 0; present = 1. .
2. ARRANGEMENT OF LEAVES:  alternate = 0; opposite or whorled = 1. .
3. TYPE OF MARGIN OF THE LEAF:  entire = 0; crenate = 1; dentate = 2.
   [nonadditive].
4. INFLORESCENCE POSITION:  axillary = 0; caulinar = 1; ramiflorous = 2.
   [nonadditive].
5. BRANCHING OF INFLORESCENCE:  absent = 0; present = 1. .
6. BRANCHING PATTERN OF INFLORESCENCE:  monopodial = 0; simpodial = 1. .
7. PEDICELS ARTICULATED:  absent = 0; present = 1. .
8. BUD SHAPE:  ovate = 1; globoso = 2. .
9. CALYX SYMMETRY:  regular = 0; subregular = 1; irregular = 2.
[nonadditive].
10. TYPE OF SEPALS MARGIN:  untoothed = 0; erose-dentate = 1;
    ciliate-fimbrate = 2. [nonadditive].
11. FORM OF COROLLA:  rotate = 0; tubuliform = 1; campaniform = 2;
urceolate = 3.
   [nonaddi
```

CONCLUSIONES GENERALES

Los fósiles son la única evidencia física y directa de la vida en el pasado, por lo cual son fundamentales para un mejor estudio y entendimiento de los grupos biológicos.

La morfolgía constituye la única fuente de información para el estudio del registro fósil, por lo que es fundamental un conocimiento profundo de la misma. En este trabajo se ejemplifica esta idea a través del establemiento de registros fósiles confiables de Celastraceae: *Baasia armendarisense*, *Cathispermum pulchrum*, *Celastrus comparabilis*, *Elaeodendroxylon* sp., *Hippocrateaceaedites*, *Lobocyclas anomala*, *Maytenoxylon perforatum*, *Salacia lombardii* y *Wuyunanthus hexapetalus*.

Los análisis morfológicos comparativos soportan la identificación de los fósiles, tal es el caso de *Salacia lombardii* (Salacioideae-Celastraceae) reconocida como una flor bisexual, con un perianto diferenciando y un disco nectarial incluida en el ámbar del Mioceno del sur de México.

La idea de relación entre los elementos florísticos preservados en el ámbar de México con taxones que actualmente crecen en la zona con base en la similitud morfológica fue puesta a prueba a través de la exploración de la posición filogenética de *S. lombardii* con sus potenciales parientes vivos más cercanos. A través de un análisis filogenético usando una matriz combinada de caracteres morfológicos y moleculares y como criterio de optimización parsiomonia se sustenta la relación cercana entre *S. lombardii* con especies actuales del Paleotrópico.

La familia Celastraceae ha sido reconocida como un linaje de origen Paleotropical, que posteriormente tuvo un evento de radiación en el Neotrópico. Esta idea es soportada a través de la presencia de una flor de *Salacia lombardii* preservada en el ámbar mexicano, la cual formaba parte de un linaje de plantas con un androceo dímero con una distribución circumtropical en el pasado.

La presencia de Celastraceae en los depósitos de ámbar de México, representa parte de la larga historia de la integración de los elementos florísticos en la región Neotropical, la cual puede ser explicada a través de la hipótesis de la Flora Boreotropical.

Este trabajo cumplió con los objetivos establecidos y constituye un ejemplo de los alcances y límites en la inclusión de los fósiles en un análisis cladístico, lo cual depende fundamentalmente de un estudio morfológico profundo con sus representantes actuales, por medio del cual sea posible el reconocimiento y establecimiento de hipótesis de relación entre ellos. Tal es el caso de la familia Celastraceae, en la cual se requiere un análisis y exploración de los caracteres mofológicos en un contexto filogenético.