



# Inclusions of flowers of *Podopterus* (Polygonaceae) in the Miocene amber of Simojovel de Allende, Chiapas, Mexico

## Inclusiones de flores de *Podopterus* (Polygonaceae) del ámbar del Mioceno de Simojovel de Allende, Chiapas, México

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### Abstract:

**Background and Aims:** The Miocene amber from Chiapas, Mexico, shows high diversity of biological inclusions such as plants, fungi, arthropods, and vertebrates, being one of the most important amber-bearing areas worldwide. The aim of this work is to describe a new record based on four bisexual flowers belonging to the fossil species *Podopterus mijangosae*, that has been described recently based on its winged fruits only.

**Methods:** The morphological and anatomical characteristics of the four fossil flowers were observed using a binocular stereoscopic microscope. The taxonomic affinity was decided by consulting specialized literature, as well as the review of herbarium material of the genera *Podopterus*, *Fallopia*, and *Neomillspaughia* of Polygonaceae.

**Key results:** The four fossil specimens are bisexual, small, and have actinomorphic flowers, with differentiated perianth, three petals and three sepals per series, stamens are free and with thread-like filaments, anthers are dithecal and basifixed, the ovary is superior, syncarpous, 3-angular, with three free styles, and capitate stigmas.

**Conclusions:** This new report of flowers of *Podopterus* adds more evidence that the family Polygonaceae was an important component of the tropical forest of Simojovel de Allende, Chiapas, Mexico, during the Miocene.

**Key words:** angiosperms, Cenozoic, flowers, Neogene.

### Resumen:

**Antecedentes y Objetivos:** El ámbar del Mioceno de Chiapas, México, presenta una alta diversidad de inclusiones biológicas como plantas, hongos, artrópodos y vertebrados, siendo una de las áreas productoras de ámbar más importantes a nivel mundial. El objetivo de este trabajo es describir un nuevo registro basado en cuatro flores bisexuales pertenecientes a la especie fósil *Podopterus mijangosae*, que ha sido descrito recientemente con base solo en sus frutos alados.

**Métodos:** Las características morfológicas y anatómicas de cuatro flores fósiles fueron observadas utilizando un microscopio estereoscópico. La afinidad taxonómica se realizó consultando literatura especializada, así como la revisión de material de herbario de los géneros *Podopterus*, *Fallopia* y *Neomillspaughia* de Polygonaceae.

**Resultados clave:** Los cuatro especímenes fósiles están representadas por flores bisexuales, pequeñas, actinomorfas, con perianto diferenciado, tres pétalos y tres sépalos por serie, estambres libres con filamentos filiformes, anteras ditecas, basifijas, ovario súpero, sincarpo, tri-angular, con tres estilos libres y estigmas capitados.

**Conclusiones:** Este nuevo reporte de flores de *Podopterus* agrega más evidencia de que la familia Polygonaceae fue un componente importante del bosque tropical de Simojovel de Allende, Chiapas, México, durante el Mioceno.

**Palabras clave:** angiospermas, Cenozoico, flores, Neógeno.

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## Introduction

The formally described fossil record based on fossil flowers from the Miocene amber from Simojovel de Allende, Chiapas, Mexico, is still scarce compared to the diversity which has not yet been described, but is observed in private and institutional collections (e.g., Colección Nacional de Paleontología (CNP), Universidad Nacional Autónoma de México (UNAM), Ciudad de México; Museo del Ámbar Lilia Mijangos, San Cristóbal de las Casas, Chiapas, Mexico). Recently, Poinar (2022) enumerated several fossil flowers and fruits from the Chiapas amber coming from different paleontological collections, although some records have not been described formally and their affinities still need more work. Among the published descriptions, there are fossil flowers and fruits belonging to Anacardiaceae, Arecaceae, Bromeliaceae, Fabaceae, Meliaceae, Metteniusaceae, Orchidaceae, Polygonaceae, Rhamnaceae, Salicaceae, and Staphyleaceae, (e.g., Miranda, 1963; Poinar and Brown, 2002; Castañeda-Posadas and Cevallos-Ferriz, 2007; Hernández-Damián et al., 2016, 2018; Hernández-Hernández and Castañeda-Posadas, 2018; Estrada-Ruiz et al., 2023), showing that the Chiapas forest was very diverse and complex.

The main distribution of the Polygonaceae family is in temperate zones of the world, although it is also well-represented in the tropics and subtropics. Approximately 43 genera and 1100 species are recognized worldwide (Arroyo, 2012). In Mexico, 17 genera with 142 extant species have been described (Solano and Ayala, 2008; Arroyo, 2012). Among the genera found in Chiapas is *Podopterus* Bonpl. (Solano and Ayala, 2008; Arroyo, 2012), an American genus comprising three species with a distribution in southern Mexico and Central America (Solano and Ayala, 2008; Estrada-Ruiz, 2023). *Podopterus* mainly grows in tropical to subtropical forests that are deciduous, as well as in thorny vegetation (Solano and Ayala, 2008; Hernández-Ledesma et al., 2015; Estrada-Ruiz, 2023). In Mexico *Podopterus* occurs in the states of Tamaulipas, Veracruz, Puebla, Yucatán, Colima, Guerrero, Michoacán, and Oaxaca (Solano and Ayala, 2008). Its species are shrubs and small trees of 1.5 to 8 m tall. Their flowers are bisexual with a perianth differentiated in two whorls; three sepals, fused at the base, decurrent wing on a pedicel; three thin flattened petals, erect with

venation, slightly elongating into fruit; stamens 6 to 8, free thread-like filaments, ovoid anthers; ovary 3-angular, styles 3, stigmas capitate (Solano and Ayala, 2008).

In Mexico, the fossil record of the family Polygonaceae is still very rare; there are only four records from the Miocene based on fossil wood (Baja California Sur), pollen grains (Chiapas), and winged fruits (Chiapas) (Palacios-Chávez and Rzedowski, 1993; Cevallos-Ferriz et al., 2014; Poinar, 2022; Estrada-Ruiz, 2023). The aim of this work is to describe a new record based on four bisexual flowers belonging to *Podopterus mijangosae* Estrada-Ruiz, that has been described recently based on its winged fruits only.

## Materials and Methods

The fossil sample has four embedded flowers, and was obtained in Simojovel de Allende, Chiapas, Mexico, directly by the artisans or amber collectors at Los Pocitos mines (Estrada-Ruiz, 2023, see page 190 for map of study area); these mines are found at 17°09'11"N, 92°46'08"W, located on the southwestern flank of the Simojovel syncline. The amber is extracted from the Los Pocitos mines and is collected in sediments from the middle Oligocene-early Miocene Simojovel Formation (De la Rosa et al., 1989; Serrano-Sánchez et al., 2015). This mine is characterized by the presence of carbonate and terrigenous sequences that resemble those exposed in the amber outcrops as observed in other localities as Montecristo, Guadalupe Victoria, El Porvenir mines in the same area. This stratigraphic mine section comes from the strata that comprise lignite with very fine and fine-grained sandstone with abundant iron oxides, some pyrite nodules deposited in facies oscillating from shallow platform to littoral conditions, where lagoon or mangrove swamps environments prevailed (Frost and Langenheim, 1974; Perrilliat et al., 2010; Serrano-Sánchez et al., 2015).

The four fossil flowers are embedded in one amber piece of ochre yellow to translucent amber with many bubble and other organic remains. All morphological and anatomical characters were observed and described using a stereomicroscope (Carl Zeiss GmbH, Göttingen, Germany). For photographing the morphological characteristics an AxioCam MRc5 camera (Zeiss AXIO Zoom V16, Oberkochen, Germany) and a SC100 digital camera of 10.5 Mpix



(OLYMPUS SZX10, Olympus, Tokyo, Japan) were used. The figures were elaborated using Corel Draw v. 2020 (Corel Corporation, 2020). To obtain the taxonomic affinity of the fossil flowers, an extensive bibliographical study including articles, fascicles, and books of Polygonaceae was carried out (e.g., Blake, 1921; Fedotov, 1991; Brandbyge, 1993; Manchester and O'Leary, 2010; Burke and Sánchez, 2011), and the database FAMEX polykey (Murguía and Villaseñor, 1993) was consulted. In addition, the fossil material was compared with material from the extant genera *Podopterus*, *Fallopia* Adans., and *Neomillspaughia* S.F. Blake (Polygonaceae) of the ENCB herbarium (Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional) (acronym as in Thiers, 2022). The specimens described (IPN-PAL 16) are deposited in the Colección de Paleontología (IPN-PAL), Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, located in Mexico City, Mexico.

## Results

### Taxonomy

#### Caryophyllales

#### Polygonaceae

***Podopterus mijangosae*** Estrada-Ruiz, Palaeoworld 32: 189. 2023. Figs. 1, 2, 3.

TYPE: MEXICO. Chiapas, Simojovel municipality, amber mines Los Pocitos, 17°09'11"N, 92°46'08"W, *Anonymous s.n.* (holotype: IPN-PAL 15!, paratype: MALM.95!, MALM.96!).

The description is based on four complete, bisexual, small, actinomorphic flowers, 6.9-8 mm long, 1.9-3 mm wide (Fig. 1A-C), pedicel slightly curved, 4-4.5 mm long (Fig. 1C); perianth differentiated into two whorls (Figs. 1B, C; 2C; 3), three sepals per series, outer ones long, each with a longitudinal groove along the main rib that expands into a thin wing (Fig. 2A-D), translucent, margin entire to undulate, partially fused at base, with a fine reticulate to fusiform venation, 2.6-3 mm long, 494-503 µm wide (Fig. 2A, B), three petals per series, flattened parts, erect, thin,

translucent with entire margin, venation irregular to reticulate (Figs. 2A, C; 3); androecium composed of eight stamens, free, filaments thread-like, anthers basifixed (Figs. 2C; 3), dithecal, ovoid, 313-376 µm long, 313-376 µm wide, dehiscence latrorse, aperture longitudinal (Fig. 2C, D); gynoecium connate at base, ovary superior, syncarpous, 3-angular, styles 3, free, 0.94-1.22 mm long; stigmas capitate (Fig. 2C, D).

Specimens studied: MEXICO. Chiapas, near the town of Simojovel de Allende, Los Pocitos mines, 17°09'11"N, 92°46'08"W, *Anonymous s.n.* (IPN-PAL 16 (Colección de Paleontología, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Mexico City, Mexico)).

Stratigraphic position and age: middle Oligocene-early Miocene, Simojovel Formation.

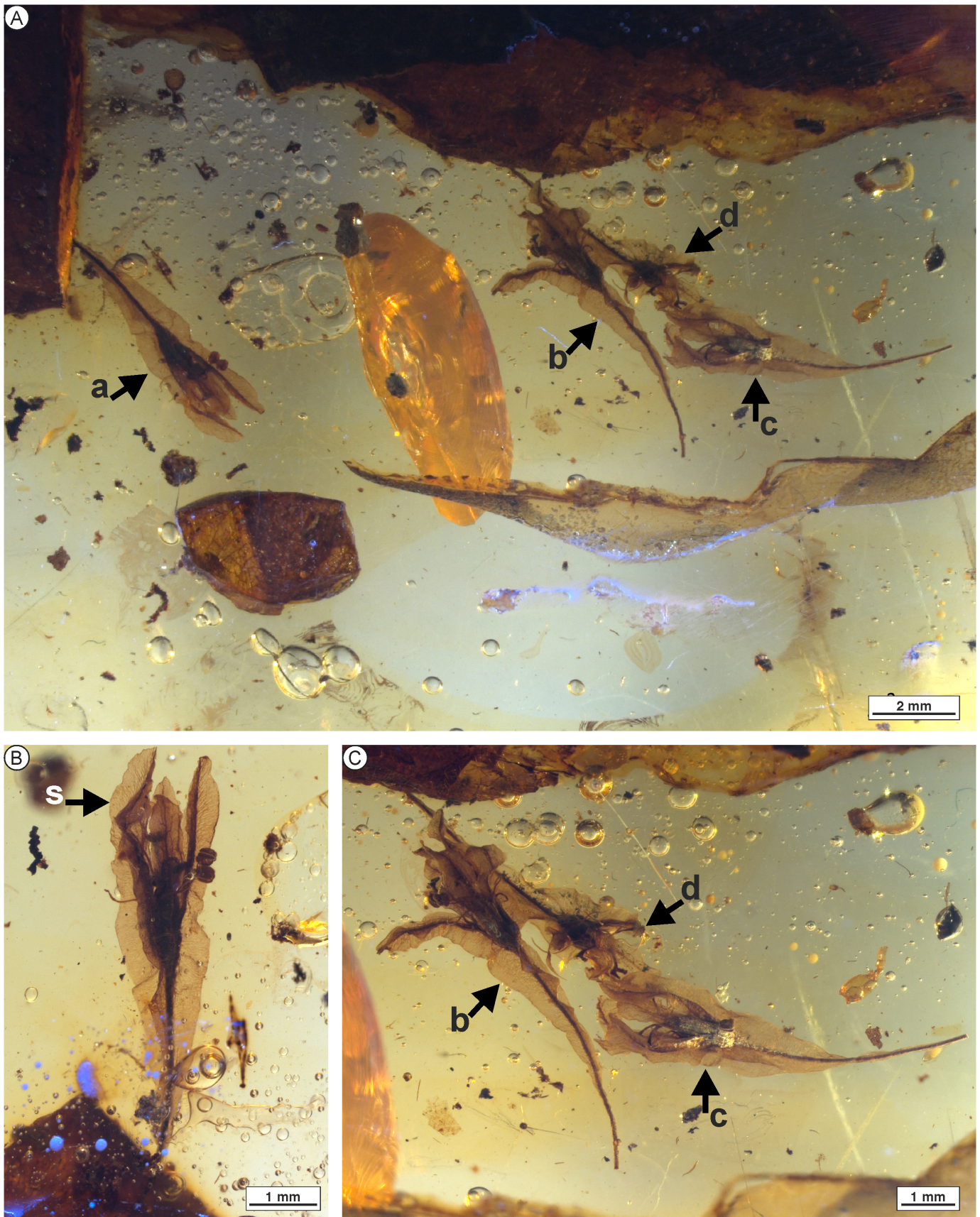
## Discussion

### Morphological comparison with extant taxa

The fossil flowers of *Podopterus mijangosae* (IPN-PAL 16) from Simojovel de Allende, Chiapas, Mexico, have the following features: inflorescences in panicles, flowers bisexual, actinomorphic, perianth differentiated into two whorls, sepals fused at the base, petals free, stamens free and filaments thread-like (8), inserted basifixed on the anthers, with superior ovary, syncarpous, as well as samaras as fruits. These features are found in the families Celastraceae, Malpighiaceae, Polygonaceae, Rutaceae, Sapindaceae and Simaroubaceae (e.g., Brandbyge, 1993; Acevedo-Rodríguez et al., 2011; Clayton, 2011; Kubitzki et al., 2011). These families can be distinguished by several differences. Celastraceae has 3-5 stamens, and the sepals are not fused at the base, unlike the others that are fused. Malpighiaceae generally has five sepals, imbricate in the bud, and a corolla with five free petals. In Rutaceae, a hypogynous flower type is more commonly found, usually 3-5-merous, with 8-10 (-many) stamens in (1-)24 whorls (Simpson, 2010; Kubitzki et al., 2011). The flowers of Sapindaceae are usually unisexual, actinomorphic, or more commonly zygomorphic, with four to seven sepals, free or sometimes more or less united, with four or five petals, nectar disc present (Calderón de Rzedowski and Rzedowski, 2006;

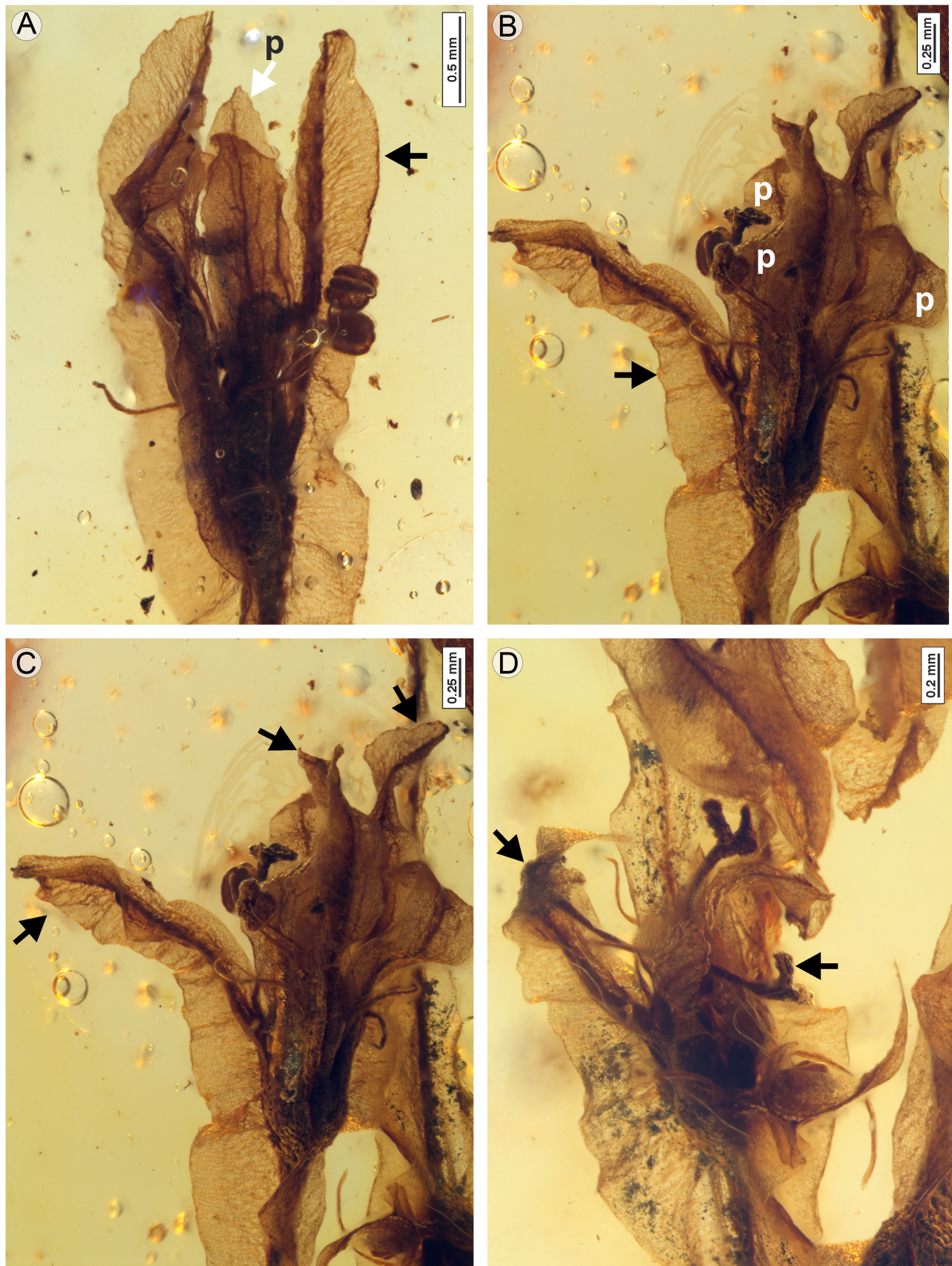






**Figure 1:** Flowers of *Podopterus mijangosae* Estrada-Ruiz, specimen IPN-PAL 16. A. general view of four flowers (arrows punt out the four specimens; a, b, c, d=specimens); B. specimen IPN-PAL 16a showing a flower with the perianth differentiated into two whorls, sepal (s) (arrow); C. three flowers of the specimens IPN-PAL 16 (b, c, d) (arrows punt out the three specimens; b, c, and d=specimens).





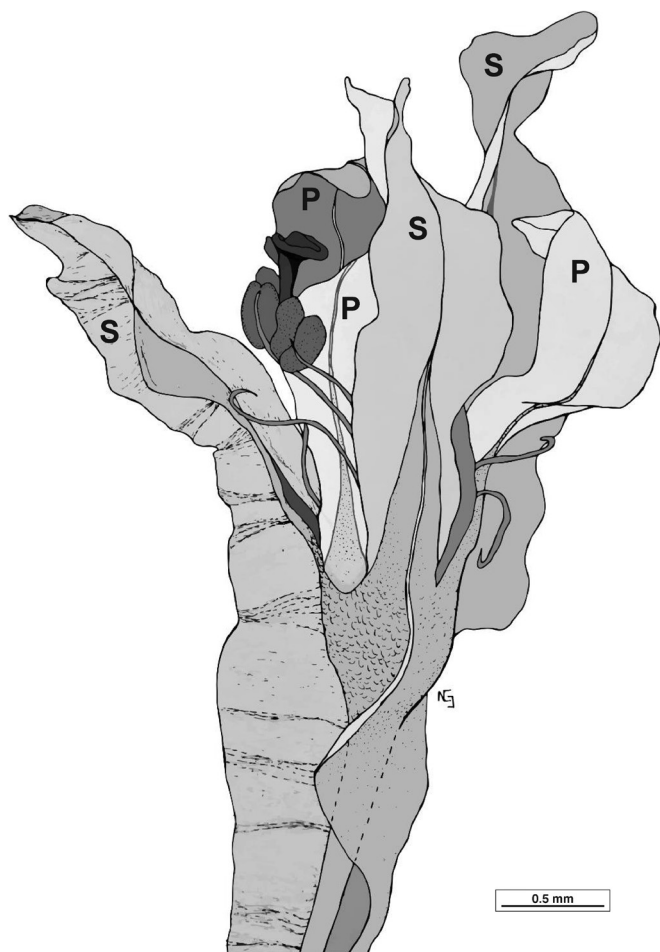
**Figure 2:** Flowers of *Podopterus mijangosae* Estrada-Ruiz, specimen IPN-PAL 16. A. general view of the specimen IPN-PAL 16a showing the wing of sepal (arrow black), and two petals, translucent with entire margin, reticulate venation (arrow white; p=petals); B. specimen IPN-PAL 16b, showing the three petals (p), and reticulate venation (arrow); C. specimen IPN-PAL 16b, is showing an anther with inserted basifixed, three sepals (arrows), capitate stigma; D. specimen IPN-PAL 16d is showing the superior ovary with three styles free (arrows).



Acevedo-Rodríguez et al., 2011). Finally, Simaroubaceae have between three and five sepals and petals, free or fused, a nectar disc between the androecium and gynoecium (Clayton, 2011), combination of characteristics not found in the fossil flowers of *Podopterus* from Simojovel de Allende, Chiapas. The fossil flowers from the Miocene Mexican amber share several features with Polygonaceae, such as the presence of three sepals and petals per series, the perianth with entire margin, with a fine fusiform-reticulate venation pattern, and emarginate apex and cuneate base, and eight stamens free with anthers dithecal, basifixed and thread-like filaments.

There are only three genera in Polygonaceae that have actinomorphic flowers, three petals or sepals, and

thin translucent wings, entire to undulate margin, partially fused at base: *Fallopia*, *Neomillspaughia* and *Podopterus*. These genera have flowers with three sepals that develop into the wings of the fruits (Brandbyge, 1993; Manchester and O'Leary, 2010). The flowers of *Fallopia* have an elliptical shape, with a long perianth that runs into the base, but there are some differences with the flowers from Chiapas. *Fallopia* has three sepals and two petals, glabrous, as well as three styles, sometimes fused toward the base or nearly to the tip, the stigmas divided into numerous, slender fringe-like lobes. *Neomillspaughia* has bisexual flowers, a perianth with three outer ovate segments (sepals), that are elongate and run to the base, but they also differ from the fossil flowers from Simojovel de Allende, Chiapas. *Podopterus mijangosae* features that rule out any taxonomic affinity with *Neomillspaughia* include a perianth differentiated into two whorls, one with three sepals and the other with three petals, and eight stamens (Blake, 1921; Burke and Sánchez, 2011). The four flowers from the Miocene Mexican amber have several features that resemble *Podopterus*, such as bisexual, small and actinomorphic flowers, with a differentiated perianth, three petals and three sepals per whorl series, free stamens with dithecal anthers, basifixed and thread-like filaments; superior ovary, syncarpous, 3-angular, with three free styles (Fig. 3). It is proposed here that the fossil flowers belong to *Podopterus mijangosae*, a recently described winged fruit (Estrada-Ruiz, 2023), due to sharing some characters such as the size, pubescence, shape, and venation pattern of the wings.



**Figure 3:** Drawing of the specimen IPN-PAL 16b of *Podopterus mijangosae* Estrada-Ruiz, showing detail of the petals (p) and sepals (s). Drawn by Naylet K. Centeno-González.

### Regional distribution of *Podopterus* during the Miocene epoch

Geological processes during the Miocene played an important role influencing the climatic conditions in the southern part of Mexico, making the environment more humid, which gave rise to floras with a similar physiognomy to those found in lowland forests or close to sea level as in the present (Cevallos-Ferriz et al., 2012). This assumption is supported by the characteristics of fossil plants that have been collected in different Miocene localities of Chiapas that suggest a tropical climate, equivalent to a tall evergreen forest, bordered by mangroves (Cevallos-Ferriz et al., 2012; Hernández-Hernández et al., 2020; Estrada-Ruiz

et al., 2023). Among these features are large leaves with entire margin, as well as wood with solitary vessels with diameter greater than 100  $\mu\text{m}$ , simple perforation plates, and abundant axial parenchyma (Castañeda-Posadas, 2007). It is possible that these climatological conditions further induced the morphological adaptations resulting in the resemblance between the fossil and extant taxa, probably indicating a closer taxonomic affinity starting since the Miocene (Cevallos-Ferriz et al., 2012). This is also supported by fossil records of other plants with a similar distribution such as *Colpothrinax* Griseb. & H. Wendl., *Swietenia* Jacq., and *Calatola* Standl., present in the amber of Chiapas and that currently have some extant species in Mexico, Caribbean and Central America (Castañeda-Posadas and Cevallos-Ferriz, 2007; Chambers et al., 2012; Estrada-Ruiz et al., 2023). Finally, although it is too early to be conclusive, this new evidence of *Podopterus* as well as other genera previously described (e.g., *Hymenaea* L., *Tapirira* Aubl., *Swietenia*, *Lunania* Hook, *Colpothrinax*, *Socratea* H. Karst., and *Calatola*) (i.e., Miranda, 1963; Poinar, 2002; Chambers et al., 2012; Hernández-Damián et al., 2016) suggest that these geological and environmental processes that gave rise to some of the extant vegetation of Mexico probably extended to Central and South America (Estrada-Ruiz, 2023; Estrada-Ruiz et al., 2023).

## Conclusions

Some plant genera currently growing in southern Mexico have been present in the region since the Miocene as evidenced by the fossil plants collected in the amberiferous sediments (e.g., *Socratea*, *Hymenaea*, *Calatola*) of Simojovel de Allende, Chiapas. Such is the case of *Podopterus*, that likely had its radiation in this part of Mexico as suggested by the number of extant species in this region. This is reinforced by this new report, which adds more evidence that this family was a component of the tropical forest of Simojovel de Allende during the Miocene.

## Author contributions

EER conceived and designed the study, took the photos, described the fossil flowers, wrote the manuscript, edited the revised version and approved the final manuscript.

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