

# *Aphananthe* Planch. (Cannabaceae) flower preserved in the Mexican amber

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**ABSTRACT.** Cannabaceae (Urticalean Rosids clade) is a small family with ten genera and a wide distribution in tropical and temperate regions worldwide. A complete understanding of the history of the lineage is fundamental to the integration of its fossil record, which needs to be better documented in low latitudes of North America. This work recognizes a new species, *Aphananthe manchesteri* Hernández-Damián, Rubalcava-Knoth et Cevallos-Ferriz sp. nov. (Cannabaceae), from the Miocene amber deposits of Simojovel de Allende, Chiapas, Mexico, based on a flower analyzed with reflected light and CT-scanning. Flowers of Cannabaceae are generally staminate or pistillate and small; staminate flowers have five sepals and opposite five stamens, and a pubescent pistillode, such as the fossil. However, the presence of three unguiculate and two ovate sepals with a puberulent surface are characteristics that allow its recognition as *Aphananthe*, the fossil is morphologically similar to *Aphananthe monoica*, an extant species that grows along the Pacific coast of Mexico. The presence of *Aphananthe manchesteri* sp. nov. in southern Mexico during the middle-early Miocene, ~23–15 Ma ago, supports the history of the lineage in low-latitude North America, representing an expansion of the Boreotropical Flora. It adds to the taxonomical diversity of angiosperms preserved in Mexican amber, comparable with amber deposits from the Dominican Republic, where another anemophilous extinct species member of the Urticalean Rosids clade has been reported. This coincidence further supports the development of similar plant communities between these fossiliferous localities.

**KEYWORDS:** *Aphananthe*, Boreotropical Flora, Cannabaceae, fossil flower, Mexican amber

## INTRODUCTION

The Urticalean Rosids clade (APG IV, 2016) comprises species such as hemp, hashish, hop, mulberry tree, fig tree, trumpet tree, nettle, and elm. These taxa belong to Moraceae, Ulmaceae, Urticaceae, and Cannabaceae families (Zavada and Kim, 1996; Sytsma et al., 2002; Zhang et al., 2011; Yang et al., 2013; Pedersoli et al., 2019). The urticalean rosids frequently have flowers that are small and inconspicuous, diclinous, monochlamydeous, or achlamydeous, with a reduced number of

organs and inflexed filaments (Yang et al., 2013, 2017; Pedersoli et al., 2019, 2022).

Cannabaceae is a small family with a circumscription that has been expanded based on molecular phylogenies (Sytsma et al., 2002; Yang et al., 2013). No wadays, it includes ten genera: *Aphananthe* Planch., *Cannabis* L., *Celtis* L., *Chaetachme* Planch., *Gironniera* Gaudich., *Humulus* L., *Lozanella* Greenm., *Parasponia* Miq., *Pteroceltis* Maxim. and *Trema*, eight of them traditional members of Ulmaceae (Celtoideae subfamily by Cronquist, 1981).

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The Late Cretaceous to Paleogene fossils of Cannabaceae (Manchester, 1987, 1989; Manchester et al., 2002) support a long and broad paleogeographical distribution of the family at middle-high latitudes of the Northern Hemisphere. This pattern is recognized in *Aphananthe* with fossils of fruits (e.g. Dorofeev, 1982; Knobloch and Mai, 1986; Manchester, 1994; Collinson et al., 2012), woods (Choi et al., 2010), and pollen (Yang et al., 2017), but fossil flowers had not been so far documented.

Mexican amber deposits are in southern Mexico, in the state of Chiapas. They are essential due to their geological age (Cenozoic) and geographical location (Solórzano-Kraemer, 2010). Unfortunately, reports of plant inclusions in the region are relatively scarce compared to other biological groups, such as insects (Avendaño-Gil et al., 2012; Hernández-Hernández et al., 2020).

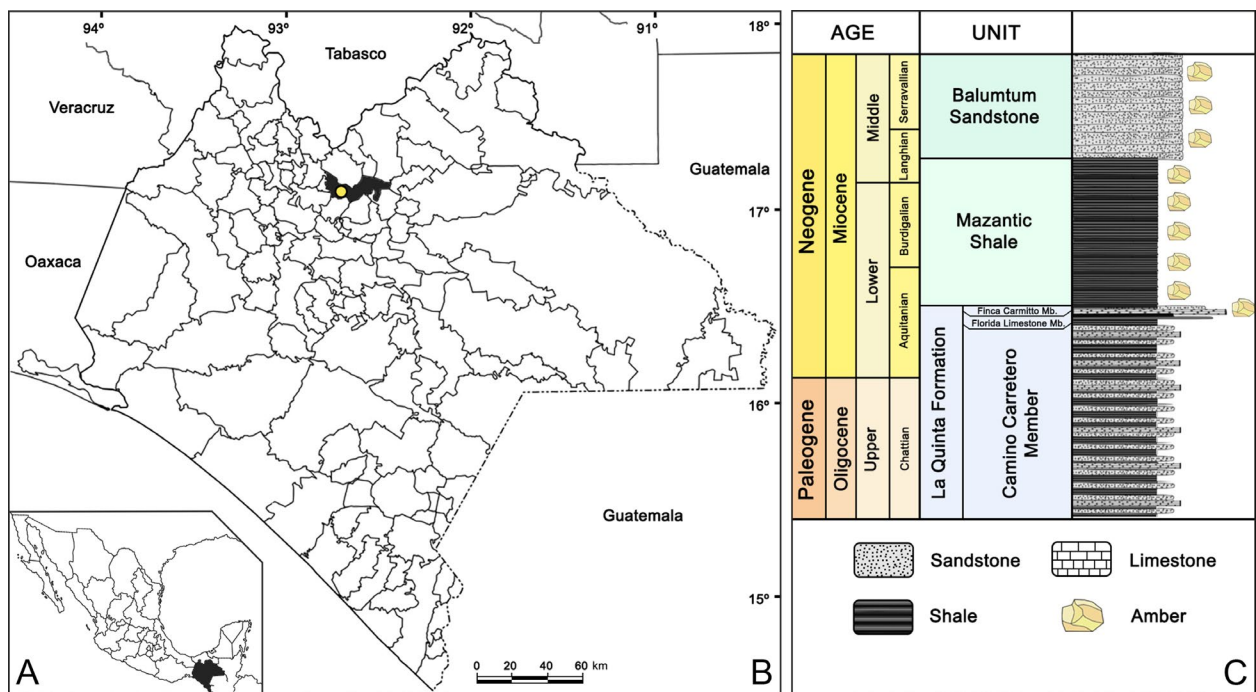
Recently, Poinar (2022), in a bibliographical revision, indicated that around 16 families of angiosperms had been reported in the Mexican amber. Some of these lineages are also documented in amber deposits in the Dominican Republic, such as *Arecaceae* (Poinar, 2002), *Celastraceae* (Chambers and Poinar, 2016; Hernández-Damián et al., 2018), *Fabaceae* (Poinar and Brown, 2002; Calvillo-Canadell et al., 2010), *Urticaceae* (Poinar et al., 2016) and *Rhamnaceae* (Chambers and Poinar,

2015; Hernández-Hernández and Castañeda-Posadas, 2018). These reports support comparing these fossiliferous localities (Poinar, 2022).

In this work, we identify and document a new species of *Aphananthe* (Cannabaceae) preserved in the Mexican amber. Its description is based on observations with light microscopy and micro-CT scanning. This new report proves the history of Cannabaceae in low-latitude North America. It further adds to the taxonomical diversity of angiosperms in the region, which is comparable to reports on the amber deposits in the Dominican Republic.

### MATERIAL AND METHODS

The specimen was recovered from Simojovel de Allende, Chiapas, Mexico. Amber from the Simojovel area is found in three lithostratigraphic formations: La Quinta or Simojovel Formation, Mazantic Shale, and Balumtum Sandstone (from base to top), which form a sequence composed mainly of calcareous sandstone and silt with lignite layers (Fig. 1). 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 (Licari, 1960; Allison, 1967). Isotopic analysis and biostratigraphy in the region suggest that the amber deposits have an age of 23–15 Ma (Vega et al., 2009; Perrilliat et al., 2010; Solórzano-Kraemer, 2010; Serrano-Sánchez et al., 2015). They were deposited in an estuarine environment along the coast of the ancient Gulf of Mexico (Serrano-Sánchez et al., 2015; Ojeda et al., 2023).



**Figure 1.** Distribution of Mexican amber deposits. **A.** Location of Chiapas state; **B.** Map showing Simojovel de Allende locality (<https://www.inegi.org.mx/>); **C.** Stratigraphic column based on Serrano-Sánchez et al. (2015)

The amber piece with the studied specimen is yellow. It was sectioned with a small diamond saw, polished with car polish and final details were obtained with Brasso®. Once the small piece was translucent, the fossil flower inclusion was photographed with transmitted white light using a Zeiss Axio Zoom.V16 microscope. In addition, X-ray computed micro-tomography (micro-CT) scanning was performed on Xradia Versa 510 Microtomograph Scanner, in the “Lumir” Laboratory, Geosciences, UNAM, Juriquilla, Mexico. From the scanning of the fossils, 676 images were taken with X-ray specifications set to 40 kV and 4.7936 microns/pixel. Virtual sections were processed using Dragonfly software, version 2020.2 for [Windows] Non-Commercial License (Object Research Systems (ORS) Inc., Montreal, Canada, 2020).

## SYSTEMATIC PALEOBOTANY

Clade: URTICALEAN Rosids APG, IV

Family: CANNABACEAE Martinov

Genus: *Aphananthe* Planch.

Species: *Aphananthe manchesteri*  
Hernández-Damián, Rubalcava-Knoth  
et Cevallos-Ferriz, **sp. nov.**

Figs 2A–D, 3A–E

Holotype. IGM-PB 1398.

Repository. Colección Nacional de Paleontología, Museo Ma. Carmen Perrilliat M., Instituto de Geología, Universidad Nacional Autónoma de México (IGM-PB).

Locality. Simojovel de Allende, Chiapas.

Stratigraphy. La Quinta Formation.

Age. Middle–early Miocene.

Etymology. The epithet recognizes Dr. Steven R. Manchester for his contributions to paleobotany and understanding the Urticalean Rosids clade.

**Diagnosis.** Staminate flower, small, pentamerous, bilaterally symmetric, short pedicel. Perianth with only one whorl, aposepalous. Perianth lobes 5, 3 unguiculate sepals, two ovate sepals. Stamens 5, uniseriate, antisepalous, inflexed. Anthers, versatile, dorsifixed, elliptic-globose, longitudinal dehiscence. Central pubescent pistillode.

**Description.** The fossil is a staminate flower ~3.0 mm long, ~3.0 mm wide. The perianth is pentamerous with bilateral symmetry and attached to a short pedicel. It comprises only one whorl of five free sepals, three unguiculate-convex ones, and two other ovate-convex, ~3.0 mm long, ~0.5 mm wide. The outer surface of the sepals is puberulent. The five stamens are positioned opposite the sepals and inflexed. The filaments are subulate, flattened and ~2.5 mm long. The anthers are elliptic-globose, versatile, dorsifixed with longitudinal dehiscence, ~0.5 mm. There is a central pistillode with simple trichomes at its base.

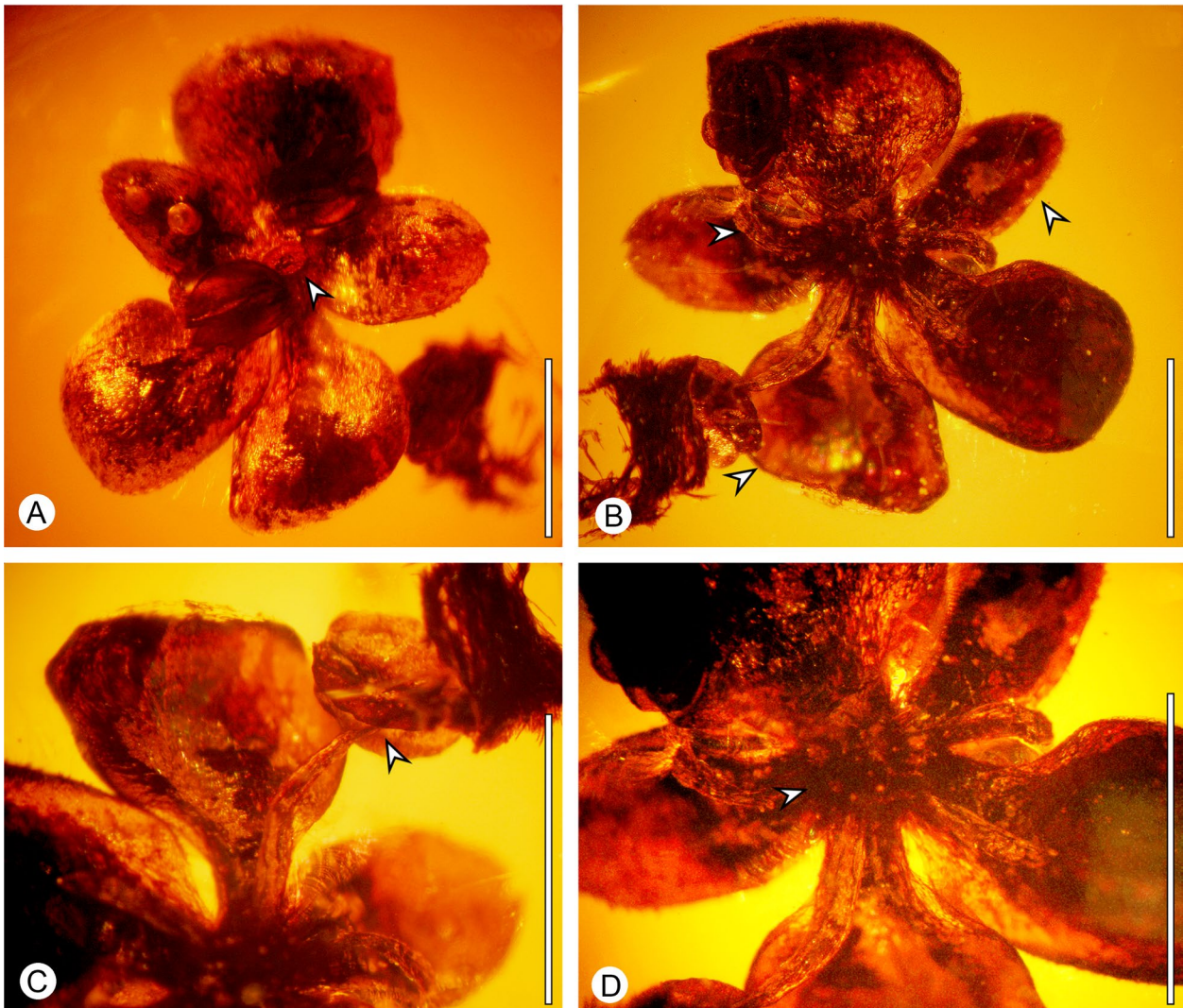
## DISCUSSION

### AFFINITIES

The Urticalean Rosids clade includes Ulmaceae, Cannabaceae, Urticaceae and Moraceae families (APG IV, 2016). Cannabaceae includes ten genera; they often have flowers with only one whorl of five perianth organs, previously interpreted as tepals (Berg, 1990), sepals (Payer, 1857; Shephard et al., 2000) or lobes of the perianth (Bechtel, 1921). We used the term sepals based on evidence of the floral development of some family members, such as *Celtis* and *Trema* (Pedersoli et al., 2019, 2022; Leme et al., 2020). Additionally, the flowers of Cannabaceae have antisepalous stamens; a character shared with Urticaceae and Moraceae (Yang et al., 2013) (Table 1, Fig 2A–D).

**Table 1.** Comparison between fossil flower and families of Urticalean Rosids based on Sytsma et al. (2002), Yang et al. (2013), Simpson (2019)

	Fossil flower	Ulmaceae (Sytsma et al., 2002; Yang et al., 2013)	Cannabaceae (Yang et al., 2013)	Urticaceae (Yang et al., 2013; Simpson, 2019)	Moraceae (Yang et al., 2013; Simpson, 2019)
Number of sepals	5	5 (2–9)	4–5	4–5 (0–1–6)	0–10
Number of stamens	5	∞	5	4–5 (1–6)	1–6
Attachment of filament to anther	dorsifixed	dorsifixed	dorsifixed-basifixed	dorsifixed-basifixed	dorsifixed-basifixed
Pubescent pistillode	present	absent	present	present	absent



**Figure 2.** Flower of *Aphananthe manchesteri* sp. nov. from Simojovel de Allende, Chiapas, Mexico. Reflected light. **A.** Abaxial view, small staminate flower, arrow pointing to short pedicel; **B.** Adaxial view, superior arrows pointing to ovate sepals, left and inferior arrow pointing to unguiculate sepal; **C.** Arrow indicates the versatile and dorsifixed anther; **D.** Arrow pointing to the central and pubescent pistillode. Scale bars = 1.0 mm in A–C; 0.5 mm in D

Unfortunately, until now, morphological synapomorphies have not been identified for Cannabaceae (Yang et al., 2013). According to Leme et al. (2020), studying the developmental pathways and anatomical characteristics of flowers will contribute to a better understanding of the group. For example, most of the members of Cannabaceae that were included traditionally within Celtoideae (Ulmaceae; Cronquist, 1981) have a floral vasculature with perianth and stamen traces departing at the same organographic level from the main vascular trace of the pedicel (Chernik, 1975), so that sepals have only one bundle (Leme et al., 2020); a characteristic also recognized in the fossil flower (Fig. 3C–E), the number of vascular bundles is variable in other urticalean rosoid species such as the case of the Moraceae family (Leite et al., 2018; Leme et al., 2020).

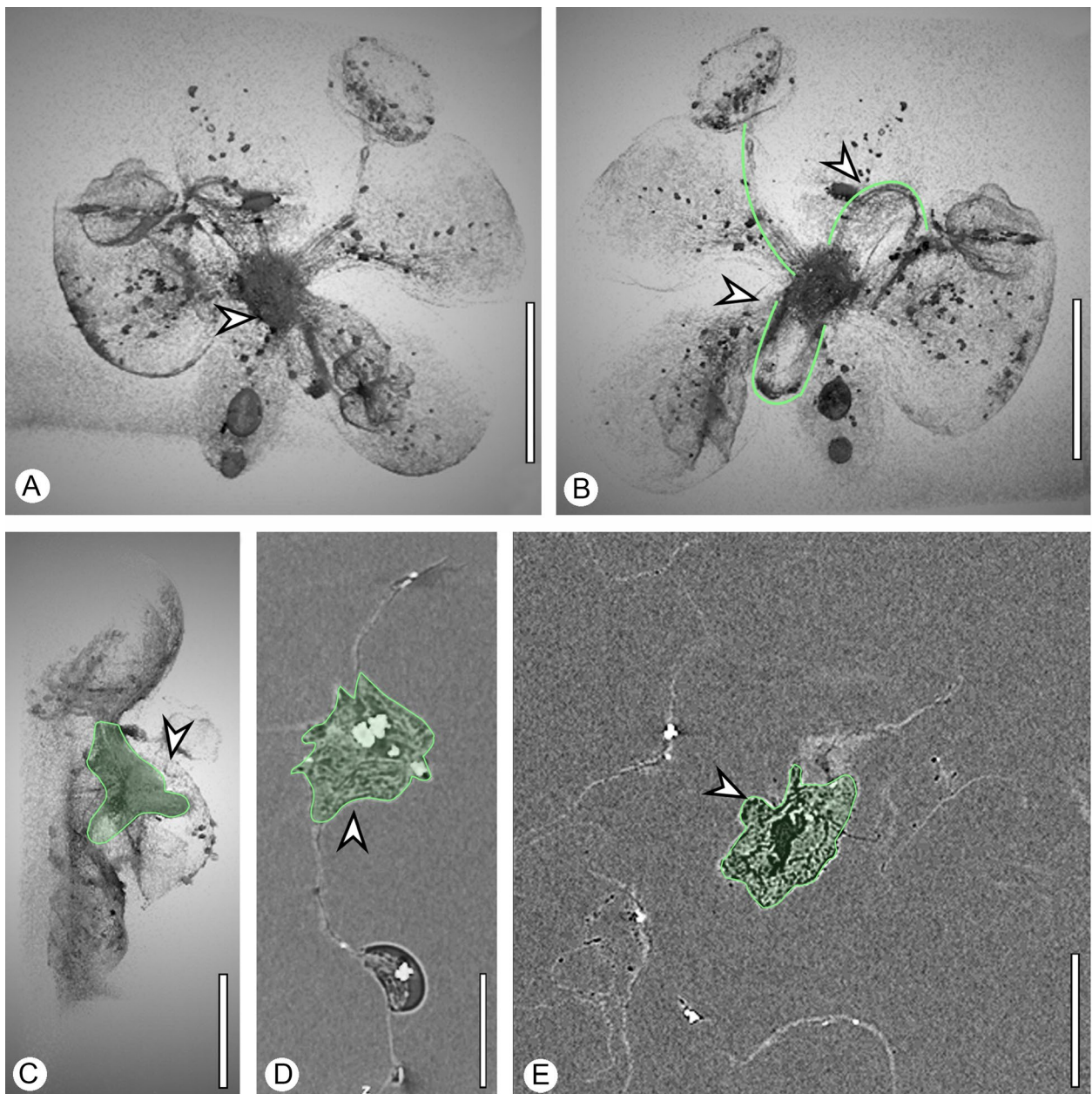
Moreover, the fossil flower and Cannabaceae have opposite stamens in equal numbers to the sepals, inflexed stamens and dorsifixed anthers (Leme et al., 2020) (Figs 2A, B; 3A, B). These coincidences strongly support that the fossil flower is most like the reproductive structures of Cannabaceae.

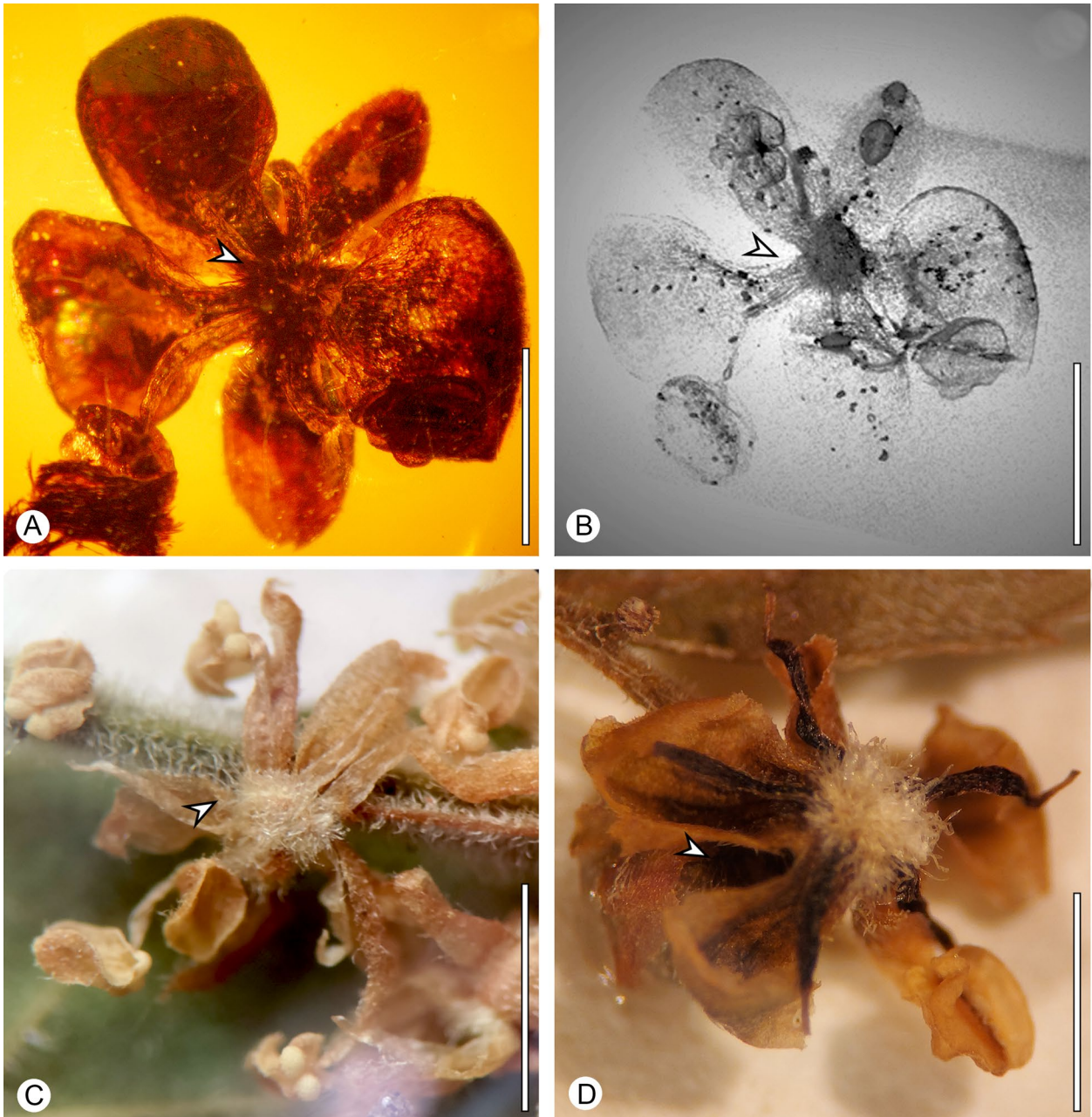
The fossil material resembles *Aphananthe*, *Gironniera*, *Celtis*, *Trema* and *Parasponia* because they all have a pubescent pistillode (Table 2, Fig. 4A–D) (Pedersoli et al., 2019; Leme et al., 2020). Nevertheless, the fossil flower resembles *Aphananthe* since both have unguiculate sepals (Table 2, Fig. 4D).

*Aphananthe* is a small genus of five semi-deciduous shrubby or tree species with an intriguing Amphi-Pacific distribution in eastern, southern and southeastern Asia, Australia, Madagascar and Mexico (Yang et al., 2017). The

**Table 2.** Comparison between fossil flower and genera of Cannabaceae based on Soepadmo (1977), Nee (1984), Pennington and Sarukhán (2016)

	Fossil staminate flower	<i>Aphanante</i> (Soepadmo, 1977; Nee, 1984; Pennington and Sarukhán, 2016)	<i>Gironniera</i> (Soepadmo, 1977)	<i>Celtis</i> (Soepadmo, 1977; Nee, 1984)	<i>Trema</i> (Soepadmo, 1977; Nee, 1984)	<i>Parasponia</i> (Soepadmo, 1977)
Unguiculate sepals	present	present	absent	absent	absent	absent
Surface of sepals	puberulent pubescent	adprissed pubescent	adprissed sparsely pubescent	adprissed sparsely pubescent	adprissed sparsely pubescent	sparsely pubescent
Apiculate anthers	absent	absent	present	absent	absent	absent
Pubescente pistillode	present	present	present	present	present	present

**Figure 3.** Flower of *Aphananthe manchesteri* sp. nov. from Simojovel de Allende, Chiapas, Mexico. In green, highlighting the characteristic. Micro-CT. **A.** Abaxial view, staminate flower; arrow pointing to the pedicel; **B.** Adaxial view, arrows pointing to inflexed filaments; **C.** Lateral view, arrow indicates the main vascular bundle; **D.** Laterally oriented specimen, arrow indicating the close of the leading vascular trace of the pedicel; **E.** Digital cross-section, arrow indicates one vascular bundle. Scale bars = 1.0 mm in A–C; 0.5 mm in D and E



**Figure 4.** Comparison between *Aphananthe manchesteri* sp. nov. from Simojovel de Allende, Chiapas, Mexico, and extant members of Cannabaceae. *Celtis caudata* 124344. Herbario de la Facultad de Ciencias (FCME), and *Aphananthe monoica* 738223. Herbario de la Facultad de Ciencias (FCME). **A.** Reflected light, *Aphananthe manchesteri* sp. nov., arrow indicates the pubescent pistillode; **B.** Micro-CT, *Aphananthe manchesteri* sp. nov., arrow indicates unguiculate sepal; **C.** Flower of *Celtis caudata*, arrow indicates the pubescent pistillode; **D.** Flower of *Aphananthe monoica* arrow indicates unguiculate sepals. Scale bar = 1.0 mm in 1–4

name *Mirandaceltis* Sharp (Sharp, 1958) was proposed for the American species, however, the fruit characteristics, including the endocarp morphology, support its inclusion in *Aphananthe* genus (Leroy, 1961; Soepadmo, 1977). Zavada and Kim (1996), based on a combined phylogenetic analysis, recognized that Asian (*Aphananthe cuspidata* (Blume) Planch.) and American species (*Aphananthe monoica* (Hemsl.) J.-F. Leroy) formed a remaining of the genus.

Floral morphology will provide relevant evidence for a better understanding of

*Aphananthe*, but the information is limited and, therefore, its availability for comparison with the fossil material is also limited. American species *Aphananthe monoica* has unguiculate-concaved sepals (Pennington and Sarukhán, 2016). However, the fossil flower and *A. monoica* have morphological differences; for example, the fossil flower has two non-unguiculate sepals (Fig. 4A, B), while in *A. monoica*, all are unguiculate (Fig. 4D). In contrast, *Aphananthe aspera* (Thunb.) Planch. has obovate-rounded sepals, while those of

*A. cuspidata* are obovate-oblong (Fu et al., 2003).

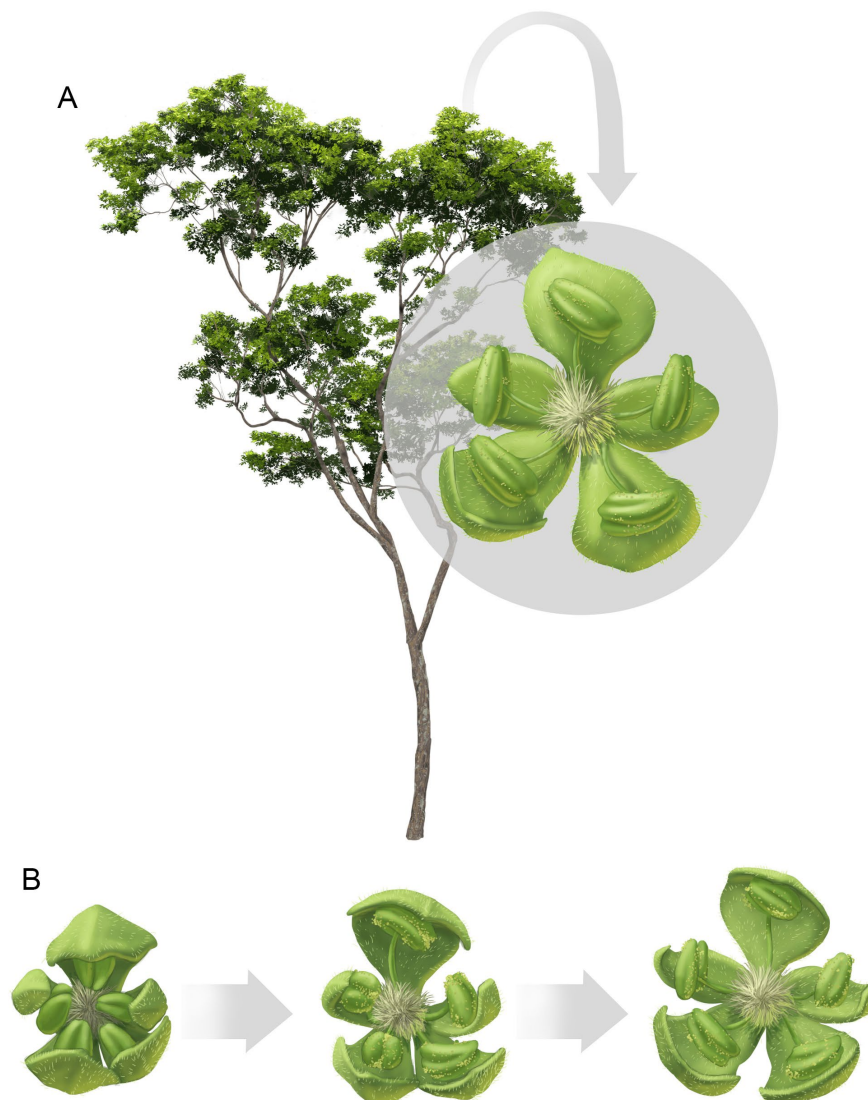
Therefore, morphological details of the new flower strongly support the recognition of new species, *Aphananthe manchesteri* Hernández-Damián, Rubalcava-Knoth et Cevallos-Ferriz, sp. nov.

According to Friis et al. (2011), two fossil flowers with affinity to Cannabaceae (including Celtidoideae) from the Cenozoic are records which can be debated. *Eoceltis dilcheri* from the Middle Eocene of Texas, USA, comprises unisexual, staminate flowers with four tepals, numerous stamens, and in situ triporate, scabrate pollen (Zavada and Crepet, 1981). Its identification is still made based on that the fossil flowers are more prominent than they are, in general, in extant taxa and have more densely crowded stamens. *Celtoidanthus*

*pseudorobustus*, from the Miocene of Germany (Weyland et al., 1958), is also uncertain.

Fossil plants reported from the Miocene in low-latitude North America have a near relative that currently grows in the region (Graham, 1999; Cevallos-Ferriz and González-Torres, 2006; Cevallos-Ferriz et al., 2012). This idea is supported here by *Aphananthe manchesteri*, which resembles *A. monoica*, a tree that nowadays grows along the Pacific coast from Nayarit to Chiapas, Mexico (Nee, 1984; Pennington and Sarukhán, 2016).

Hence, we propose a hypothetical whole-plant reconstruction of *Aphananthe manchesteri* and its flower (Fig. 5A, B). It is similar to *A. monoica* based on the presence of the unguiculate sepals. However, the fossil flower of *Aphananthe* is also comparable with Asian extant species because they have similar pubescent flowers; for this



**Figure 5.** A. Hypothetical whole plant reconstruction of *Aphananthe manchesteri* sp. nov. based on its comparison with its nearest living relatives by Aldo Domínguez de la Torre; B. Reconstruction of flower with explosive release of pollen

reason, their affinity needs to be evaluated in a phylogenetic context.

Until now, ~16 families of angiosperms have been recognized in the Mexican amber (Poinar, 2022), among them Urticaceae with *Ekrixanthera ehecatli* (Poinar et al., 2016). The latter and *Aphananthe manchesteri* are part of the Urticalean Rosids clade (APG IV, 2016); both are staminate and small flowers with inflexed stamens and pubescent pistillode, which are characters related to an explosive release of pollen in the wind-pollinated plants (Fig. 5A) (Pedersoli et al., 2019, 2022). This mechanism is a dispersal syndrome frequently reported in Cannabaceae and Urticaceae (Yang et al., 2017). However, they have significant differences. *Ekrixanthera ehecatli* has glabrous and three wedge-shaped tepals (Poinar et al., 2016), while *A. manchesteri* has puberulent and three unguiculate sepals. Furthermore, the continuous floral vasculature recognized in *A. manchesteri* supports its inclusion in Cannabaceae (Fig. 3C–E), because it is a character shared by several species of the family as *Trema* and *Celtis* (Leme et al., 2020); even more, their sepals have a single vascular bundle (Leme et al., 2020), while other urticalean rosids have five vascular bundles, including Ulmaceae (Leme et al., 2018).

According to Solórzano-Kraemer (2007), Mexican amber deposits can be related to the Dominican Republic since both stratigraphic sequences have lignite beds and a similar botanic origin of amber from extinct species of *Hymenaea* (Fabaceae). They further share a comparable fossil record of insects (40%). Poinar (2022) recently highlighted this similarity by identifying angiosperm families in both deposits.

Indeed, the new flower is a member of Urticaceae and belongs to the Urticalean Rosids clade. This family has been reported from amber deposits in Mexico and the Dominican Republic with the extinct genus *Ekrixanthera* (Poinar et al., 2016). Here, the flower fossil of *Aphananthe* further corroborates the presence of pollen grains of members of the Urticalean Rosids clade in amber deposits in Chiapas and the Dominican Republic, as well as in other localities in low-latitude North America (Palacios-Chávez and Rzedowski, 1993; Graham, 1999; Poinar et al., 2016).

Though comparing taxonomical floristic elements is premature due to relatively few

reports from Mexican amber in contrast with the Dominican Republic deposits, this new taxonomic report also suggests similar ecological dynamics in the vegetal communities preserved in both localities due to the presence of extinct plants of the Urticalean Rosids clade with an explosive release of pollen. This process is more frequent in open areas of vegetation (Pedersoli et al., 2019). To further elaborate on this idea, it is essential to continue documenting the diversity of plants that grew in the past in southern Mexico. Furthermore, these organisms should be compared to other contemporaneous plants from amber deposits worldwide.

#### BIOGEOGRAPHICAL IMPLICATIONS

The Late Cretaceous to Paleogene fossils of Cannabaceae (Manchester, 1989; Manchester et al., 2002) support a long and broad paleogeographical distribution of the family in the Northern Hemisphere. Moreover, an early diversification of the family coincides with the expansion of Boreotropical flora in the northern mid-latitudes during a warm phase, peaking in the late Paleocene–early Eocene thermal maximum (Wolfe, 1975; Manchester, 1999; Zachos et al., 2001).

This idea is supported by Jin et al. (2020) based on a biogeographical approach; the authors suggested that the movement of genera across the North Atlantic and Beringian land bridges explain some of the more northerly and temperate distributions in the group, while long-distance dispersal was probably the process involved in tropical intercontinental disjunctions like that of *Trema* genus (Stevens, 2001 onwards).

Yang et al. (2017) discussed the evolution and diversification of *Aphananthe* in detail; the authors suggested that *Aphananthe* had an origin during Late Cretaceous (~71.5 Ma), its crown group differentiated during the early Miocene (~19.1 Ma), and that the long-distance dispersals explain better its disjunct distribution.

We suggest based on this new member of Cannabaceae, *Aphananthe manchesteri* in Chiapas, that probably during the Miocene, or slightly earlier, as high-latitude North America began a cooling phase, an extension of the Boreotropical flora extended its distribution to low-latitude North America, southern Mexico, ~23–15 Ma ago. To support this hypothesis it is necessary to integrate different sources of evidence.



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