



## Miocene *Hymenaea* flowers preserved in amber from Simojovel de Allende, Chiapas, Mexico

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### ARTICLE INFO

#### Article history:

Received 1 November 2009

Received in revised form 17 February 2010

Accepted 19 February 2010

Available online 26 February 2010

#### Keywords:

Chiapas  
early Miocene  
Leguminosae  
Caesalpinioideae  
*Hymenaea*

### ABSTRACT

A diverse biota included in the amber of the early Miocene La Quinta Formation, Simojovel de Allende, Chiapas, Mexico, includes nicely preserved flowers of the legume genus *Hymenaea* (Caesalpinioideae: Detarieae), the same plant that produced the amber-forming resin. Our observations confirm the presence of two distinct species. *Hymenaea mexicana* Poinar and Brown is characterized by sub-equal clawed petals, and a verrucose and basally hirsute ovary, resembling the flower of extant *Hymenaea verrucosa* Gaertner (section *Trachylobium*), an African species. In contrast, the new species *Hymenaea allendis* Calvillo-Canadell, Cevallos-Ferriz & Rico-Arce is distinguished by its prominent nectariferous disc, and smooth glabrous ovary, thus resembling *Hymenaea courbaril* L. (section *Hymenaea*) with an American lineage of the genus. Different maturation stages of these flowers are preserved, with recognition of a development series that parallels that of extant relatives. Presence of these two species of *Hymenaea*, ca. 23 my ago in southern Mexico has interesting biogeographic implications for the development and history of neotropical floras during the mid-Cenozoic.

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### 1. Introduction

The importance of Leguminosae in Mexican floristic communities stands out since the family represents the third most diverse group among angiosperms today (Sousa and Delgado, 1993). The world's oldest currently recognized fossils of legumes are Paleocene in age (Lewis et al., 2005); nevertheless, there are reports of legumes that doubtful and need reevaluation (Herendeen et al., 1992; Lewis et al., 2005).

In Mexico, the oldest bona fide legume fossils are fruits of *Inga* (Mimosoideae), *Chamaecrista* and *Senna* (Caesalpinioideae (Calvillo-Canadell and Cevallos-Ferriz, 2005)) from the Eocene La Carroza Formation from La Popa, Nuevo León. This age is based on physical geology and biostratigraphy (Vega-Vera et al., 1989), but a U–Pb radiometric date based on 5 detritic zircon grains indicates it could be as old as Paleocene but this ages has to be confirmed using more material (Lawton, T. 2010, per. comm.). Caesalpinioideae, in particular, is an important group present at almost every Cenozoic Mexican plant fossil locality. Representatives of this subfamily include *Copiaferoxylon* from the Oligocene–Miocene El Cien Formation (Baja California Sur); *Apuleia*, *Bahucis*, and *Caesalpinia* from the Oligocene Coatzingo Formation (Puebla) (Calvillo-Canadell and Cevallos-Ferriz,

2002, 2005; Cevallos-Ferriz and González Torres, 2005); and *Hymenaea* from the Miocene La Quinta Formation (Chiapas; Poinar and Brown, 2002).

Amber deposits containing fossil plant and insect remains have been recognized around the world in rocks as old as Carboniferous (Langenheim, 1966, 2003); however, the amount of amber and preservational quality of included organisms varies. Not all resins produced by trees form amber. According to Ross (1998) among extant plants only two are known to produce suitable amounts of resin to generate amber: *Agathis australis* (Lamb.) Steud., from New Zealand and the legume *Hymenaea* from Central and South America. The amber of Chiapas has been interpreted as being produced during the late Oligocene to early Miocene (ca. 30–20 mybp) by plants related to *Hymenaea* (Langenheim, 1966). Langenheim and Beck (1965) and Lambert et al. (1989) compared through chemical and physical characteristics this amber to the resin produced by trees growing today in Chiapas; and examined several genera including *Hymenaea*, *Amyris*, *Myroxylon*, *Pistacia*, *Bursera*, *Protium*, *Picea*, *Taxodium*, and *Pinus* and concluded that the amber was produced by a member of the first genus. The presence of isolated reproductive organs of a *Hymenaea* plant in amber gives further support to this idea (Poinar and Brown, 2002). Initially it was thought these remains were related to *Hymenaea courbaril* L., an extant Central-South American species. However, recent observations and detailed comparison of amber materials and analysis of the reproductive organs led to recognition of an extinct species, *Hymenaea mexicana* Poinar & Brown,

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which is thought to be similar to *Hymenaea verrucosa* Gaertner, a living species from east Africa (Poinar and Brown, 2002). Other remains have been identified and described from the amber samples based on different plant organs, including a leaf fragment of *Acacia* (Leguminosae; e.g., Gómez-Bravo, 2005). In addition to the legumes found in this amber, a flower of *Tapirira durhamii* Miranda (Anacardiaceae) (Miranda, 1963), a bryophyte, *Lejeunea palaeomexicana* von Riclef (1984), palms of the subtribes Iriarteinae (*Socratea brownii*; Poinar, 2002a), and Euterpeinae (Poinar, 2002b), and flowers of Meliaceae (*Swietenia miocenica* Castañeda-Posadas & Cevallos-Ferriz; Castañeda-Posadas and Cevallos-Ferriz, 2007) have been reported.

In this paper, we augment the description of *Hymenaea mexicana* with observations from new material, including an almost complete flower, and recognize a new species of the genus based on Miocene flowers preserved in the amber of Simojovel de Allende, Chiapas. The biogeographic significance of these species in relation to the origin of the extant Mexican megabiodiversity is highlighted.

## 2. Materials and methods

### 2.1. Locality and age

The fossil material was collected in the Simojovel de Allende municipality, located in the northern zone of the state of Chiapas, at 17.80801900 N latitude and 92.84300000 W longitude (Fig. 1), at an altitude of 600 m. The area is limited to the north by the Huitiupán, Sabanilla, and Tila municipalities; to the east by the Chilón municipality; to the south by the Pantheló, Chalchihuitán, and El Bosque municipalities; and to the west by the Jitotol and Pueblo Nuevo Solistahuacán municipalities (Centro Estatal de Estudios Municipales [CEEM], 1988). The strata exposed in this region include Upper Cretaceous limestones, Oligocene shale and sandstone, and Miocene sandstone. The amber bearing strata are associated with a marine sequence that Frost and Langenheim (1974) assigned to the Oligocene by the presence of planktonic foraminifera—such as *Globigerina ciproensis* and *Globorotalia kugleri*. However, Grimaldi

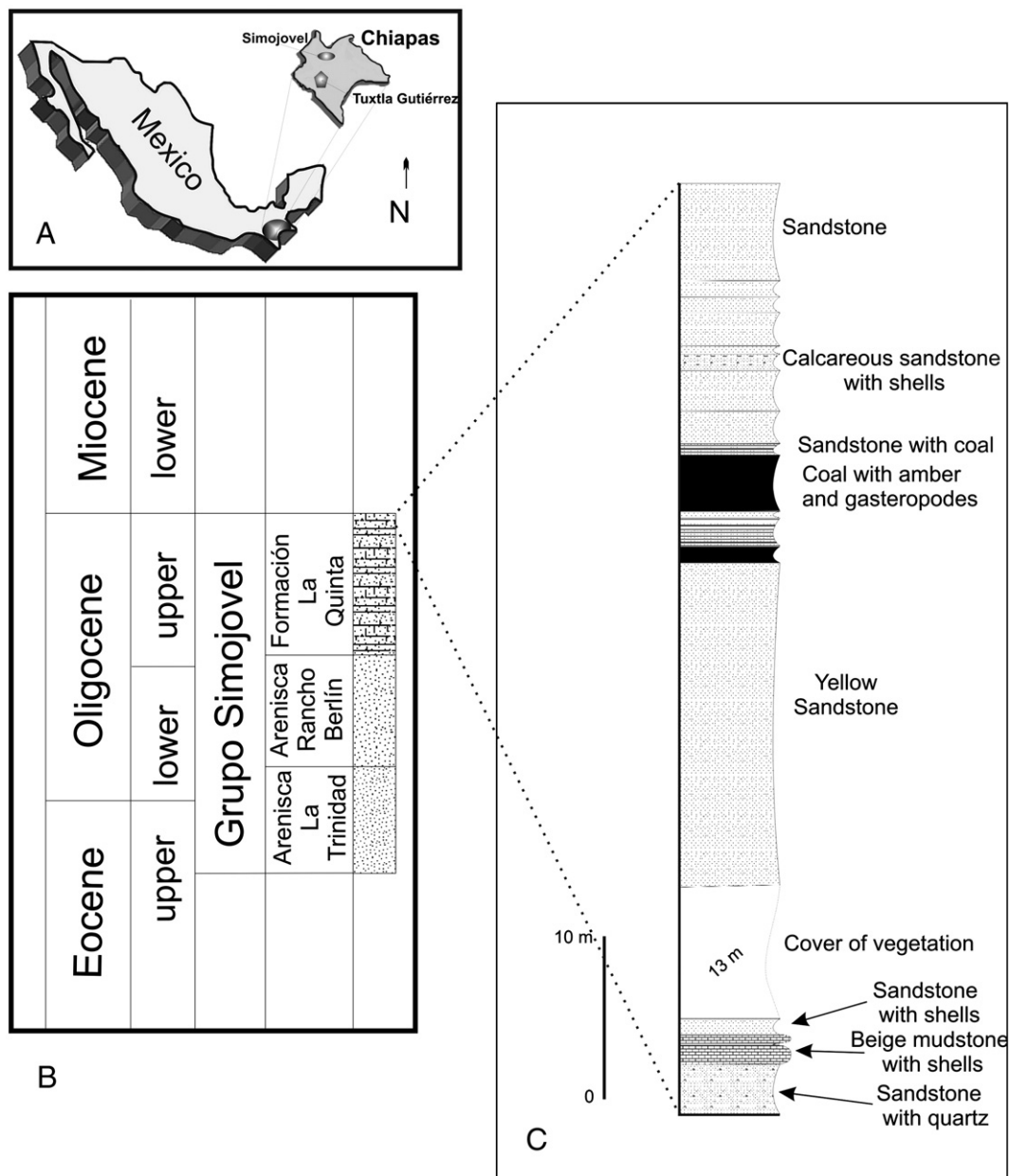


Fig. 1. A) Geographic location of Simojovel de Allende, with (B) stratigraphic position of the La Quinta Formation, and (C) detailed column locating fossiliferous strata (Modified from Castañeda-Posadas and Cevallos-Ferriz, 2007).

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