

A FOSSIL FLOWER OF THE GENUS *PROTIUM* (BURSERACEAE) IN MID-TERTIARY AMBER FROM THE DOMINICAN REPUBLIC

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ABSTRACT

Protium callianthum (Burseraceae) is described as a new species of fossil flower from amber deposits in the Dominican Republic. The flower is functionally staminate and is characterized by a cupular calyx with 5 triangular lobes, 5 widely recurved petals (1 missing through insect predation or mechanical damage), 10 incurved stamens with laterally dehiscent anthers, and an enlarged, annular disc surrounding a small pistillode. The ovary is glabrous and 5-lobed, with a fused style and spreading, 10-lobed stigma. Features consistent with many extant *Protium* species are petals with papillate margins and a minutely papillate adaxial surface, and stamens of two slightly unequal series, the antepetalous being longer than the antesepalous. This is the 12th angiosperm species recently described in Mid-Tertiary amber from Neotropical Caribbean forests.

RESUMEN

Se describe **Protium callianthum** (Burseraceae) como una nueva especie de flor fósil procedente de los depósitos de la República Dominicana. La flor es funcionalmente estaminada y se caracteriza por un cáliz cupular con 5 lóbulos triangulares, 5 pétalos ampliamente recurvados (1 perdido por predación de insectos o daño mecánico), 10 estambres incurvados con anteras dehiscuentes lateralmente, y un disco anular ensanchado que rodea un pequeño pistilodio. El ovario es glabro y 5-lobulado, con un estilo fusionado y extendido, estigma 10-lobulado. Sus características consistentes con muchas especies vivientes de *Protium* son pétalos con márgenes papilosos y superficie adaxial dilatamente papilosa, y estambres de dos series ligeramente desiguales, los antepétalos más largos que los antesépalos. Esta es la duodécima especie de angiosperma recientemente descrita en ámbar del terciario medio en bosques Neotropicales Caribeños.

INTRODUCTION

Previously described fossil angiosperms from the Dominican amber deposits include 3 species of Arecaceae (Poinar 2002a, 2002b), 3 of Meliaceae (Chambers et al. 2011b; Chambers & Poinar 2012), 2 of Lauraceae (Chambers et al. 2011a, 2012b), 1 of Fabaceae (Poinar 1991), 1 of Chrysobalanaceae (Poinar et al. 2008a; re-vised by Chambers & Poinar 2010), and 1 possibly of Moraceae (Poinar et al. 2008b). The habitat for these taxa was a moist tropical forest, from which numerous amber-embedded insect and plant fossils are known (Poinar & Poinar 1999). The family Burseraceae, order Sapindales, is most closely related to family Anacardiaceae (Stevens 2001 onwards; Wannan 2006). It contains about 700 species in 19 genera found principally in tropical and subtropical areas of the Old and New Worlds (Daly et al. 2011). Based on DNA evidence from plastid and nuclear markers, the age of Burseraceae has been estimated as 64.92 (60.33–69.67) Ma, near the Cretaceous/Tertiary boundary (De-Nova et al. 2012). This is considerably younger than the estimated date of 92.7 Ma of Becerra et al. (2012). Fossil evidence of the Burseraceae, principally in the form of fruits and pyrenes, first becomes abundant in the Early Tertiary (Daly et al. op. cit., p. 87). *Protium* is one of the largest genera in the family, with ca. 180 species, ranging in the New World from southern Mexico to Amazonia and in the Old World from Madagascar to India, tropical China, and the Malesian region (Daly et al. op. cit.). It is almost entirely arborescent, with various species providing sources of resin and durable timber (Mabberley 2008).

MATERIALS AND METHODS

The described flower, together with an accompanying one missing its reproductive organs (see Fig. 5), are in a single piece of amber collected from mines in the Dominican Republic, in the Cordillera Septentrional between the cities of Puerto Plata and Santiago. The amber is principally deposited in turbiditic sandstones of the Upper

Eocene to Lower Miocene Mamey Group (Draper et al. 1994). The age of the amber is controversial, the oldest assigned dates being 45–30 Ma, based on coccoliths (Cépek in Schlee 1999), and the youngest being 20–15 Ma, based on foraminifera (Iturralde-Vinent & MacPhee 1966).

DESCRIPTION

Protium callianthum K.L. Chambers & Poinar, sp. nov. (Figs. 1–5). TYPE: HISPANIOLA. DOMINICAN REPUBLIC: amber mine in the northern mountain range (Cordillera Septentrional), 2010, *unknown amber miner s.n.* (HOLOTYPE: catalogue number Sd-9-191, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

Flower 5-merous, staminate, width at anthesis (estimated from fully developed petals) 6.0 mm (Figs. 1, 2), calyx glabrous, cupular (Fig. 4), 1.4 mm long overall, sepals connate, the fused portion 1.0 mm, the lobes broadly triangular, acute, 0.4 mm long, 0.7 mm wide at base; petals 5 (1 missing and 1 truncated near base), lanceolate from a broad base, acute, spreading, distal portion recurved, length 2.4 mm including the recurved part, the tip inflexed (Fig. 4), margin papillate (Fig. 4), abaxial surface glabrous, adaxial surface minutely papillate; stamens 10, strongly incurved, of 2 different lengths, the antepetalous ones up to 1.1 mm, the antesepalous ones up to 0.9 mm, anthers lance-linear, basifixed (Fig. 2), 0.5 mm long, laterally dehiscent; disc intrastaminal, glabrous, annular, swollen, 1.7 mm in diameter, the central depression 0.7 mm in diameter, occupied by a reduced pistilode (Fig. 2), ovary ovoid, glabrous, ca. 5-lobed, style fused, stout, 0.15 mm long, distally 10-lobed or sulcate (Figs. 1, 2), floral pedicel papillate at base, otherwise glabrous, 2.8 mm long (Fig. 3).

Etymology.—From Greek “kallos,” beauty, and “anthos,” flower.

DISCUSSION

Petals of *Protium* may be either erect or reflexed at anthesis (Engler 1931), and the fossil is in the latter category. Petals are variously glabrous or pubescent in the genus, e.g., villous abaxially and adaxially in *P. alvarezianum* Daly & P. Fine and adaxially short-papillate in *P. carolense* Daly. The fossil resembles the latter species in this respect as well as in its widely recurved petals, but differs in other features (e.g., flowers 5-merous versus 4-merous). The form of calyx seen in *P. callianthum* is well represented in the genus, as described for many of its species by Swart (1942). Anthers with basal rather than dorsal insertion are common in the genus and characterize *P. callianthum* (Figs. 2, 3). They are illustrated for *P. altsonii* Sandw., *P. bahianum* Daly, and others (Daly 1989, 1992a). Staminate flowers possessing a thick intrastaminal disc whose central depression contains a reduced, nonfunctional but structurally complete pistil, are common in *Protium* (see illustrations of *P. bahianum* [Daly 1992a] as well as *P. morii* Daly and other taxa [Daly 1992b]). The ease with which the fossil keys to *Protium* on floral traits (Swart 1942; Daly et al. 2011), as well as its similarity to the various illustrated taxa mentioned above, strongly support its assignment to this genus.

Several features of the fossil are worth noting. Papillate margins allow postgenital fusion between the valvate petals before they finally separate at anthesis. This occurs through interdigitation of the papillae, as explained by Bachelier and Endress (2009). A striate cuticular ornamentation, which they also mention, is not visible in the fossil. The occurrence of antepetalous stamens longer than the antesepalous ones, as in the fossil, was noted for *Protium morii* by Bachelier and Endress (2009) from floral bud cross-sections. However, this differs from the description of the species by Daly (1992), who gives 1.7–1.85 and 1.85–2.05 mm for the antepetalous versus antesepalous ones, respectively. Other species for which the descriptions mention longer antesepalous than antepetalous stamens are *P. carolense* (Daly 1992) and *P. alvarezianum* (Daly & Fine 2011). The frequency, in *Protium*, of the stamen length relationship shown by *P. callianthum* is uncertain.

Tribe Protieae (the *Protium* Alliance per Daly et al. [2011]) is a well-supported clade in recent molecular analyses (Clarkson et al. 2002; Weeks et al. 2005; Thulin et al. 2008; Becerra et al. 2012; Fine et al. in review). It presently comprises the genera *Protium*, *Crepidospermum*, and *Tetragastris*, although the need for some taxonomic revision is often suggested (e.g. Thulin et al. 2008), and the latter 2 genera may soon have to be merged with *Protium* (P. Fine, pers. comm.). Relationships in the tribe were reviewed by Daly (1989), who offered criteria by which to distinguish among the 3 genera. Using his proposals, *P. callianthum* is separated from the small

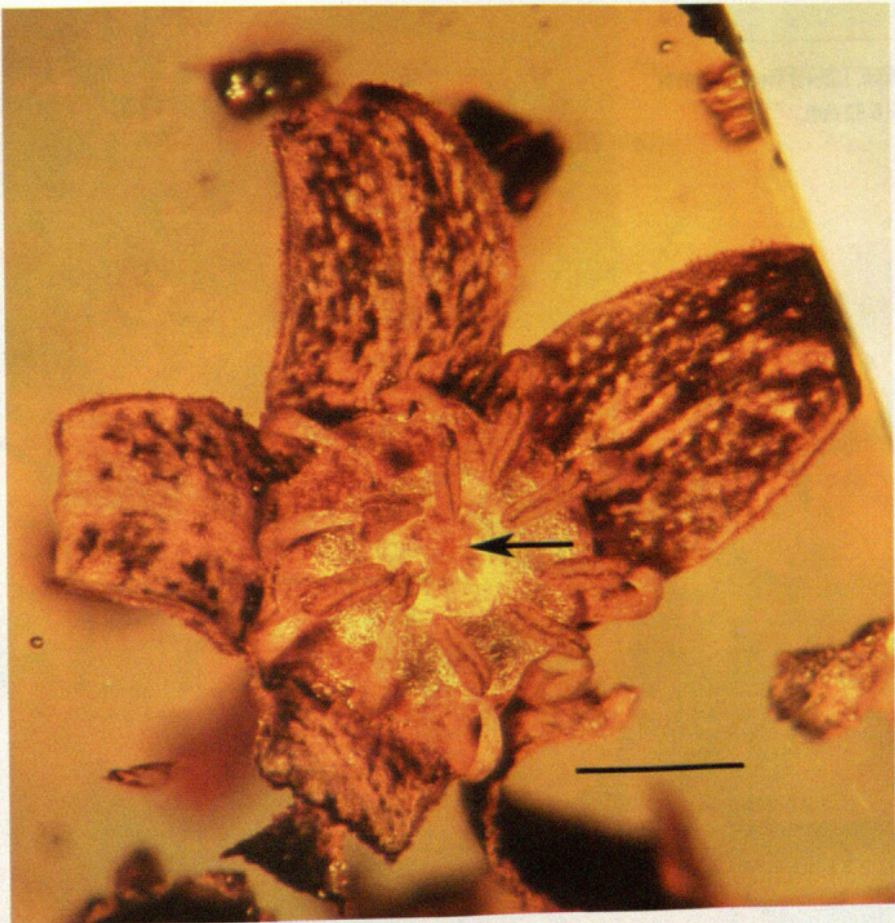


FIG. 1. *Protium callianthum*. Apical view of flower. Arrow indicates lobed stigma of pistillode. Scale bar = 0.80 mm.

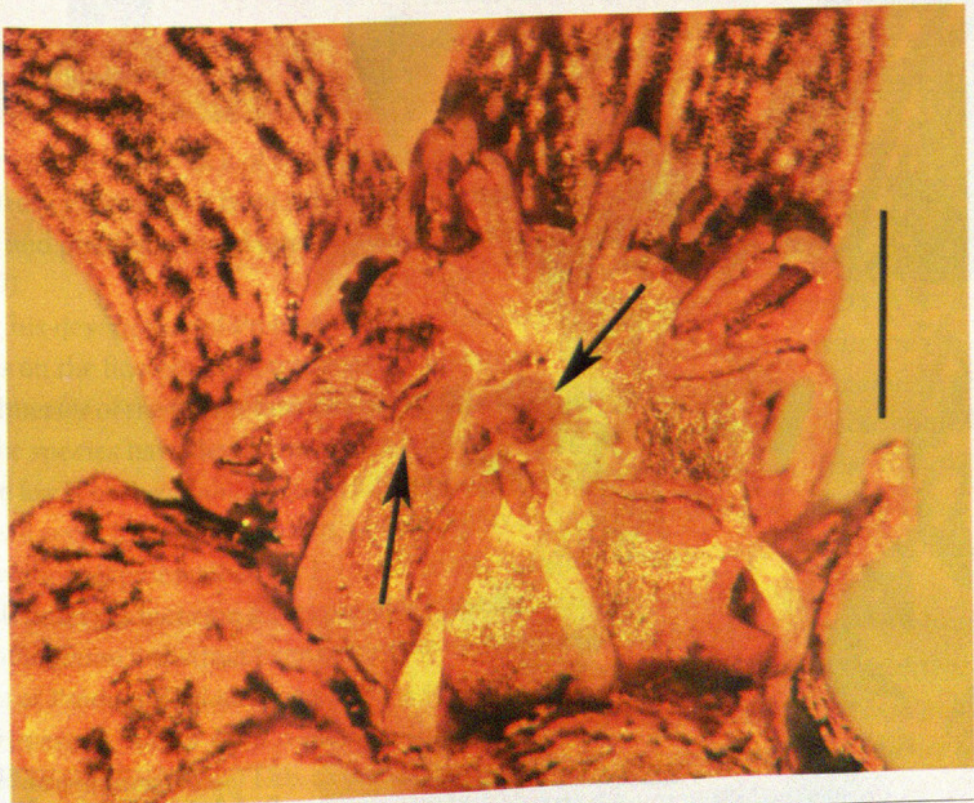


FIG. 2. *Protium callianthum*. Magnified apical view. Upper arrow is on lobed stigma, lower arrow shows basal insertion of anther on filament. Scale bar = 0.74 mm.

FIG. 3. *Protium callianthum*. Lateral view of flower and pedicel. Scale bar = 0.92 mm.

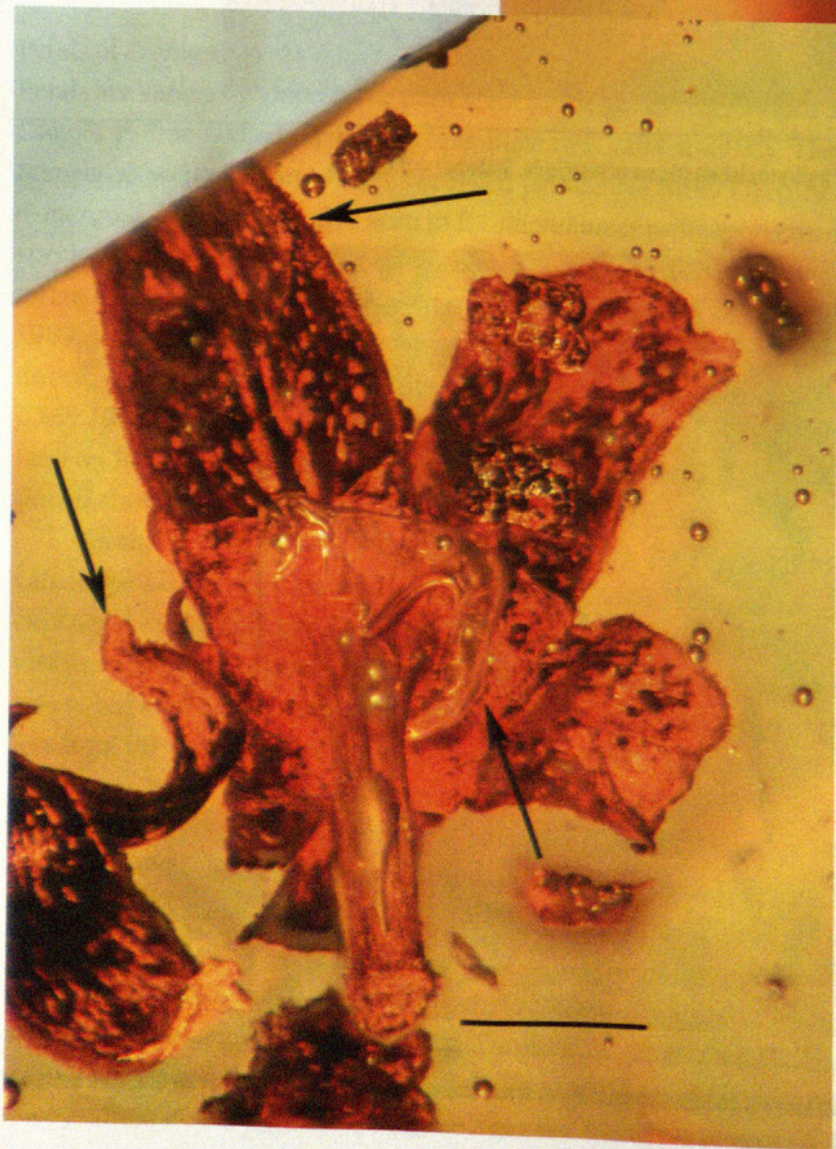


FIG. 4. *Protium callianthum*. Basal view of flower. Top arrow shows papillate margin of petal, left arrow is on inflexed petal tip of adjacent flower, lower arrow indicates calyx cup. Scale bar = 1.67 mm.

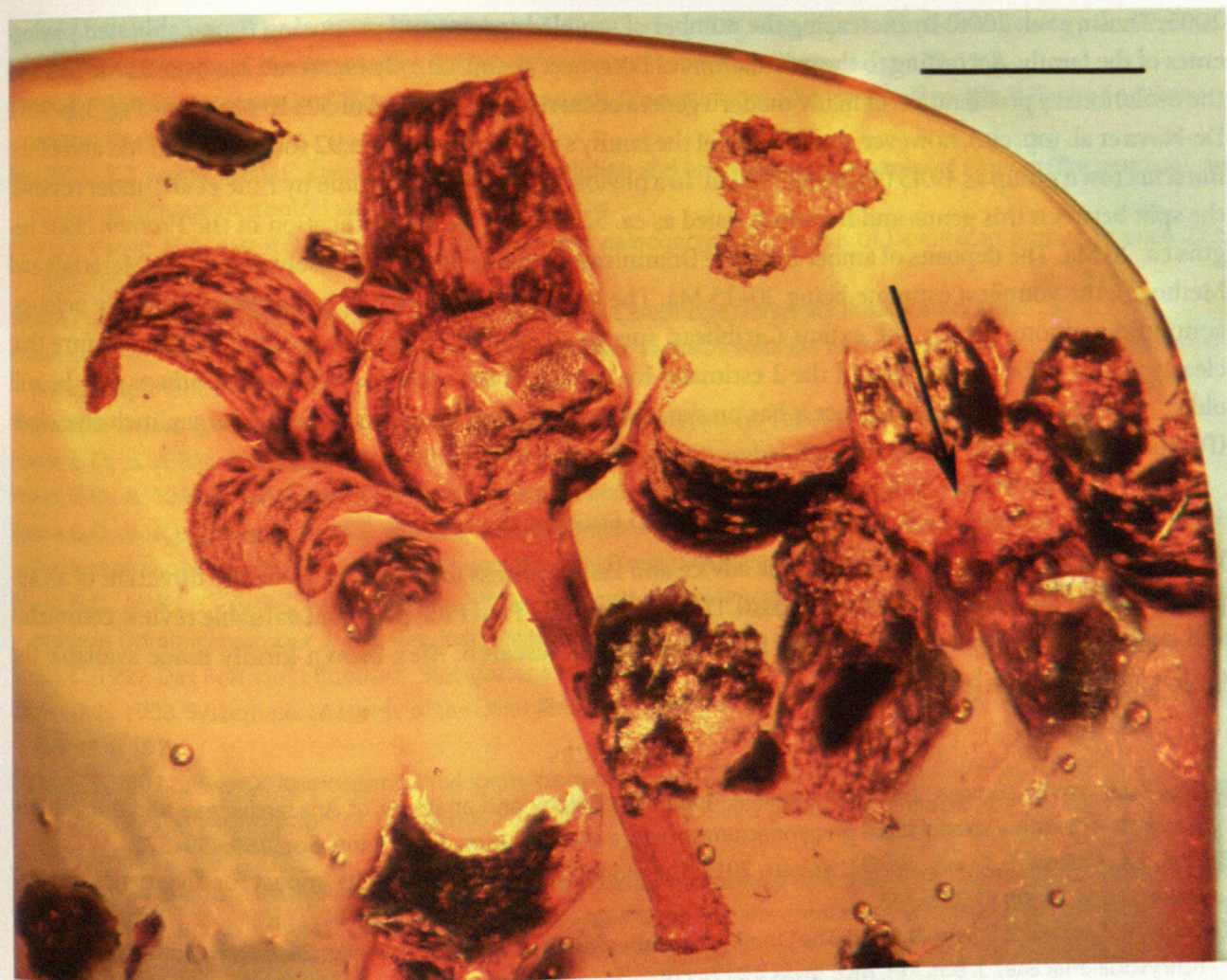


FIG. 5. *Protium callianthum*. Two adjacent flowers, the right one damaged by insect predation. Arrow is on partially eaten disc. Scale bar = 1.37 mm.

genus *Crepidospermum* by the lack of snail-shaped trichomes (Solereder 1908) on external organs. *Tetragastris* usually differs from *Protium* and from the fossil in having the anthers basifixed on short, broadly laminar filaments, the disc and pistillode fused into a conical "ovariodisc" in staminate flowers, and the petals partly connate (Daly 1989).

Following his description of *Protium carolense*, Daly (1992) mentions a relationship of this taxon with an insect that feeds on the flowers. He found that in a majority of collections, all the buds are infested with a larva, which eats the interior of the flower but does not prevent regular enlargement of the remaining perianth. Other collections of the species have developing fruits with no evidence of the infestation. In the block of amber containing the type fossil of *P. callianthum* is an adjacent staminate flower (Fig. 5) in which the stamens and top of the disc and pistil seem to have been eaten, quite possibly by an herbivorous insect of some kind. Whether the insect/flower relationship described for *P. carolense* might also have characterized *P. callianthum* is, of course, unknown, but it deserves mention for its possible botanical and entomological interest.

Protium callianthum is distinct from other taxa of the genus occurring today in the Caribbean region. One modern species of *Protium*, *P. glaucescens* Urb., is endemic to the Dominican Republic but differs from *P. callianthum* in its 4-merous, rather than 5-merous, flowers. The 5 species endemic to Cuba also have 4-merous flowers, while *P. attenuatum* (Rose) Urb. of the Lesser Antilles, with a 5-parted perianth, differs from *P. callianthum* in its ovate, dorsifixed anthers and 5-lobed stigma, among other floral traits.

The two most recent molecular phylogenetic studies of Burseraceae (Becerra et al. 2012; De-Nova et al. 2012), although emphasizing the genus *Bursera*, go beyond previous studies (Clarkson et al. 2002; Weeks et al.

2005; Thulin et al. 2008) by increasing the number of sampled species and proposing time-calibrated phylogenies of the family. According to the calculations of Becerra et al. (op. cit.), Burseraceae are over 92 Ma old, and the evolutionary proliferation of many modern genera occurred in the period of 30 ± 10 Ma (their Fig. 3, p. 339). De-Nova et al. (op. cit.), however, give the age of the family's crown group as 64.92 (60.33–69.67) Ma and of the *Bursera* crown group as 49.43 (45.38–53.77) Ma. In a phylogenetic study of *Protium* by Fine et al. (under review), the split between this genus and *Bursera* is dated as ca. 52 Ma, and the diversification of the *Protium* clade begins ca. 20 Ma. The deposits of amber from the Dominican Republic are not precisely dated (see Materials and Methods), the youngest estimate being 20–15 Ma. The large clade to which *P. callianthum* probably belongs, containing, among others, the extant Caribbean species of *Protium*, diverged around 15 Ma, a figure that clearly would favor the younger of the 2 estimates for the age of the amber. *Protium callianthum* may be still older, on the stem of this clade, since it has no synapomorphies that match those in the larger, inclusive clade (P. Fine, pers. comm.).

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