TREPTOSTEMON (LAURACEAE), A NEW GENUS OF FOSSIL FLOWER FROM MID-TERTIARY DOMINICAN AMBER

Kenton L. Chambers
Department of Botany and Plant Pathology
Oregon State University
Corvallis, Oregon 97331, U.S.A.
chamberk@science.oregonstate.edu

George O. Poinar, Jr.
Department of Zoology
Oregon State University
Corvallis, Oregon 97331, U.S.A.

Andre S. Chanderbali
Department of Biology
University of Florida
Gainesville, Florida 32611, U.S.A.

ABSTRACT

A fossil flower of family Lauraceae is described from amber of Late Oligocene-Early Miocene deposits in the Dominican Republic, island of Hispaniola. The flower is staminate and lacks a visible pistillode. It has 6 equal, lanceolate, spreading tepals and at least 6 fertile stamens. The 4 anther pores of the stamens of whorls 1 and 2 are arranged in pairs, one above the other. The pores are open and in some cases have the torn remains of apical valves. The 3 stamens of whorl 3 have at least 2 pores, whose raised valves are visible, but the total number of pores is uncertain. It is not known whether these stamens are functional or staminodial. Whorl 4 staminodes appear to be absent. A distinctive feature of the flower is that all 6 anthers of whorls 1 and 2 stamens are extrorse in dehiscence. Due to this unique characteristic, the flower cannot be assigned to any modern genus, and it is here described as the new genus and species **Treptostemon domingensis**.

RESUMEN

Se describe una flor fósil de la familia Lauraceae procedente de ámbar de depósitos del Oligocenetardío- Miocene temprano en la República Dominicana, isla de la Española. La flor es estaminada y carece de un pistilodio visible. Tiene 6 tépalos iguales, lanceolados extendidos, y al menos 6 estambres fértiles. Los 4 poros de las anteras de los estambres de los verticilo 1 y 2 están colocados en pares, uno encima del otro. Los poros están abiertos y en algunos casos tienen restos de desgarros de las valvas apicales. Los 3 estambres del verticilo 3 tienen al menos 2 poros, cuyas valvas elevadas son visibles, pero el número total de poros es incierto. No se conoce cuantos de estos estambres son funcionales o son estaminodios. El verticilo 4 de estaminodios parece estar ausente. Una característica distintiva de la flor es que las 6 anteras de los verticilos de estambres 1 y 2 tienen dehiscencia extrorsa. Debido a esta característica única, la flor no puede ser asignada ningún género moderno, y se describe aquí como el nuevo género y especie **Treptostemon domingensis.**

INTRODUCTION

Amber deposits of the Cordillera Septentrional, Dominican Republic, continue to yield interesting fossil angiosperm flowers from the low-elevation tropical forests characteristic of Mid-Tertiary Caribbean vegetation (Poinar & Poinar 1999). We have recently described fossils assignable to *Licania* (Chrysobalanaceae) (Poinar et al. 2008a, revised by Chambers & Poinar 2010), *Persea* (Lauraceae) (Chambers et al. 2011a), *Trichilia* (Meliaceae) (Chambers et al. 2011b), *Swietenia* (Meliaceae) (Chambers & Poinar 2012), and *Trochanthera* (possibly Moraceae) (Poinar et al. 2008b). A second flower of Lauraceae is described in the present paper. It has several well-marked features, including 6 fertile stamens in whorls 1 and 2, whose anthers have 2 pairs of pores that open extrorsely. The stamens of whorl 3 display 2 upright valves but are possibly staminodial, since their terminal portion is dissimilar in size and shape from the fertile anthers. The anthers are closely adjacent and are on short filaments. The epidermis of the anthers and staminodes is densely covered with minute trichomes. No pistillode or whorl 4 staminodes are visible. Because of the extrorse dehiscence of the 6 anthers of whorls 1 and 2, the fossil cannot easily be accommodated in any modern genus of Lauraceae. We therefore propose to separate it as the new genus and species *Treptostemon domingensis*.

MATERIALS AND METHODS

All the amber fossils referred to above came from mines in the Cordillera Septentrional, between Puerto Plata and Santiago, Dominican Republic. Dating methods applied to the deposits are thus far equivocal. An age of 45–30 mybp was assigned by Cépek in Schlee (1999) based on fossil coccoliths, and one of 20–15 mybp was determined by Iturralde-Vinent and MacPhee (1996) based on foraminifera. The amber is found in turbiditic

sandstones of the Upper Eocene to Lower Miocene Mamey Group (Draper et al. 1994). Animals and plants of the forest vegetation present at the time of amber deposition were described by Poinar and Poinar (1999), the original resin having been a product of the arborescent genus *Hymenaea* (Fabaceae). In Poinar and Poinar (op. cit.), the present flower was inadvertently assigned to the genus *Nectandra* (Pg. 21, Fig. 10).

DESCRIPTION

Treptostemon K.L. Chambers, Poinar, & A.S. Chanderbali, gen. nov. TYPE SPECIES: *Treptostemon domingensis* K.L. Chambers, Poinar, & A.S. Chanderbali, sp. nov. (**Figs. 1–2**).

Diagnosis.—Flower staminate, radially symmetrical (Fig. 1), receptacle flat, pedicel remnant strigose, tepals 6, in 2 whorls of 3, separate, approximately equal, spreading, lightly strigose on both surfaces, margins involute, glabrous (Fig. 2), stamens 9, in whorls of 3, at least the outer 2 whorls fertile, anthers minutely puberulent, those of whorls 1 and 2 with 4 pores arranged as 2 pairs, one above the other, all extrorse, opening by apical valves, stamens of whorl 3 functional or staminodial, their distal portion dissimilar in size and shape from the fertile anthers (Fig. 2), 2 or 4 small pores probably present, the distal pair opening extrorsely by upturned valves, glands of whorl 3 stamens small, whorl 4 staminodes and pistillode not evident. Pistillate flower unknown.

Etymology.—From Greek "treptos," turned, and "stemon," stamen.

Treptostemon domingensis K.L. Chambers, Poinar, & A.S. Chanderbali, sp. nov. TYPE: HISPANIOLA. DOMINICAN REPUBLIC: amber mine in the northern mountain ranges (Cordillera Septentrional), 1995, *unknown amber miner s.n.* (HOLOTYPE: catalogue number Sd-9-64, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.)

Description.—Tepals lanceolate, acute, laterally spreading, 3.1 to 4.0 mm long, 1.1 to 1.6 mm wide (Fig. 1), anthers of whorls 1 and 2 0.9 to 1.0 mm wide, ca. 1.0 mm long, with short filaments, pores extrorse, circular to oblong, ca. 0.3 mm in diameter, valve remnants visible in a few cases (Fig. 2), connective forming an adaxial ridge, stamens of whorl 3 club-shaped, distal portion cylindrical, 0.7 mm in diameter, pores extrorse, the distal pair defined by small, upturned valves (Fig. 2), otherwise not observable, glands of whorl 3 stamens 0.19 mm wide (only 1 observed).

Etymology.—From source of amber in Dominican Republic.

DISCUSSION

Examination of the fossil is best done from above, as in Figures 1 and 2. In a lateral view, obtained with difficulty, the outer anthers display all 4 extrorse pores, although in apical view, the lower pair may be barely visible (Fig. 2). The filaments of the outer stamens are quite short and curve at the tip, so that the anthers face dorsolaterally. The positioning of the stamens does not allow observation of pores on whorl 3, and their number is uncertain. The upraised valves of the distal pores (Fig. 2) are in an extrorse position. Despite the reduced size and cylindrical shape of these anthers, it is uncertain whether the whorl 3 stamens are fertile or staminodial. A staminodial condition is possible, considering the report by Kubitzki and Kurz (1984) that in staminate flowers of 3 dioecious species of *Ocotea* they studied, "[t]he staminodes often possess valves that open after the wilting of the stigma" (i.e., stigma of the pistillode). Only one gland of the whorl 3 stamens is in view (Fig. 2). On some anthers, small, black air bubbles that have settled among the surface trichomes may be confused for pores, but these are artifacts. The extrorse dehiscence in all androecial whorls of *Treptostemon* is unique in Lauraceae, although in *Pleurothyrium* there are 9 tetrasporangiate, latrorse anthers which may look almost extrorse (J. Rohwer, pers. comm.).

The shortness of the stamens of *Treptostemon* and their close positioning in the flower are features similar to *Aniba* and *Aiouea* (Kubitzki and Renner 1982), among other genera, although a close relationship to these 2 taxa, which are hermaphrodite, with upright tepals and only 2 pores per anther, is not likely. Furthermore, the usual laurad introrse dehiscence of whorls 1 and 2 anthers occurs in the 2 genera. Stamens with short filaments also occur in the New World dioecious genera *Rhodostemonodaphne* (Madriñán 2004) and *Ocotea* (the latter

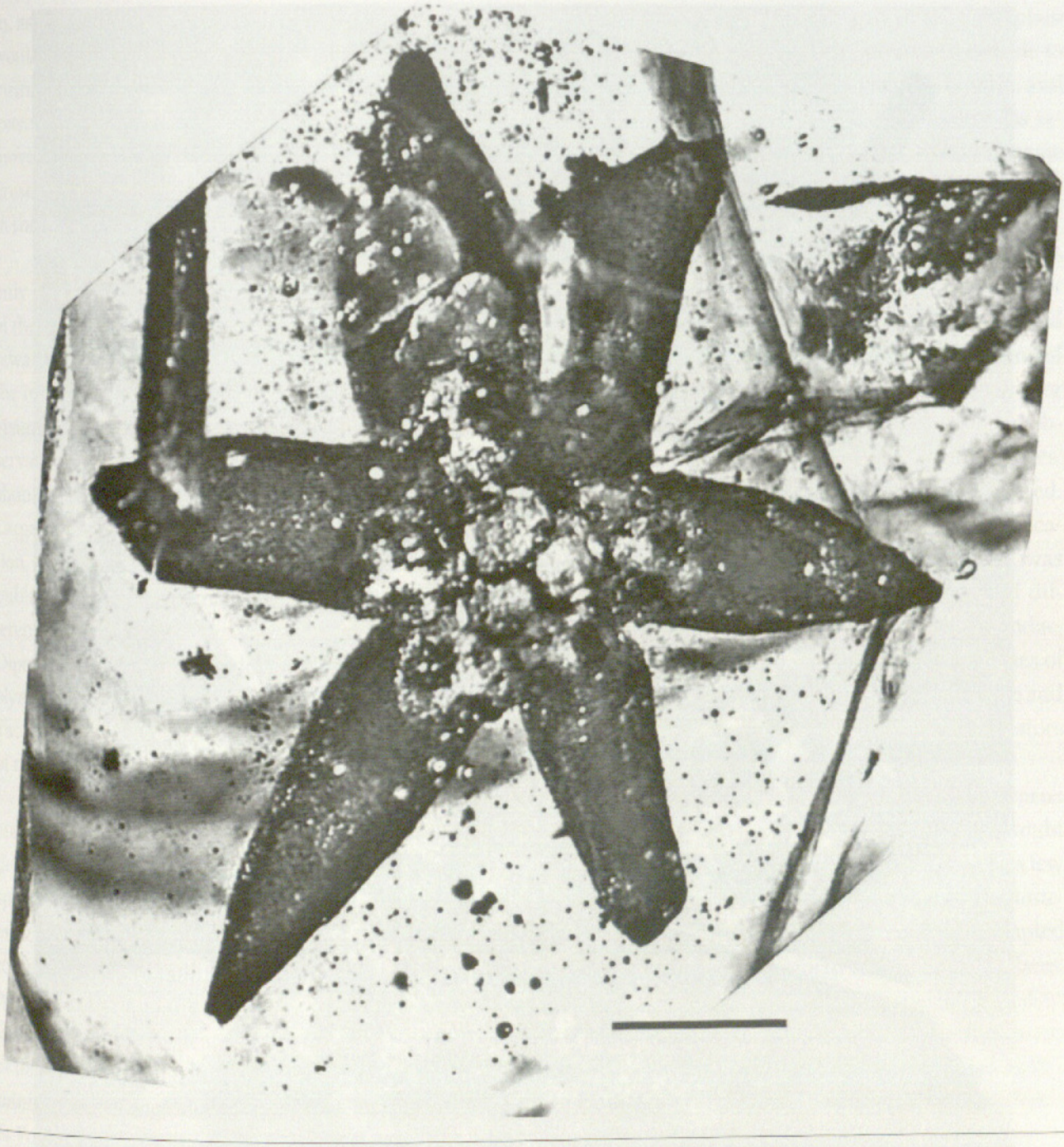

Fig. 1. *Treptostemon domingensis*, apical view of complete flower. Scale bar = 1.4 mm.

with bisexual or unisexual flowers). Both have 4-pored, introrse anthers, but in *Rhodostemonodaphne* the pores form a more or less horizontal row (Rohwer 1993; van der Werff 1991, Fig. 2E), unlike the pores of *Treptostemon* anthers. The latter two genera are similar in lacking staminodes of whorl 4 but differ in their receptacle, which is narrowly tubular in *Rhodostemonodaphne* (Rohwer op. cit.). The closest relative among genera with 4-pored anthers is probably *Ocotea*, a species-rich and variable taxon characterized by Rohwer (1993, p. 382) as "the dustbin of the Perseae." Dioecious species such as *O. pyramidata* (Allen 1945) may have anthers 1.0 mm long, with the filament only 0.5 mm. (As an aside, although pollen is shed inwards by these anthers, it is also released outwards from the 2.15 mm-long stamens of whorl 3). According to Rohwer (op. cit.) the whorl 4 staminodes of *Ocotea* are absent in unisexual flowers, the receptacle varies from flat to deeply tubular, and the pistillode in male flowers may be present or absent. The principal difference between *Ocotea* and *Treptostemon*, therefore, is that the former has anthers of whorls 1 and 2 dehiscing introrsely.

Pollen had recently been discharged from the *Treptostemon* flower before it became immersed in tree res-

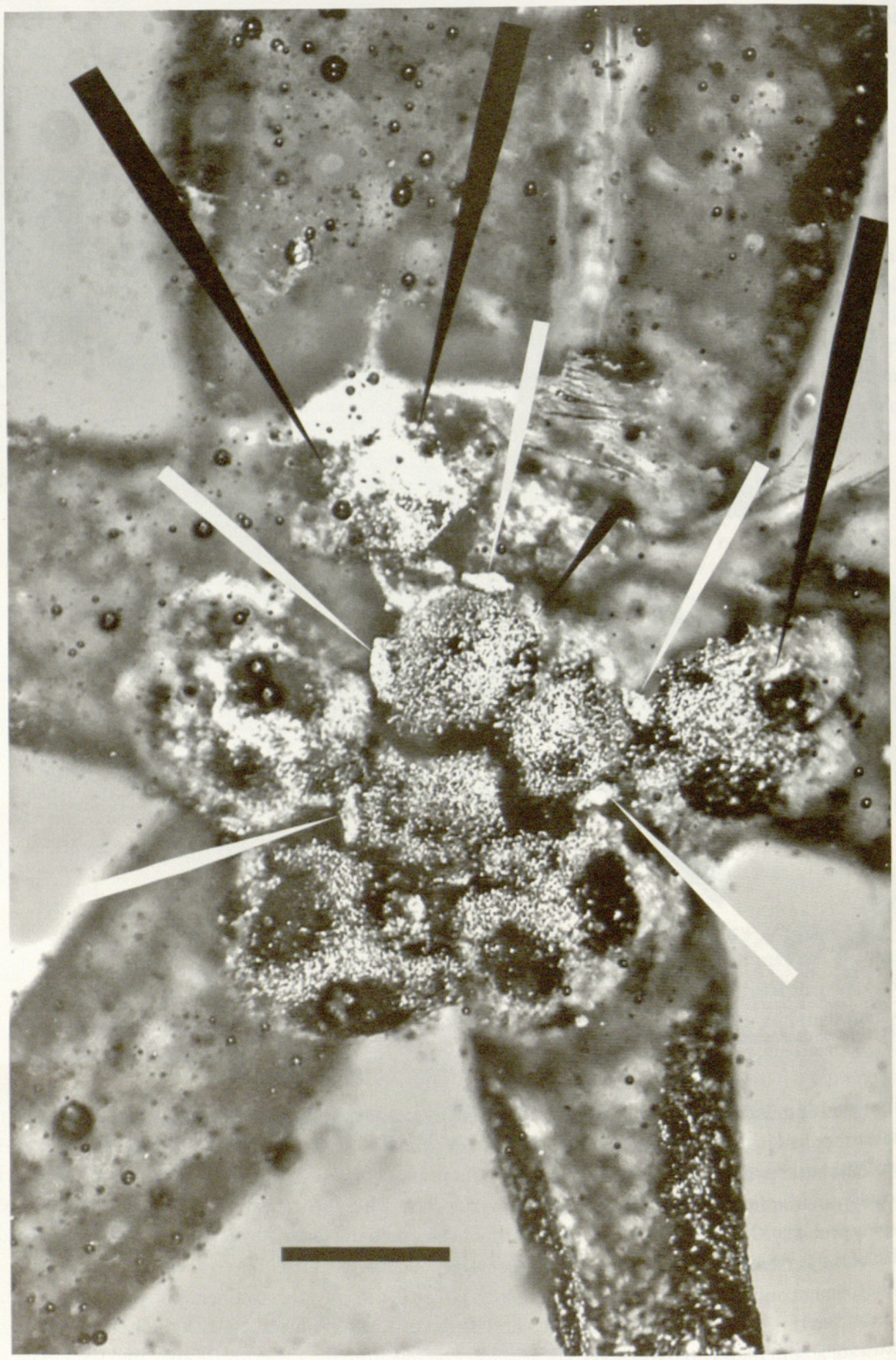

Fig. 2. *Treptostemon domingensis,* enlarged view. White arrows indicate 5 of 6 upraised valves on stamens of whorl 3; long black arrows show 3 apical valve remnants by pores on anthers of whorl 1; short black arrow points to gland of whorl 3 staminode. Note involute, glabrous margins of tepal at lower right. Scale bar = 0.7 mm.

in, as shown by a cloud of tiny pollen grains below 2 tepals on one side of the fossil. Being dioecious, the plant would have had to release pollen from the staminate flowers in such a way that it would be easily available to visiting insects for transfer to pistillate flowers on another tree. It is likely that dioecy, nectar production, and extrorse anther dehiscence were adaptive features of the species' pollination syndrome, but we are too far removed in time to reconstruct other details of its floral biology. A brief review of reports on pollination in some present-day Lauraceae may be of interest, nonetheless, in conjunction with a discussion of available pollinators in the insect fauna already known from Dominican amber (Michener & Poinar 1997; Poinar & Poinar 1999).

A report on pollinators identified from modern tropical rain forests in Costa Rice (Bawa et al. 1985) lists only one member of Lauraceae, an unidentified species of *Ocotea*. It is cited as hermaphroditic and a member of the subcanopy, its major pollinators being beetles. Whether the flowers offer both nectar and pollen as food rewards is not mentioned. However, in her generic description of *Ocotea*, Allen (1945) states that stamens of the inner series always bear two sessile or stipitate glands, presupposing the presence of a nectar reward for visitors. In a study of dichogamy and dioecy in Neotropical Lauraceae, Kubitzki and Kurz (1984) included observations of pollinators for 3 dioecious species of *Ocotea*. Two species were seen to be visited by brown bees, about 1 cm in length, while small diptera, wasps and moths sucking nectar were occasionally encountered. Larger flies were observed visiting flowers of *O. guianensis* and *O. opifera* but could not be caught for identification. A more detailed study of pollination in a single dioecious species, *Laurus azorica* of Macaronesia, was published by Forfang and Olesen (1998). In a sample of over 200 trees, flower visitors included at least 11 different insect species. These were: Hymenoptera–2 species of Halictidae, 1 of Apidae, and 1 of Ichneumonidae; Diptera–1 species of Musicidae, 1 of Syrphidae, 1 of Tachinidae, and 1 of Bibionidae; Lepidoptera–1 species of Nymphalidae; Coleoptera–1 species of Nitidulidae; Hemiptera–1 species of Pentatomidae. Only Halictidae and Tachinidae were common, comprising 97% of the visits. Bees are also considered to be the principle pollinators of the avocado, *Persea americana*, even though flies and other insects also visit the flowers (Free 1993).

Generalized, radially symmetrical flowers of Lauraceae, with spreading perianth and exposed stamens and pistil, are open to visits by many different groups of anthophilous insects. A potential pollinator might develop a specific attraction to the odor of pollen or nectar in such a flower and become faithful to one or a few species (Faegri & van der Pijl 1979). However, it is unlikely that an unspecialized flower like that of *Treptostemon*, even with its modified form of pollen presentation atypical of the family, would have been closely adapted to a single kind of pollinator. Since their origination in the Early Cretaceous (Danforth & Poinar 2011), bees, which rear their young on pollen, have been among the most dependable pollinators of angiosperms. Based on the above reports indicating that bees are frequent visitors of present-day Lauraceae, it is likely that this group of insects also visited and pollinated *T. domingensis* in the Tertiary forests of Hispaniola. The bee fauna of Dominican amber includes representatives of families Apidae, Andrenidae, Colletidae, and Halictidae (Michener & Poinar 1997). Of these, the most common bee in Dominican amber is the small, stingless *Proplebia dominicana* (Apidae, tribe Meliponini), which could well have been significant in the pollination system of *Treptostemon*. Despite their presence in the fossil record, stingless bees do not occur in Hispaniola today. Their disappearance as keystone species could have led to the elimination of many plant species, including *Treptostemon*.

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