MIMOSOIDEAE (FABACEAE) DIVERSITY AND ASSOCIATES IN MID-TERTIARY DOMINICAN AMBER

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ABSTRACT

The present work provides a survey of mimosoid (Fabaceae: Mimosoideae) fossils and their associates in Dominican amber. Included are 6 different flower types and 8 different leaflet types. Two flowers are described as **Campopetala dominicana** gen. & sp. nov. and **Entada hispaniolae** sp. nov., respectively. The new combination **Senegalia eocaribbeanensis** is proposed. Also presented is an example of a flower pollinator (Hymenoptera: Apidae), a flower herbivore (Hemiptera: Pentatomidae), leaflet parasitism by fungi, ants associated with pinnae, and indirect evidence of damage from insect herbivores. These fossils are a partial record of mimosoid diversity and associated organisms that existed in the Mid-Tertiary forests preserved in amber from the Dominican Republic.

RESUMEN

El presente trabajo aporta un estudio de los fósiles mimosoides (Fabaceae: Mimosoideae) y sus asociados en el ámbar dominicano. Se incluyen 6 tipos diferentes de flor y 8 tipos diferentes de foliolos. Se describen dos flores como **Campopetala dominicana** gen. & sp. nov. y **Entada hispaniolae** sp. nov., respectivamente. Se propone la nueva combinación **Senegalia eocaribbeanensis.** También se presenta un ejemplo de un polinizador de flores (Hymenoptera: Apidae), un herbívoro de flores (Hemiptera: Pentatomidae), parasitismo de foliolos por hongos, hormigas asociadas con pinnas, y evidencias indirectas de daños por insectos herbívoros. Estos fósiles son un registro parcial de la diversidad mimosoide y organismos asociados que existieron en los bosques del Terciario medio preservados en ámbar de la República Dominicana.

INTRODUCTION

Mimosoids (Fabaceae: Mimosoideae) are widespread throughout the world and represent a very successful group with variable growth habits and a tolerance for climatic changes (Allen & Allen 1981). However, compared with other Fabaceae, mimosoids have a mediocre fossil record (Herendeen 1992). Fossil remains of mimosoids in Dominican amber were portrayed as part of the vegetation in a reconstructon of the Mid-Tertiary Dominican amber forest (Poinar & Poinar 1999).

The present work surveys mimosoid remains in Dominican amber, including 6 different flower types, 8 different pinna types, and a seed. Two of the flowers are described, one as a new species in the genus *Entada* and the other as a new genus and species. Also presented is the first fossil evidence of a pollinator (Hymenoptera: Apidae), a flower herbivore (Hemiptera: Pentatomidae), leaflet parasitism by fungi, leaf-visiting ants, and damage to leaflets from attacks by insect herbivores. These fossils give a view of mimosoid diversity and associated organisms that characterized the Dominican amber forests. Fossil flowers of some 11 other families of angiosperms have been identified from these forests, as listed in Poinar and Chambers (2015).

MATERIALS AND METHODS

Dating of Dominican amber is uncertain, with the youngest proposed ages of 20–15 mya based on foraminifera (Iturralde-Vincent & MacPhee 1996) and the oldest ages of 45–30 mya based on coccoliths (Cépek in Schlee 1990). These dates are derived from microfossils recovered from the strata containing the amber, which had been re-deposited in Upper Eocene to Lower Miocene turbiditic sandstones of the Mamey Group (Draper et al. 1994). Dilcher et al. (1992) felt that because the amber had already matured by the time it was redeposited into the marine basins, it could as old as late Eocene. The discovery of Early Oligocene amber in Puerto Rico and Maastrichtian-Paleocene amber in Jamaica (Iturralde-Vinent 2001) shows that amber of various ages ranges

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throughout the Greater Antilles. Examination and photographs were made with a Nikon stereoscopic microscope SMA-10-R at 80× and a Nikon Optiphot microscope at 800×.

RESULTS

The Mimosoideae are characterized by bipinnate leaves (with certain exceptions) with entire margins and asymmetrical outlines. The flowers are actinomorphic, having a 5-parted cupulate calyx, valvate corolla lobes equal in number to the sepals, and many (at least twice the number of petals) equal stamens (Croat 1978; Herendeen 1992). Additional characters are discussed below under specific fossils.

In 1992 Dilcher et al. described *Acacia eocaribbeanensis* from three flowers in Dominican amber. The species represents one of the commonest mimosoid flowers in this amber, and four additional flowers of the species are shown here in Fig. 1. One of these is perfect, and since the flowers of *A. eocaribbeanensis*, as published, are staminate, the pistil is briefly described below along with other measurements of the four flowers. Because some of the measurements differ from those in the original description, these new flowers show the diversity that was present in different populations of *A. eocaribbeanensis*.

Senegalia eocaribbeanensis Poinar & K.L. Chambers, comb. nov. (**Figs. 1–3**). Basionym: *Acacia eocaribbeanensis* D.L. Dilcher, P.S. Herendeen, & F. Huber. 1992. In: P.S. Herendeen & D.L. Dilcher, eds. Advances in legume systematics. Part 4, the fossil record. Pp. 33–42. Type: HISPANIOLA. Dominican Republic: Paleobotanical Collections, U.S. National Museum, Washington D.C., *unknown amber miner s.n.*, specimens obtained from the Jacob and Marianella Lopez-Penha Brodzinsky amber collection, Santo Domingo, Dominican Republic (holotype: USNM 458372; paratype: USNM 458373).

Description based on 4 flowers in a single piece of amber.
Flowers small, sessile, regular, 5-parted, with a very small, synsepalous calyx 0.5–0.8 mm long and 0.3–0.8 mm wide, corolla funnelform, longer than calyx, petals free, 1.4–1.8 mm long and 0.4–0.5 mm wide, stamens numerous, free, long-exserted, from 50–80 per flower, filaments 2.6–4.8 mm long, anthers minute, 125–146 µm long, apical glands spherical, 54–56 µm in diameter, ovary simple, flat, 1.0–1.2 mm long, glabrous, with rugose surface, stipe narrow, 127 µm long, style shorter than stamens, sharply bent near base, 222 µm long, stigma elongate, 48–55 µm long, ratio of calyx length to corolla length 0.36–0.44.

A NEW GENUS AND SPECIES OF MIMOSOIDEAE FLOWER

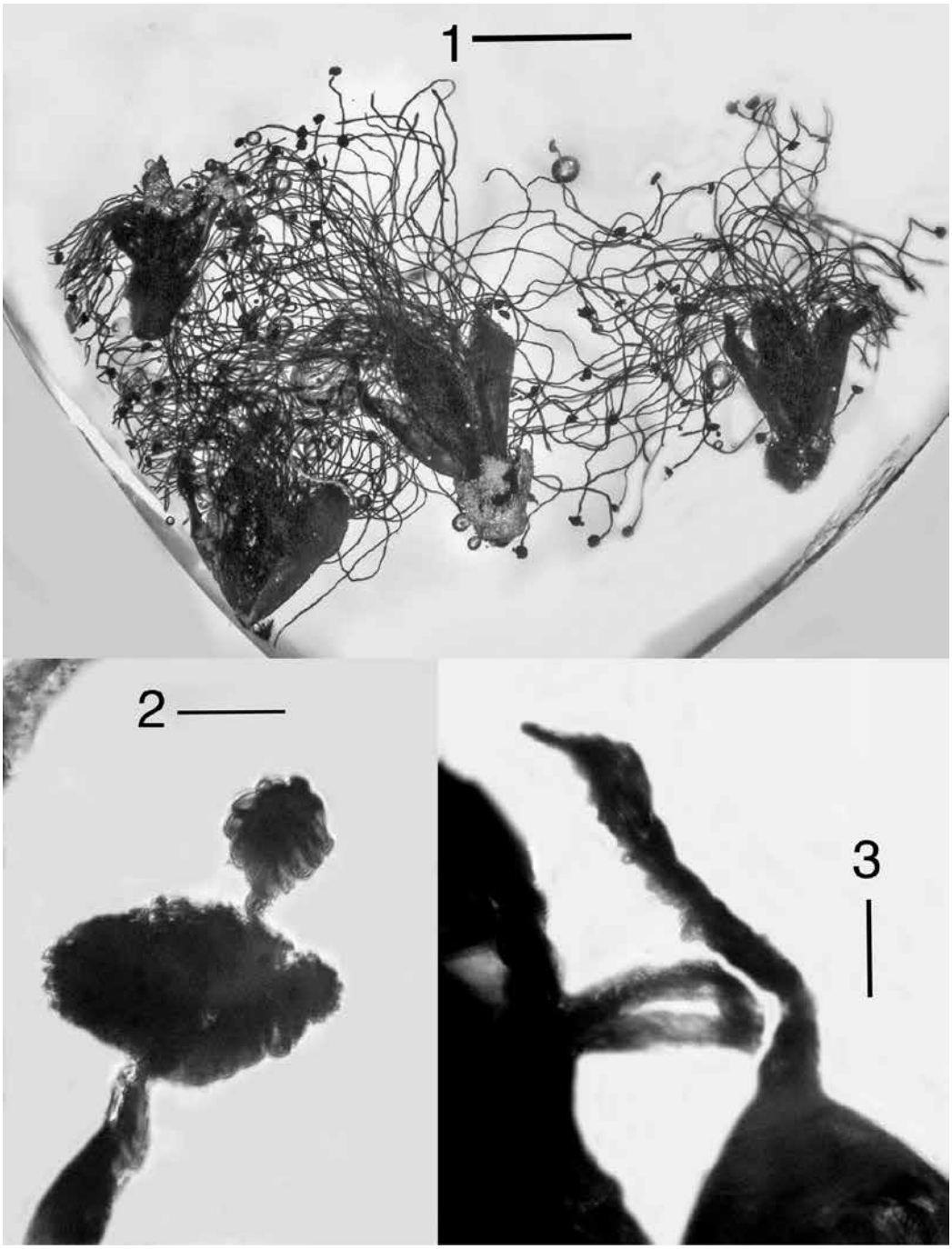
While examining additional mimosoid flowers in Dominican amber, a flower was discovered that appears to represent a new genus. Distinguishing features of this genus are the presence of reflexed petals, numerous, extremely long filaments, and the anthers transverse with protruding pollen sacs on either end.

Campopetala dominicana Poinar & K.L. Chambers, gen. & sp. nov. (**Figs. 4, 5**). Type: HISPANIOLA. Dominican Republic: amber mine in the northern mountain ranges (Cordillera Septentrional) between Puerto Plata and Santiago, 19.4°N, 70.4°W, *unknown amber miner s.n.* (holotype: accession number Sd-9-50, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.)

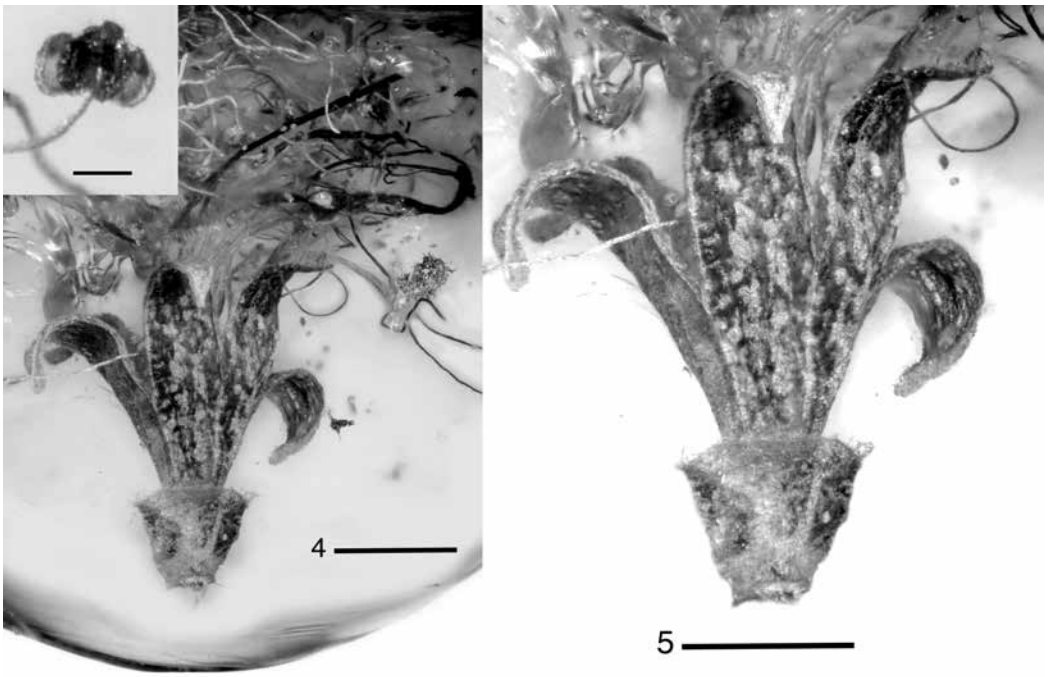
Flower regular, small, sessile, 5-parted, calyx synsepalous, cup-shaped, puberulent, length 0.9 mm, width 1.3 mm, sepals united, the lobes represented only by veins on surface of calyx cup, corolla funnelform, petals spreading, reflexed, length 3.9–4.2 mm, width 0.8–0.9 mm at base, fused for 35–38% of their length, glabrous except for some long trichomes on tips, stamen number 20–30, mostly free, with some irregularly united at base, filaments exserted, length 8.6–11.0 mm, anthers small, 220–284 µm long, transverse, with protruding pollen sacs on either end, apical glands not observed and presumed to be lacking, style simple, shorter than stamens, floral disc not observed.

Etymology.—Generic name from the Greek "kamptos" = curved and "petalon" = petal, in reference to the reflexed petals. The specific epithet is based on the geographic origin of the fossil.

The above characters as well as the absence of anther glands separate the fossil from other Mimosoideae presently found in Hispaniolae and Puerto Rico (Liogier 1985, 1988; Barneby & Zanoni 1989) as well as from *Senegalia eocaribbeanensis* (Dilcher et al. 1992).



Figs. 1–3. Mimosoid flowers in Dominican amber. **1.** Four flowers of *Senegalia eocaribbeanensis*. Scale bar = 1.2 mm. **2.** Anther of *S. eocaribbeanensis* with stalked apical gland. Scale bar = 46 µm. **3.** Style of *S. eocaribbeanensis*. Scale bar = 50 µm.



Figs. 4–5. Holotype of *Campopetala dominicana* gen. et sp. nov. in Dominican amber. 4. Complete flower. Scale bar = 1.5 mm. Insert shows detail of anther. Scale bar = 0.16 mm. 5. Enlargement of perianth. Scale bar = 1.3 mm.

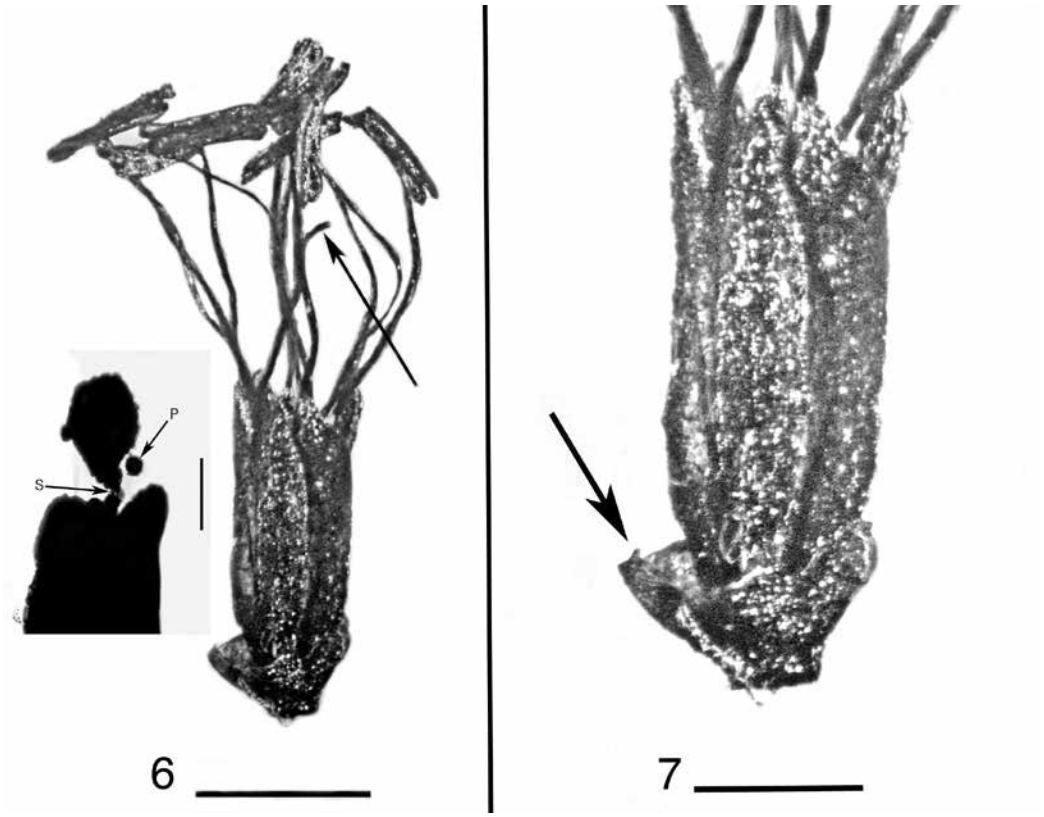
A NEW SPECIES OF *ENTADA*

Members of the genus *Entada* are woody climbers, shrubs and trees unarmed or with prickles. The flowers are small, sessile, variously colored, bisexual or polygamous and borne in axillary racemes or terminal panicles. They occur in lowland rain forests as well as in streamside forests, riverine areas, coastal thickets with sandy soils and savannas (Allen & Allen 1981). The seeds are unusually large and capable of surviving in sea water 21 months or more (Mabberley 2008).

The following new species was discovered during the examination of mimosoid flowers from the same amber deposits as the above *Senegalia* species. Diagnostic characters that place it within the genus *Entada* are small, sessile, 5-merous, valvate flowers with a synsepalous, barely toothed calyx, 5 free to slightly connate petals, 10 free, shortly-exerted stamens, anthers with glands, a slender style, and a terminal, blunt-tipped stigma.

Entada hispaniolae Poinar & K.L. Chambers, sp. nov. (**Figs. 6, 7**). Type: HISPANIOLA. Dominican Republic: Amber mine in the in the northern mountain ranges (Cordillera Septentrional) between Puerto Plata and Santiago, 19.4°N, 70.4°W, *unknown amber miner s.n.* (holotype: Accession number Sd-9-21, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

Flower small, sessile, regular, calyx small, 5-parted, synsepalous, glabrous, length 0.4 mm, width 0.9 mm, sepal tips represented by minute teeth, 0.08–0.10 mm long; corolla glabrous, much longer than calyx, with 5 free, narrow (5–6 times longer than broad), valvate, linear-lanceolate petals 1.7–1.8 mm long and 0.26–0.29 mm wide, stamens 10 (two anthers missing) with free, exerted, filaments, 2.8–3.1 mm long, anthers relatively large dorsifixed, 0.7–0.8 mm long with longitudinal dehiscence, apical anther glands spherical to oval, greatest length 0.124 mm, greatest width 0.117 mm, pollen grains round to ovate, greatest diameter 0.028–0.036 mm, style slender, 1.8 mm long, with a blunt tip.



Figs. 6–7. Holotype of *Entada hispaniolae* sp. nov. in Dominican amber. 6. Complete flower. Arrow shows tip of style. Scale bar = 1 mm. Insert shows tip of anther with stalk (S) of anther gland and pollen grain (P). Scale bar = 0.12 mm. 7. Perianth of *E. hispaniolae*. Note long, narrow petals. Arrow shows mucronate tip of calyx lobe. Scale bar = 0.5 mm.

Etymology.—Species epithet based on the geographic origin of the fossil.

The small flowers with very small sepals, narrow petals with acute apices, and relatively long anthers distinguish the fossil from extant members of the genus. The new species differs from present day Caribbean members of *Entada* by the above-listed characteristics. Regarding the size of the floral parts, the fossil most closely resembles the extant *E. polystachya* (L.) DC., which occurs not only in Hispaniola but also throughout the Antilles and tropical America (Liogier 1985, 1988). However the petals of *E. polystachya* are 2 mm long and only 2–4 times longer than broad, while the petals of *E. hispaniolae* are less than 2 mm long and 5–6 times longer than broad.

The genus, which has a world-wide tropical distribution, is considered native to the Old World tropics, with some 18 species in central and East Africa and Madagascar, 10 species in Asia and 4 species in tropical America (Brenan 1970). While some use is made of the bark and root decoctions of *Entada* species in Africa, the genus is best known for its oversized fruit pods, the largest known for any member of the family (Allen & Allen 1981).

This is the first known fossil *Entada* flower and the second New World fossil of the genus. Berry (1921) reported a seed of what he determined as *Entada boweni* Berry (1920) in Tertiary shales in Venezuela. A second previously described fossil is *Entada palaeoscandens* Awasthi & Prasad (Awasthi & Prasad 1990) based on a single leaf impression and some seeds from the Middle Miocene to Early Pleistocene Khola beds in Nepal.

The presence of deciduous apical anther glands is a diagnostic character for the genus (Rock 1920; Allen

& Allen 1981; Liogier 1985, 1988). The surface of these glands on *Entada hispaniolae* is rough and uneven, very similar to the surface of anthers that are shedding pollen. Some of the anther glands contain spherical bodies that protrude from the surface. The stalk connecting the gland to the tip of the anther connective contains a transparent slender cell in the center, where gland detachment may occur (Fig. 6, insert). When discussing anther glands in mimosoids from an evolutionary perspective, Tybirk (1997) suggested that their likely function is to secrete an odor to attract pollinators shortly after the flowers open.

ADDITIONAL MIMOSOID REMAINS

Flowers (Figs. 8–10)

In addition to the examples presented above, two other mimosoid flower types were found in Dominican amber. One has a unique, non-flaring perianth structure and 12 stamens and could be a member of the Mimoseae (Figs. 8, 9). The other is quite large (20 mm in diameter) and had numerous stamens (Fig. 10). Its systematic position has not been determined.

Leaflets (Figs. 11–18, 26, 27)

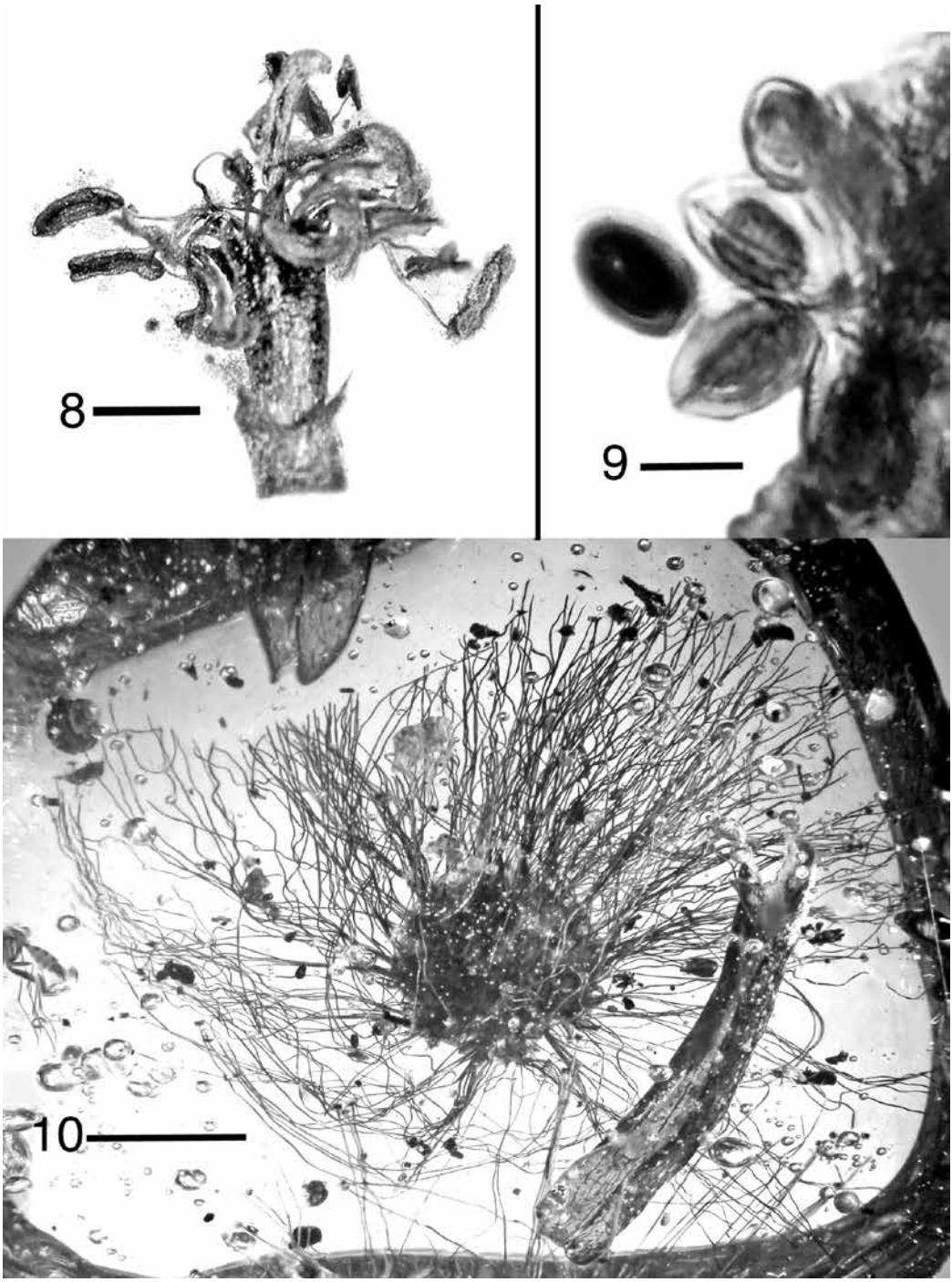
Mimosoid leaflets also occur in Dominican amber, as was mentioned by Dilcher et al. (1992). Leaves of Mimosoideae, when bipinnate, characteristically have pinnules that are straight to slightly curved, with an apex that is ordinarily acute but can be obtuse, round, truncate, emarginate, or sometimes mucronate, and a base that is usually asymmetrical and acute to obtuse. The pinnules are usually closely spaced and opposite on the axis. Each pinnule commonly has 1–2 prominent veins arising near the base of the midrib that run parallel to the margins. However, veins are difficult to recognize in amber, since the pinnules generally darken over time. A variety of mimosoid leaflet types occur in Dominican amber, some of which are depicted here. The shape of the pinnules can vary from broadly oblong with rounded tips (Fig. 11) to linear with acute tips (Fig. 14), subulate-gladiate with acute tips (Figs. 13, 17), or oblong with mucronate tips (Fig. 16). The pinnules can be glabrous (Figs. 15, 16) or densely pubescent (Fig. 18). On some pinnae, the pinnules are folded inward and lie adjacent to the rachis, sometimes touching the opposite pinnules (Figs. 14, 15, 17). This arrangement has been termed a "sleep posture" and is characteristic of leaflet behavior at night or during periods of drought (Dilcher et al. 1992).

Seed (Figs 19, 20)

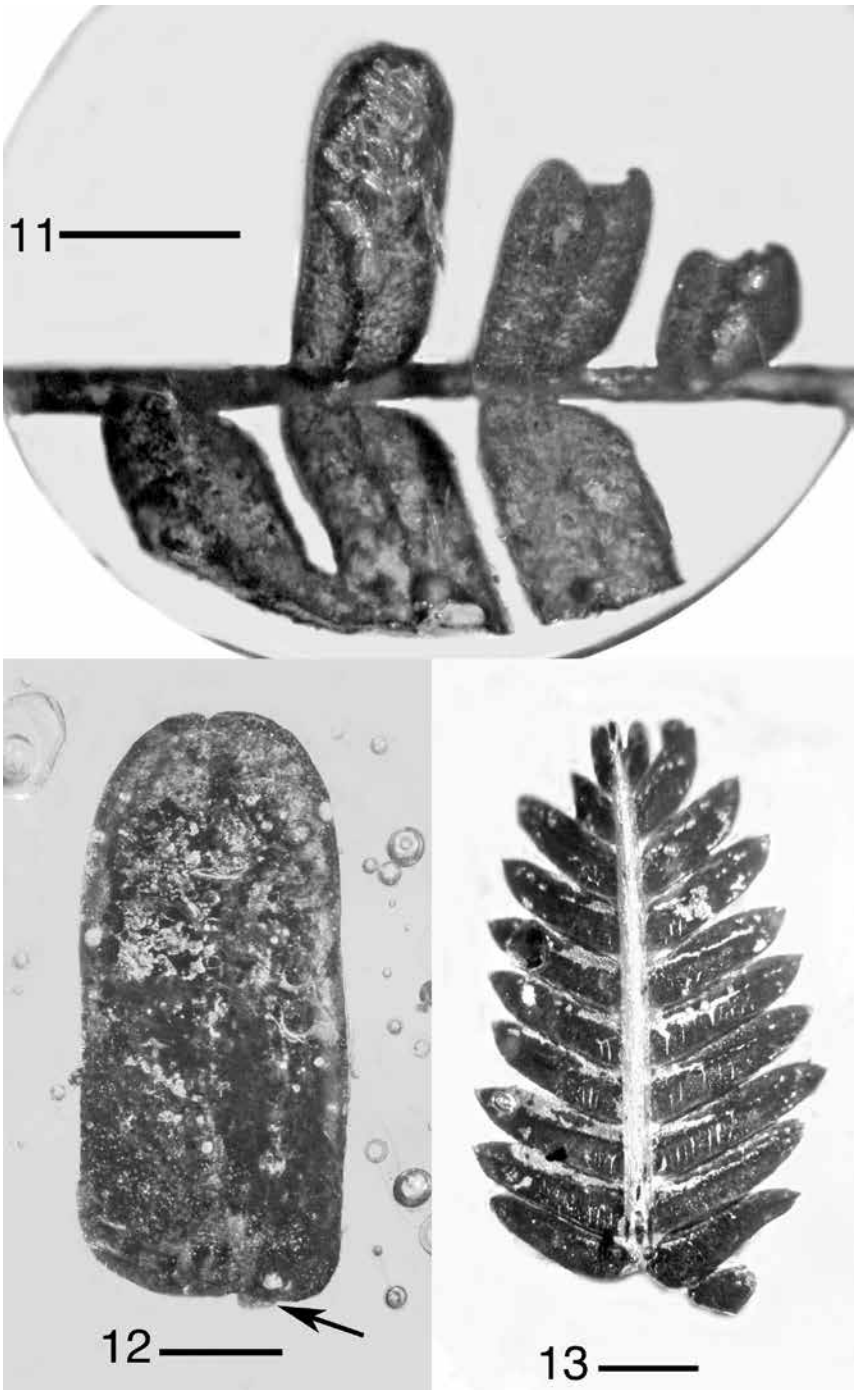
Mimosoid seeds are usually straight, compressed, and range from 5–7 mm in length. They are normally dark brown or black and disk-shaped, but can be elliptical, oblong, orbicular, or suborbicular. They are symmetrical about their longitudinal axis with an apical funicular attachment at the radicle end. Seeds of Mimosoideae differ from those of Papilionoideae, which are usually curved or asymmetrical near the radicle with a subapical funicular attachment (Rock 1927; Croat 1978; Herendeen 1992). The seed in Figs. 19 and 20 is compressed, disk-shaped, and has a funicular attachment at the radicle end. These features and its size (4 mm long) place it within the range of mimosoid seeds.

Flower pollination (Fig. 21)

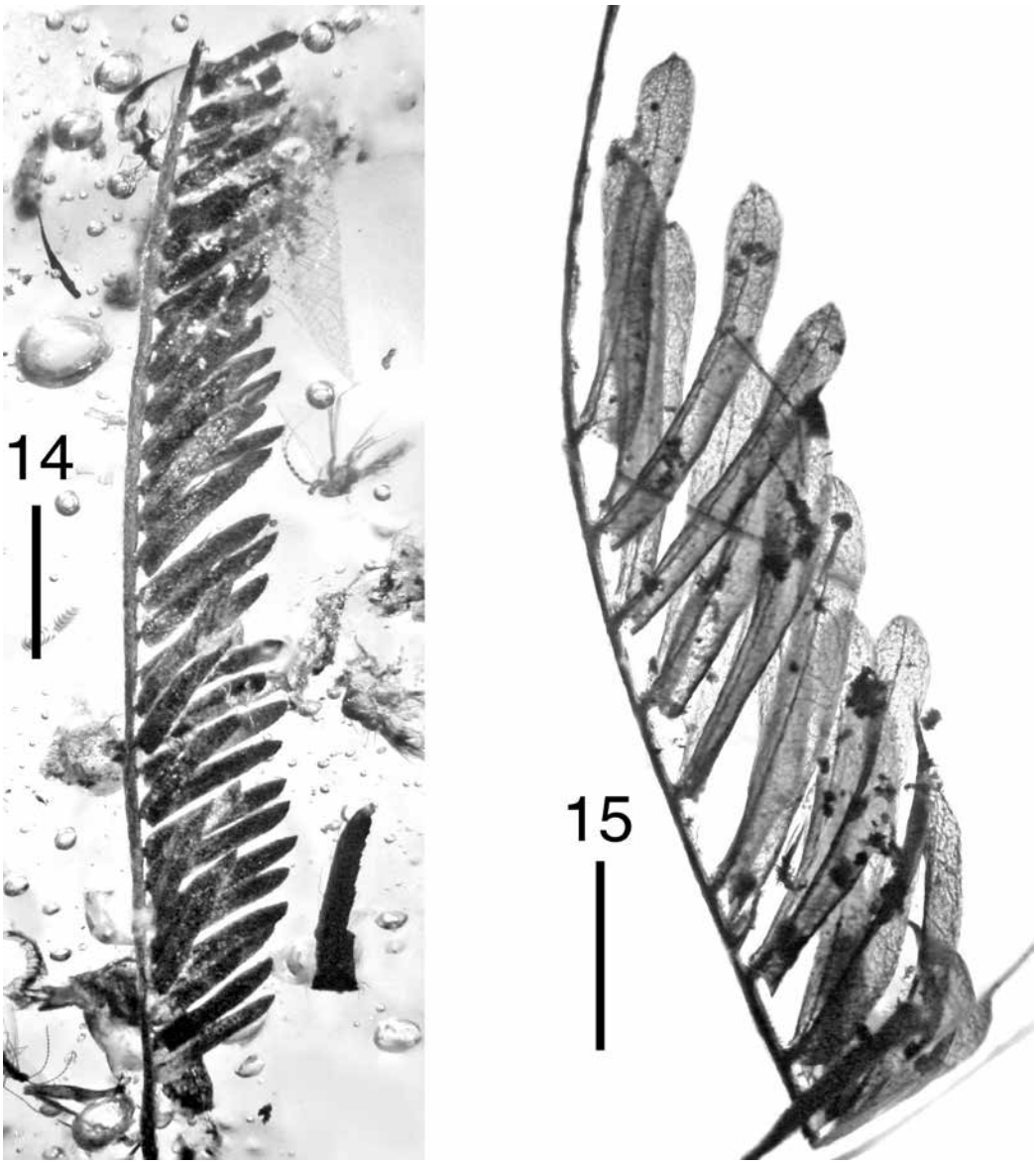
A separate piece of amber contained a flower of *Senegalia eocaribbeanensis* with a stingless bee, *Proplebia dominicana* (Hymenoptera: Apidae) entangled within the filaments (Fig. 21). Evidently these hymenopterans pollinated ancient mimosoids in the Dominican amber forest. Bee pollination is common in extant legumes, and bees are considered important in the radiation of the Fabaceae (Herendeen et al. 1992). Stingless bees such as *Proplebia* are examples of unspecialized pollinators that crawl over the surface of the entire inflorescence, which represents the plant's pollination unit. While the pollen is easily accessible, the anther glands may offer additional rewards for bees. Stingless bees are extinct in the Greater Antilles today, and if they were important pollinators of mimosoids, their disappearance may explain the absence of some mimosoid lineages from the West Indies. Mimosoids in Hispaniola today have native solitary bees, as well as introduced honeybees and other flower-visiting insects, for pollination. Just what role the anther glands play in attracting pollinators is not known; however, they may have co-evolved with stingless bees. It is interesting that none of the Australian



Figs. 8–10. Mimosoid flowers in Dominican amber. **8.** Small flower with the petals fused for most of their length and 12 stamens with short filaments and long anthers. Scale bar = 2.0 mm. **9.** Pollen grains from flower in Fig. 8. Scale bar = 20 µm. **10.** Large flower with numerous stamens. Scale bar = 3.7 mm.



Figs. 11–13. **Mimosoid pinnules in Dominican amber. 11.** Broadly oblong pinnules with central venation. Scale bar = 2.6 mm. **12.** Broad pinnule with faintly emarginte tip and central venation. Arrow = minute stalk of pinnule. Scale bar = 1.2 mm. **13.** Oblong, gladiate pinnules with acute tips and submarginal venation. Scale bar = 2.3 mm.

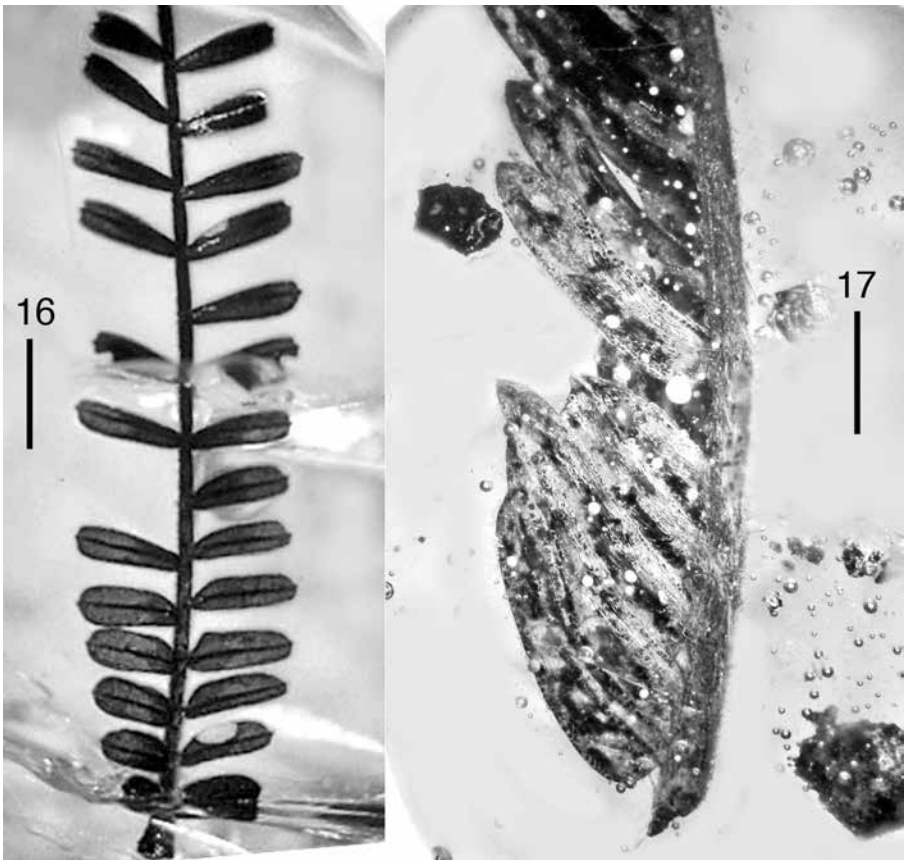


Figs. 14–15. Mimosoid leaflets in Dominican amber. **14.** Subulate pinnules with acute tips and subcentral venation. Scale bar = 7 mm. **15.** Gladiate pinnules with obtuse tips. Scale bar = 2 mm.

Acacia s. l. species are known to have anther glands and none of the few native social stingless bees were recorded visiting the inflorescences (Bernhardt 1989).

Floral herbivory (Figs. 22–24)

There is both direct and indirect evidence of herbivory on mimosoid flowers and leaves in Dominican amber. Direct evidence is represented by an immature (probably the first or second stage) stink bug (Hemiptera: Pentatomidae) clasping a floral part of *S. eocaribbeanensis* (Fig. 22). Indirect evidence is shown by a pinna in which



Figs. 16–17. Mimosoid leaflets in Dominican amber. 16. Oblong pinnules with mucronate tips. Note unequal spacing of the leaflets with not all directly opposite on the rachis. Scale bar = 3.4 mm. 17. Oblong, pubescent pinnules with acute tips and submarginal venation. Scale bar = 1.8 mm.

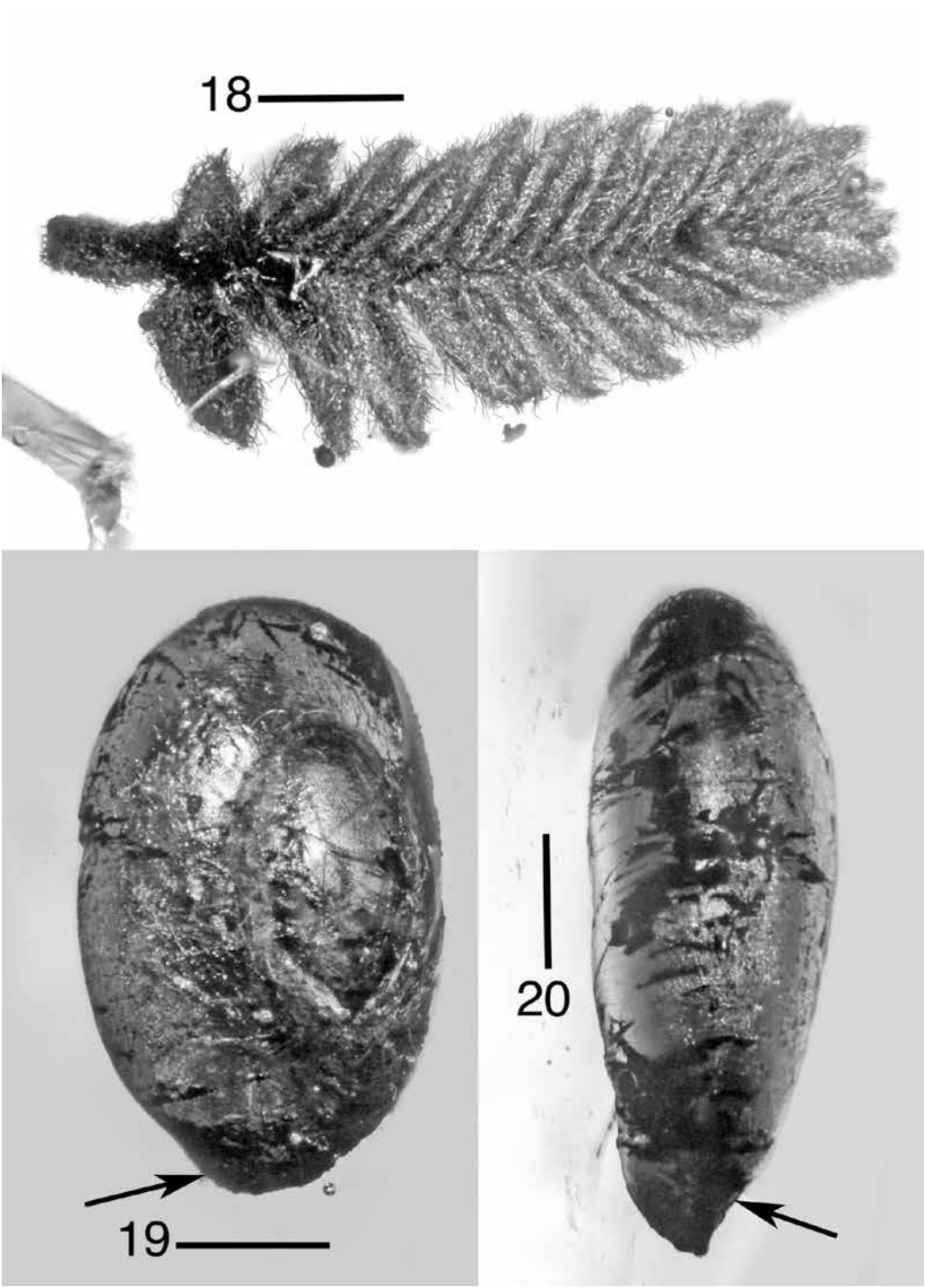
the epidermis and underlying tissues are removed (Fig, 23), and one in which a section of the margin has been eaten (Fig. 24).

Fungi attacking pinnules (Fig. 25)

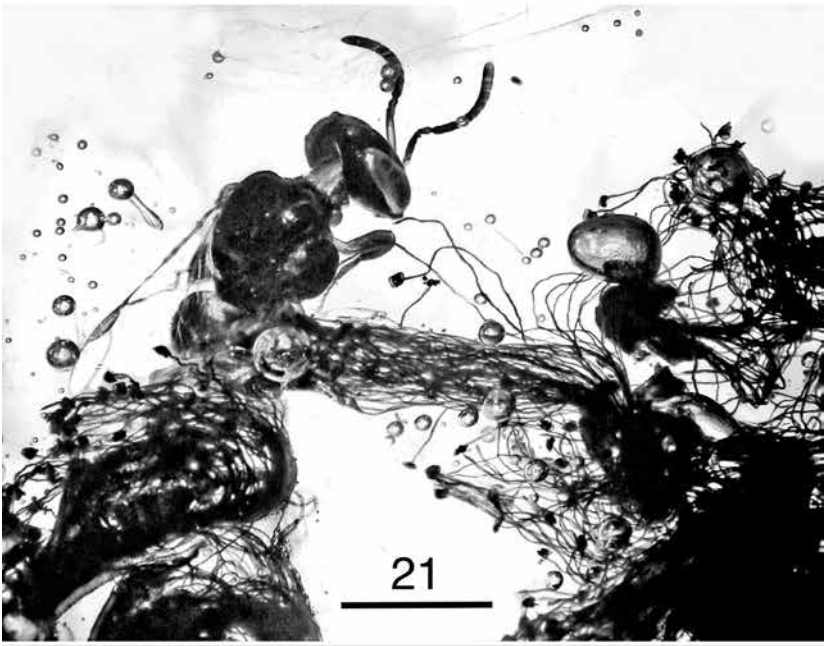
Several mimosoid pinnules in Dominican amber had hyphomycetous fungi growing on their surfaces (Fig. 25).

Association with ants (Figs. 26–28)

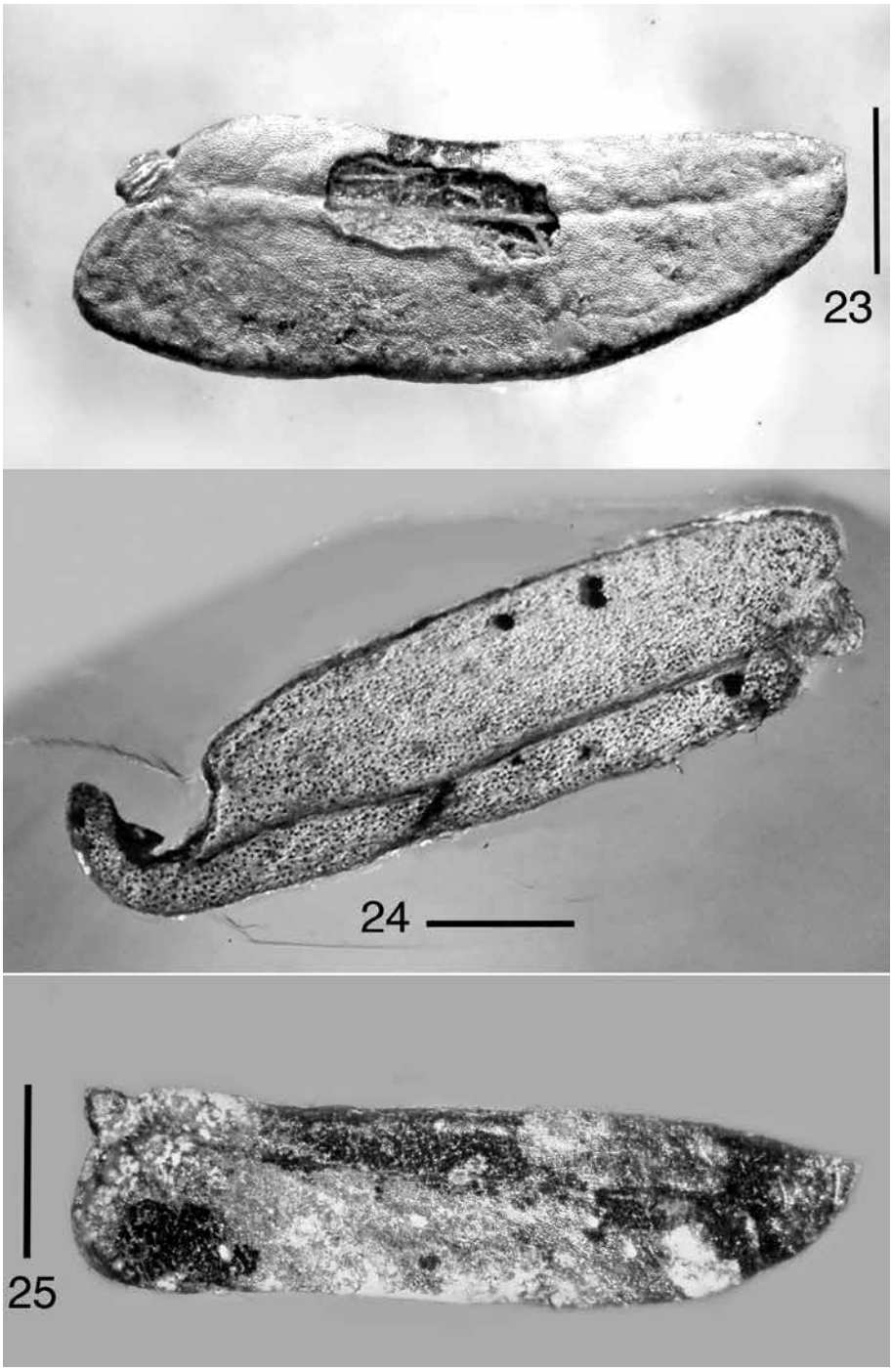
Representatives of different ant genera visit the foliage of extant mimosoids (Janzen 1983). Some may come to obtain nectar from petiole glands while others may be searching for prey. Carpenter ants of the genus *Camponotus* (Hymenoptera: Formicidae) (Fig. 26) and honey ants of the genus *Azteca* (Hymenoptera: Formicidae) (Fig. 27) are common arboreal ants, so it is not surprising that they are preserved in the amber. One of the most interesting cases of ant symbiosis with mimosoids is the genus *Pseudomyrmex* (Hymenoptera: Formicidae), especially those species that live in the thorns of certain species of *Acacia s. l.* and defend the plant against various herbivores (Jansen 1983; Seigler & Ebinger 1995). While there is no evidence yet of ant-acacias in Dominican amber, several species of *Pseudomyrmex*, including *P. nexilis* Ward (1992) (Fig. 28) establish the presence of this genus in the Dominican amber forest.



Figs. 18–20. Mimosoid leaflet and seed in Dominican amber. **18.** Pilose pinnules. Scale bar = 1.0 mm **19.** Face view of suborbicular-shaped seed. Arrow shows funiculus. Note circular pleurogram on middle right side. Scale bar = 1.2 mm. **20.** Edge view of seed shown in Fig. 19. Arrow shows funiculus. Scale bar = 1.0 mm.



Figs. 21–22. Insects associated with mimosoid flowers in Dominican amber. **21.** A worker stingless bee (*Proplebeia dominicana*) entangled in the stamens of *S. eocaribbeanensis.* Scale bar = 2.2 mm. **22.** An immature stink bug (Hemiptera: Pentatomidae) on a flower of *S. eocaribbeanensis*. Scale bar = 0.5 mm.



Figs. 23–25. **Insect and fungal damage to mimosoid leaflets in Dominican amber. 23.** Evidence of insect damage to the epidermal surface of leaflet. Scale bar = 0.8 mm. **24.** Evidence of chewing insect damage to a leaflet. Scale bar = 0.5 mm. **25.** A hyphomycetous fungus growing on the surface of a leaflet. Scale bar = 1.0 mm.

Figs. 26–28. Ants (Hymenoptera: Formicidae) associated with mimosoid leaflets in Dominican amber. **26.** *Camponotus* sp. worker. Scale bar = 3 mm. **27.** *Azteca* sp. worker. Scale bar = 1.2 mm. **28.** Queen of *Pseudomyrmex nexilis*. Scale bar = 1.0 mm.

PREVIOUS FOSSIL RECORDS OF MIMOSOIDEAE FROM THE NEW WORLD

The fossil history of the Mimosoideae dates from the Lower Eocene, based on megafossils of fruits, leaflets, and flowers from Europe, North America and Africa, with the greatest known fossil diversity occurring in tropical America and Africa. Pollen microfossils have been used to establish records of specific genera, since many have their pollen in distinctive polyads (Herendeen et al. 1992).

Mesoamerican records of mimosoid fossils include leaflets in Oligocene Mexican amber and pollen from the Middle Pliocene of Mexico. Fossil remains of mimosoids from the Caribbean are limited. Aside from those reported in the present work, these include pollen from the Oligocene of Puerto Rico and the Lower Miocene and Middle Pliocene of Panama (Graham 1992).

Fossil mimosoid flowers are rare, with only four species previously described. These are *Senegalia eocaribbeanensis* (see above), *Protominosoidea buchananensis* Crepet and Taylor (1986) from the Paleocene-Eocene boundary in Tennessee (the earliest fossil of subfamily Mimosoideae), and portions of an inflorescence described as *Eomimosoidea plumosa* Crepet and Dilcher (1977) from the Middle Eocene Claiborne Formation in Tennessee. This taxon was also reported from the Oligocene of Texas (Daghlian et al. 1980).

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