SALPINGANTHIUM HISPANIOLANUM GEN. ET SP. NOV. (FABACEAE: DETARIEAE), A MID-TERTIARY FLOWER IN DOMINICAN AMBER

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ABSTRACT

Salpinganthium hispaniolanum gen. et sp. nov. is described as a new fossil legume from mid-Tertiary forests of Hispaniola. Arborescent legumes of tribe Detarieae previously described from these forests include *Hymenaea protera* and *Prioria dominicana*. Flowers of the new genus and species have a bilaterally symmetrical corolla of five petals, 10 free stamens, an elongate, cylindrical hypanthium, and one or two persistent sepals, the others perhaps being deciduous. The petals are of three markedly different shapes. The pistil is exserted from the hypanthium and is densely hirsute. The bracteoles, sepals, and petals are gland-dotted, as is appropriate for members of the resin-producing Detarieae of subfamily Detarioideae.

RESUMEN

Salpinganthium hispaniolanum gen. et sp. nov. se describe como una nueva leguminosa fósil de los bosques del Terciario medio de Hispaniola. Las leguminosas arborescentes de la tribu Detarieae descritas anteriormente en estos bosques incluyen *Hymenaea protera* y *Prioria dominicana*. Las flores del nuevo género y especie tienen una corola simétrica bilateralmente de cinco pétalos, 10 estambres libres, un hipanto alargado y cilíndrico y uno o dos sépalos persistentes, los otros quizás caducifolios. Los pétalos tienen tres formas marcadamente diferentes. El pistilo se extrae del hipanto y es densamente hirsuto. Las brácteas, sépalos y pétalos están salpicados de glándulas, como es propio de de los miembros de las Detarieae productoras de resina de la subfamilia Detarioideae.

INTRODUCTION

Amber mines in the mountains of the Dominican Republic on the island of Hispaniola have yielded a rich trove of insects, flowers, and other long-extinct fossil organisms representative of a mid-Tertiary Caribbean tropical forest (Poinar & Poinar 1999). Among the amber-embedded fossil flowers, pictured by these authors, that have since been formally described are *Trichilia glaesaria* (Meliaceae; Chambers et al. 2011), *Swietenia dominicensis* (Meliaceae; Chambers & Poinar 2012), *Treptostemon domingensis* (Lauraceae; Chambers et al. 2012), *Virola dominicana* (Myristicaceae; Poinar & Steeves 2013), *Prioria dominicana* (Fabaceae; Poinar & Chambers 2015), *Lobocyclas anomala* (Celastraceae; Chambers & Poinar 2016), and *Strychnos electri* (Loganiaceae; Poinar & Struwe 2016). *Hymenaea protera* (Fabaceae) was described earlier (Poinar 1991). The present fossils were mentioned by Poinar and Poinar (1999) as possibly representing the genus *Peltogyne*, but upon further study they are here being recognized as a distinct new genus and species.

At least five flowers of this taxon have been recovered over the past several years, and four of these are well enough positioned in their blocks of amber to be useful in illustrating the new taxon. The corolla of the flowers is bilaterally symmetrical, the largest of the five petals probably being held in an erect, adaxial position (referred to as "median" by Bruneau et al. 2014). In addition, there are two oblong-elliptic, laterally spreading petals and a pair of shorter, spreading or downward-pointing petals (Fig. 1). The hypanthium is elongate-cylindrical and bears at the apex 10 free stamens whose anthers are basifixed on long filaments. The hirsute ovary is almost completely exserted from the hypanthium, with a slender style and slightly enlarged stigma. Only one or two well-developed calyx lobes remain on the flowers examined, although more may have been present at an earlier stage. The paired bracteoles below each flower, as well as the sepals and petals, are conspicuously gland-dotted.

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MATERIALS AND METHODS

Amber from mines in the Cordillera Septentrional of the Dominican Republic is principally deposited in turbiditic sandstones of the Upper Eocene to Lower Miocene Mamey Group (Draper et al. 1994). It has been suggested (Dilcher et al. 1992) that "…the amber clasts, from all physical characteristics, were already matured amber at the time of re-deposition into marine basins. Therefore, the age of the amber is greater than Miocene and quite likely is as early as late Eocene." Dating by marine coccoliths (Cépek in Schlee 1990) gave a date of 45–30 Ma, while a later study based on foraminifera (Iturralde-Vinent & MacPhee 1996) assigned a more recent date of 20–15 Ma. The reports of Maastrichtian–Paleocene amber in Jamaica and of Early Oligocene amber in Puerto Rico (Iturralde-Vinent 2001) indicate that amber-producing forests existed in the Caribbean region from the Late Cretaceous to at least the mid-Tertiary.

The holotype flower is contained in a block of amber measuring 12 mm × 10 mm × 8 mm. Examination and photographs were made with a Nikon stereoscopic microscope SMA-10-R at 80× and a Nikon Optiphot microscope at 800×. Helicon Focus Pro X64 was used to stack photos for better clarity and depth of field. Paratype flowers were examined in a similar way.

DESCRIPTION

Salpinganthium Poinar & K.L. Chambers, **gen. nov.** Type: *Salpinganthium hispaniolanum* Poinar & K.L. Chambers, sp. nov.

Diagnosis.—Flowers perfect, bilaterally symmetrical, basal bracteoles 2, opposite, elliptic-lanceolate, subtending the floral stipe, stipe glabrous, hypanthium tubular, glabrous, with distinct longitudinal veins, calyx and corolla gland-dotted (Figs. 1–5), remaining calyx lobes 1 or 2, lanceolate, sessile, petals unequal, the adaxial one erect, broadly ovate, acute, sessile, with 6+ longitudinal veins from the base, lateral petals 2, spreading, oblong-elliptic, acute, slenderly attenuate toward the base, with a single midvein, lower petals 2, spreading or abaxially reflexed, lanceolate, acute, stamens 10 (2 sometimes staminodial, Fig. 4), free, filaments linear, equal, inserted on rim of hypanthium, glabrous throughout, anthers ellipsoid, basifixed, 4-loculed, dehiscing by longitudinal slits, pistil 1, stipe glabrous, ovary exserted from mouth of hypanthium, elongate-fusiform, densely hirsute, probably multiovulate, style curved, stigma slightly enlarged, pollen unknown.

Etymology.—From Greek "salpinx, -ingos," tube, trumpet, and "anthos," flower, with reference to the tubular hypanthium.

Salpinganthium hispaniolanum Poinar & K.L. Chambers, **sp. nov.** (**Figs. 1–5**). Type: HISPANIOLA. Dominican Republic: Amber mine in the northern mountain range (Cordillera Septentrional), 2013, *unknown amber miner s.n.* (holotype: catalogue number Sd-9-26, Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.). Paratypes: catalogue number Sd-9-26A, catalogue number Sd-9-26B, catalogue number Sd-9-26C, Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.

Description.—Basal bracteoles 2.0–3.4 mm long, 0.8–1.5 mm wide (Figs. 1, 2), stipe 1.7 mm long (Fig. 2), hypanthium 1.8–2.9 mm long, 0.6 mm wide (Figs. 2, 3), remaining calyx lobes 2.2–3.0 mm long, 1.0–2.2 mm wide (Figs. 1–3), adaxial petal 3.0–5.0 mm long, 2.0–2.5 mm wide, (Figs. 3–5), lateral petal pair 4.0–5.5 mm long, 1.3–1.6 mm wide (Figs. 1–3), lower petal pair 2.0–3.0 mm long, 0.8–1.0 mm wide (Figs. 1, 2), stamen filaments 3.8–5.0 mm long, anthers 0.8–1.0 mm long, connective prominently ridged (Figs. 1, 2, 5), ovary 1.4–2.4 mm long, 0.5–0.6 mm wide (Figs. 1, 3, 5), style 0.4 mm long.

Etymology.—From source of the amber on the island of Hispaniola.

DISCUSSION

The legume subfamily Detarioideae, comprising 81 genera and ca. 760 species, is a segregate of what was previously recognized as the traditional subfamily Caesalpinioideae (The Legume Phylogeny Working Group 2017). In revising the tribal classification of this subfamily, de la Estrella et al. (2018) recognized a group of 21 arborescent, resin-producing genera as tribe Detarieae, separating it from the related tribe Amherstieae with

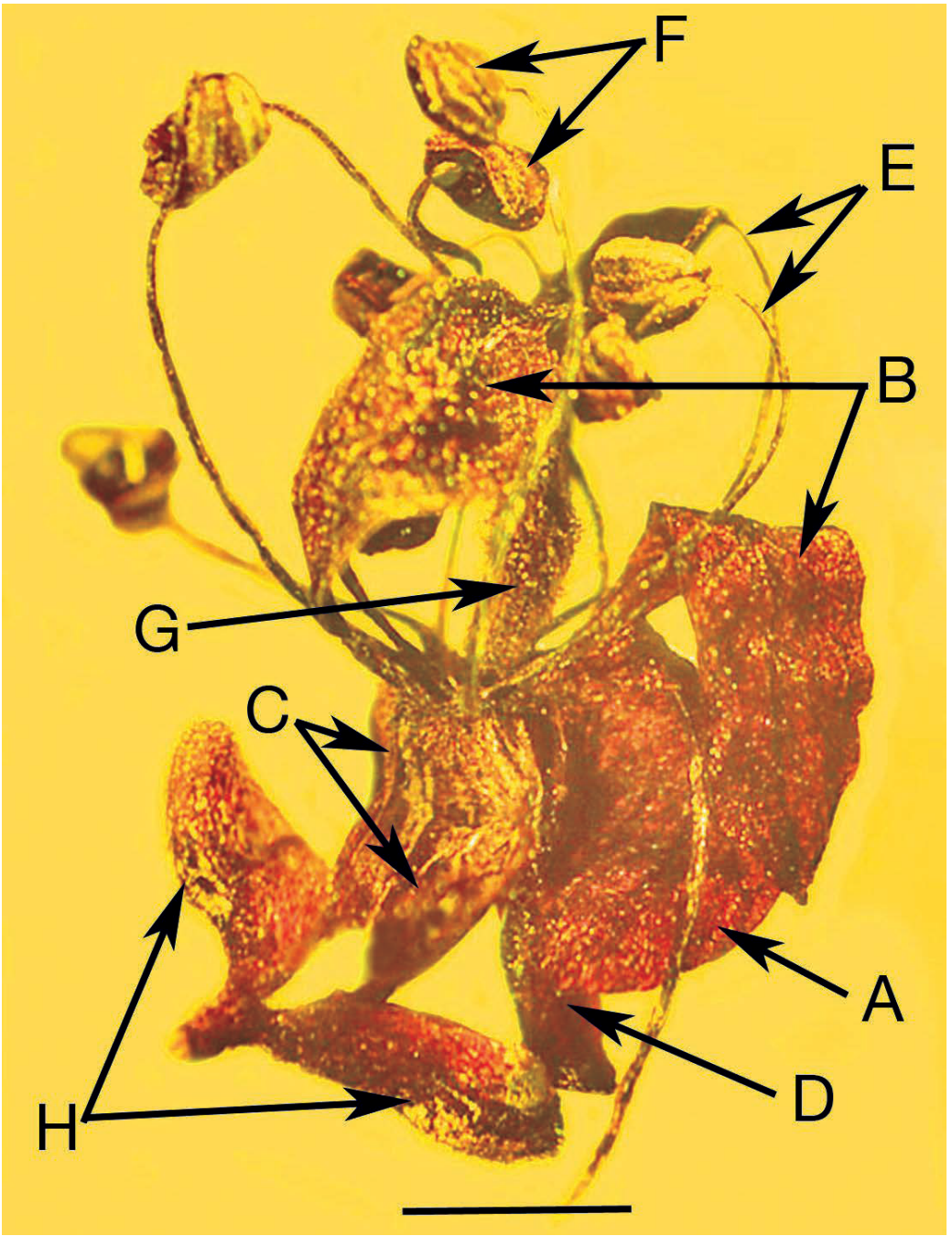

Fig. 1. *Salpinganthium hispaniolanum*. Holotype, lateral view. **A.** Adaxial petal. **B.** Lateral petals. **C.** Lower petals. **D.** Tip of sepal. **E.** Stamen filaments. **F.** Anthers. **G.** Ovary. **H.** Subtending bracts. Scale bar = 1.5 mm.

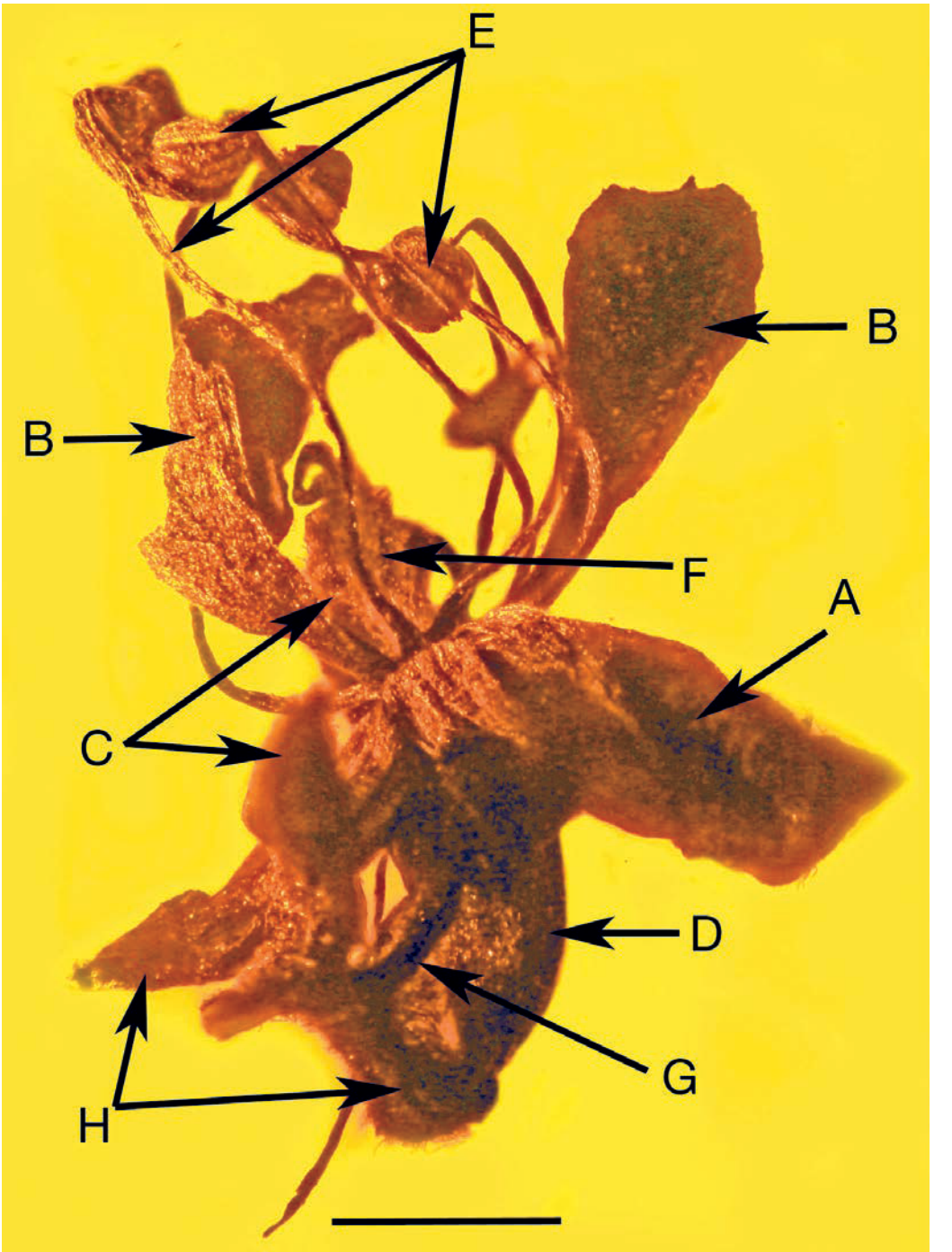

Fig. 2. *Salpinganthium hispaniolanum*. Paratype 1, lateral view. **A.** Adaxial petal. **B.** Lateral petals. **C.** Lower petals. **D.** Sepal. **E.** Stamens. **F.** Ovary. **G.** Stipe. **H.** Subtending bracts. Scale bar = 1.8 mm.

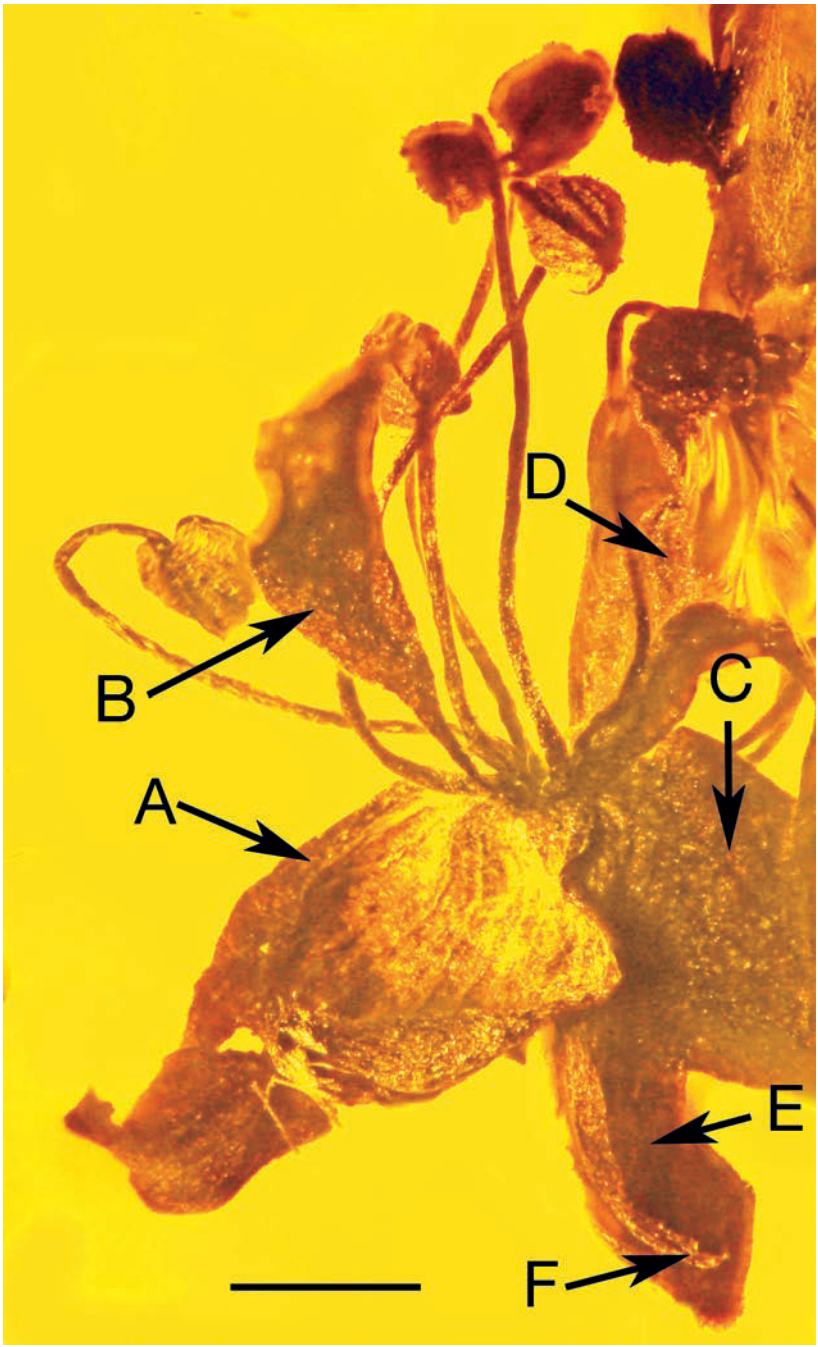

Fig. 3. *Salpinganthium hispaniolanum*. Paratype 2, lateral view. **A.** Adaxial petal. **B.** Lateral petal. **C.** Sepal. **D.** Ovary. **E.** Hypanthium. **F.** Stipe remnant. Scale bar = 1.3 mm.

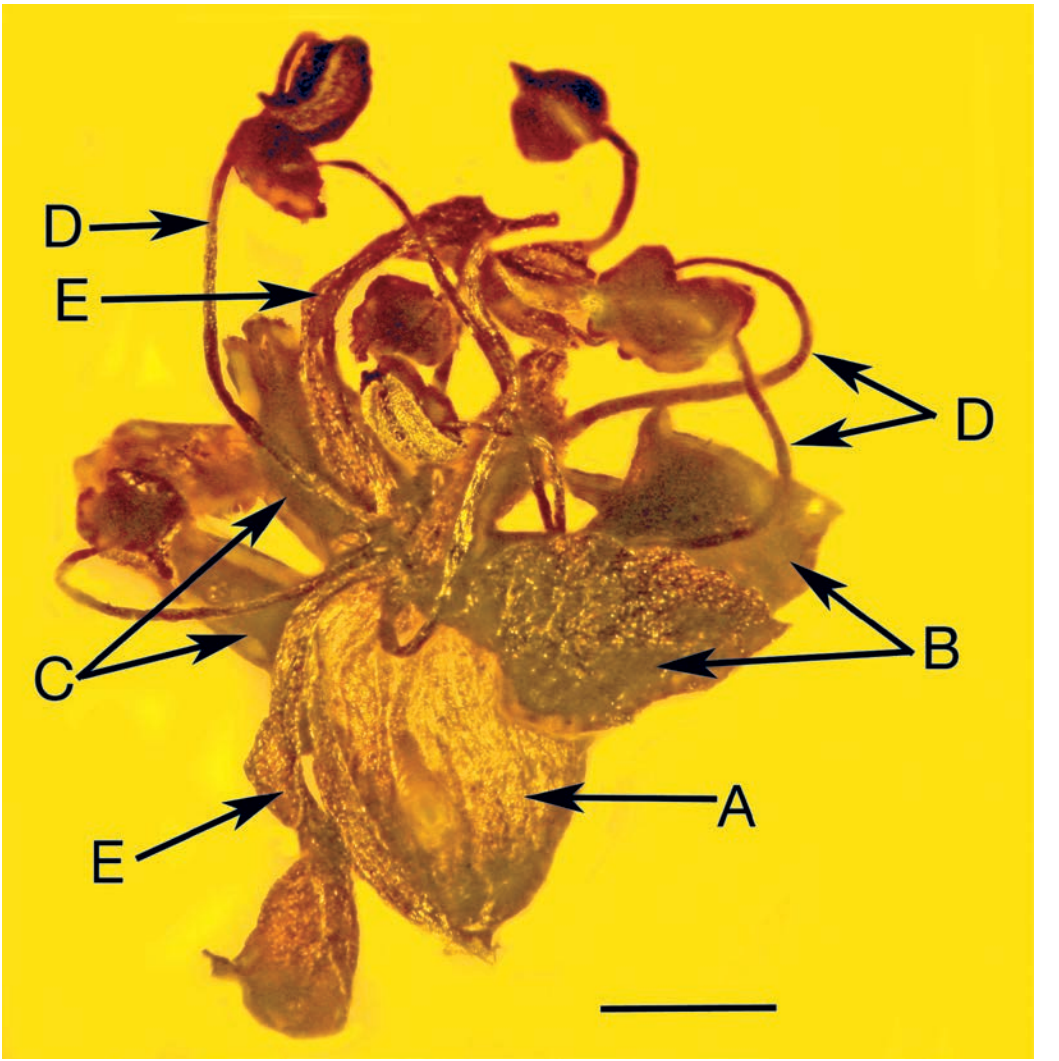

Fig. 4. ***Salpinganthium hispaniolanum*****. Paratype 3, face view. A. Adaxial petal. B. Lateral petals. C. Lower petals. D. Stamens. E. Staminodes. Scale bar = 1.2 mm.**

which it had been united by Mackinder (2005) and Bruneau et al. (2008, 2014). They also established two new tribes, Shotieae and Barnebydendreae for three genera previously assigned to Detarieae, noting among other things their lack of resin production. The phylogenetic analysis by de la Estrella et al. (op. cit.), based on three regions of the chloroplast genome and one nuclear gene, identified Detarieae as a monophyletic group, essentially as had been reported by Fougère-Danezan et al. (2007, 2010) and Bruneau et al. (2008) using chloroplast genes alone. Genera of Detarieae are widespread in the Old World tropics, extending from Africa to Madagascar, India, and Malesia. *Eperua* and *Peltogyne* are limited to the New World, while *Copaifera, Guibourtia, Hymenaea,* and *Prioria sens. lat.* (Breteler 1999) are amphi-Atlantic in distribution (Mabberley 2008). The fossils described here as *Salpinganthium* possess gland-dotted bracteoles, sepals, and petals (Figs. 1, 2), which are strong evidence for their placement among the resinous Detarieae.

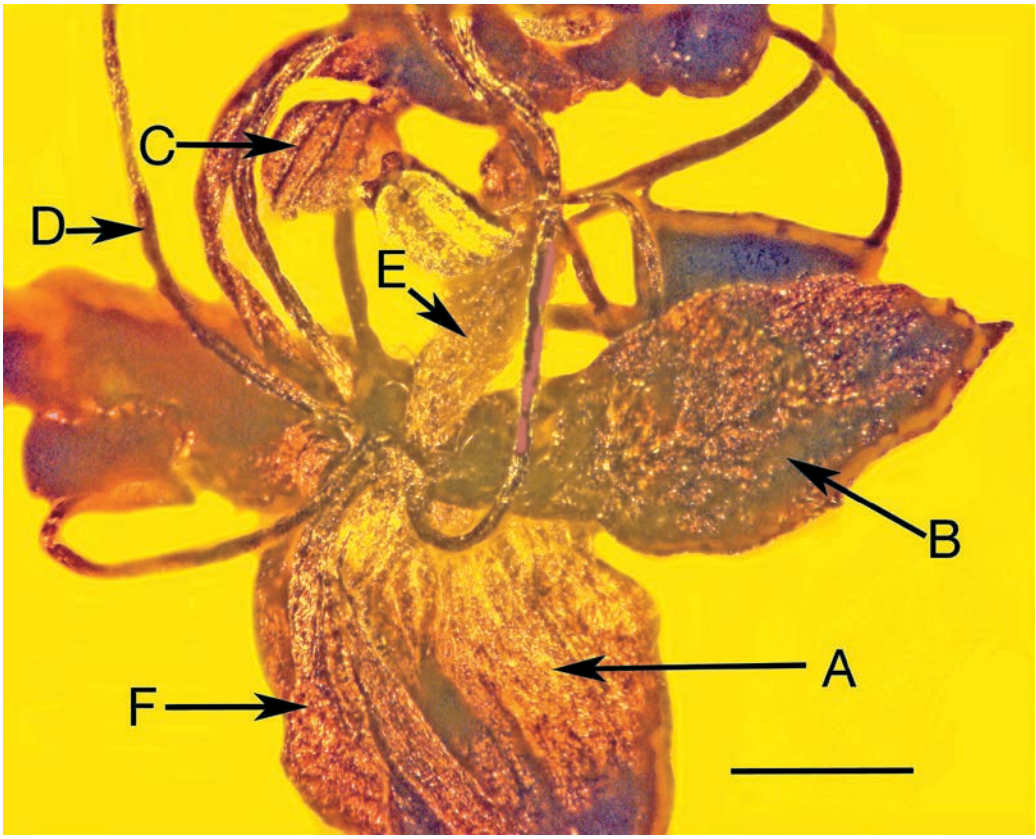

Fig. 5. *Salpinganthium hispaniolanum*. Paratype 3, face view. **A.** Adaxial petal. **B.** Lateral petal. **C.** Anther. Note prominent connective. **D.** Filament. **E.** Ovary. **F.** Staminode. Scale bar = 1.0 mm.

It has been noted that a "remarkable range and complex pattern of floral modifications" are found in detarioid legumes (Mackinder 2005). In studying our suite of fossils, we reviewed the floral diversity in Detarieae *sens. str.*, looking for a extant genus having the combination of bilaterally symmetrical flowers, an enlarged adaxial petal, and paired lateral and abaxial petals differing in size and shape from the adaxial one. To match the fossils, the stamens should be free and equal and the hypanthium well developed and elongate. Among New World genera, *Copaifera* and *Prioria* lack petals entirely and have a short hypanthium, while in *Eperua*, the corolla consists of a single large, revolute petal, and its stamen filaments are basally connate (Taubert 1894). In the New World genus *Peltogyne*, the corolla is regular (Kochanovski et al. 2020) or is sometimes irregular due to the adaxial (internal) one being narrower than the other four (da Silva 1976). In *Hymenaea,* only the African species *H. verrucosa* and the mid-Tertiary fossils *H. protera* (Poinar 1991) and *H. mexicana* (Poinar & Brown 2002) have irregular corollas, three of the five petals being enlarged, possessing a narrow claw and expanded limb. In the other 20 extant species, the corolla is regular, and in all species the hypanthium is shallowly cup-shaped, not elongate (Barbosa Pinto 2017). The amphi-Atlantic *Guibourtia* lacks petals and a hypanthium (Barbosa Pinto et al. 2017).

Available descriptions of the 15 strictly Old World genera of Detarieae (e.g., Taubert 1894; Watson & Dallwitz 1983) and floral images available on the web do not include any examples of flowers with the combined corolla, androecium, and hypanthium characteristics of *Salpinganthium*. Nine genera, with examples

such as *Detarium*, *Gilletiodendron*, *Hardwickia*, *Neoapaloxylon*, and *Sindoropsis*, are excluded for having a short or almost nonexistent hypanthium. An androecium with connate filaments or fewer than 10 fertile stamens characterizes *Augourdia*, *Baikiaea*, *Sindora*, and *Stemonocoleus*. Genera lacking a corolla or with only one petal include *Colophospermum*, *Daniella*, *Detarium*, *Eurypetalum*, *Hylodendron*, and *Sindora*. The irregular corolla of *Tessmania*, unlike that of *Salpinganthium*, comprises four large, unguiculate petals and one smaller, elliptical petal.

Phylogenetic dating of the stem node of the Detarieae *sens. str.* clade very much depends on fossil evidence from Dominican amber, the age of which "is problematic because there are differing opinions as to whether the amber has been reworked from the original depositional sediments and how much older it might be than the Miocene age deposits in which the amber is found" (Bruneau et al. 2008). These authors provide a divergence time estimate of 46.1 Ma in their consensus Baysian tree (op. cit., table 3; fig 2, node 4, which excludes the *Prioria* clade). It is unfortunate that fossiliferous Dominican amber does not have a better defined age, given that it includes the detarioid genera *Hymenaea* and *Prioria*, as well as various fossils from the Mimosoid clade (Dilcher et al. 1992; Poinar & Chambers 2016) as useful markers for calibrating the ages of these groups of Fabaceae.

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