

***Hymenaea protera* sp.n. (Leguminosae, Caesalpinoideae) from Dominican amber has African affinities**

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Abstract. *Hymenaea protera* is described from amber originating from La Toca mine in the Dominican Republic. The fossil species is characterized by the presence of reduced petals as well as distinctly clawed showy petals with cordate to reniform bases and a glabrous, verrucose ovary with long hirsute hairs at its base and along one margin. The fossil species most closely resembles the extant *H. verrucosa* Gaertner which occurs in East Africa and adjacent islands. These findings are interpreted as supporting a hypothesis that the genus *Hymenaea* arose in the late Cretaceous on the combined South American-African continents and that Cretaceous and early Tertiary landmass movements were significant in determining the present amphi-Atlantic distribution of the genus. It is proposed that at least the majority, if not all, of the amber recovered from La Toca mine and other mines in the vicinity with similar-aged deposits originated from *H. protera*.

Key words. *Hymenaea*; Leguminosae; Caesalpinoideae; fossil; amber; Dominican Republic.

Investigations of angiosperms in amber from the Dominican Republic have been limited by the scarcity of plant material and by the difficulty of assigning floral and vegetative structures in separate pieces of amber to the same plant species. This problem is confounded by the fact that there are two major areas in the country that contain amber mines and both of these areas contain multiple mines that vary in age¹. Most of the amber is mixed together by those involved in the distribution and sale of the material and it is often impossible to determine from which mine a piece has originated. For these reasons, a concentrated effort was made by the author to obtain plant fossils from a single amber mine in the Dominican Republic. This mine, La Toca, is very fossiliferous and contains some of the oldest amber recorded from the Dominican Republic¹. By obtaining a series of *Hymenaea* floral and vegetative fossils from La Toca mine, it could be assumed that all of the fossils were formed roughly during the same period. Many of the pieces contained multiple *Hymenaea* fossils (bracts, calyxes and pistil or petals and stamens) providing strong evidence of different floral structures originating from the same plant species (probably the same plant in many instances).

The present paper describes the first fossil species of *Hymenaea* and provides morphological evidence that its closest extant relative occurs in East Africa.

Materials and methods

Amber containing vegetative and floral portions of *Hymenaea* were personally collected by the author and his assistants from La Toca mine, located between Santiago and Puerto Plata in the Cordillera Septentrional of the Dominican Republic. In addition, specimens containing *Hymenaea* floral and vegetative parts have been sent to the author during the past seven years from reliable sources in the Dominican Republic. La Toca mine is in the altimira facies of El Mamey Formation (upper

Eocene) which is shale-sandstone interspersed with a conglomerate of well-rounded pebbles². Differences in the magnitudes of absorption peaks in nuclear magnetic resonance spectra of the exo-methylene group of amber¹ from different mines in the Dominican Republic were used to calibrate the ages of the various mines, with the age (20 million to 23 million years; based on foraminifera counts in the surrounding bedrock) of the Palo Alto mine used as a standard³. The ages of various specimens of Dominican amber ranged from 15 to 40 million years; that from La Toca mine was the oldest, some 35 million to 40 million years old (lower Oligocene to upper Eocene).

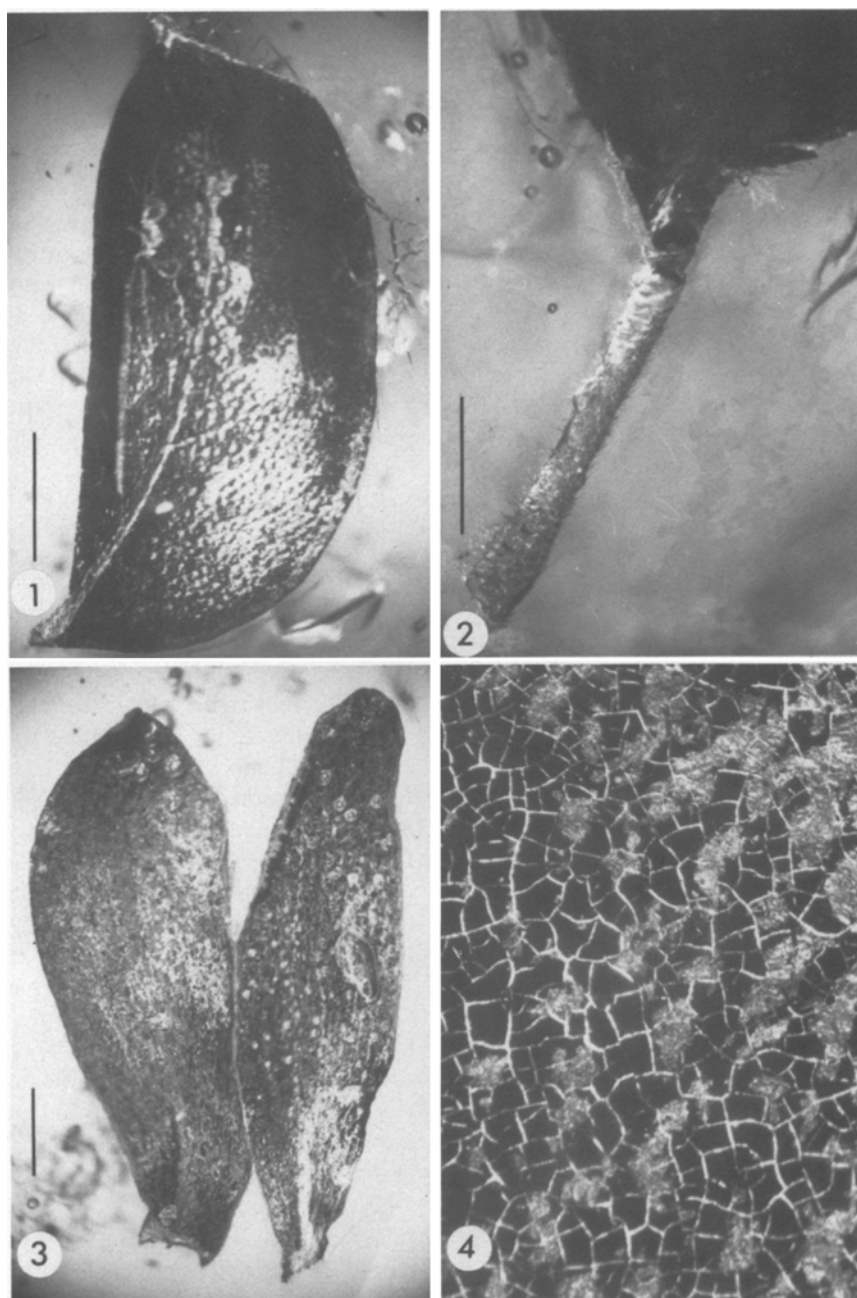
For the present investigation, 80 pieces of amber from La Toca were examined. Of these, only 56 were chosen for figures and measurements since they contained complete, easily visible and measurable specimens. All of the above pieces of amber are numbered and are maintained in the Poinar collection of Dominican amber residing at the University of California at Berkeley.

Drawings were made with the aid of an image drawing tube mounted on a Nikon SMZ-10 stereoscopic microscope. Photographs were made with a Nikon Microflex AFX attached to a Nikon SMZ-10 stereoscopic microscope. Measurements were taken directly from plant material in the amber when specimens were near the surface; otherwise they were calculated from drawings made with the image drawing tube.

Results

Taken in combination, the floral and vegetative structures of the *Hymenaea* found in La Toca amber pieces showed variation well within the range of a single species. The characters did not match those of any existing species in the genus and the fossil species is described as new.

Leaf structures. The leaves were stipulate and bifoliate. Two points of insertion at the apex of the petiole contained the two leaflets.



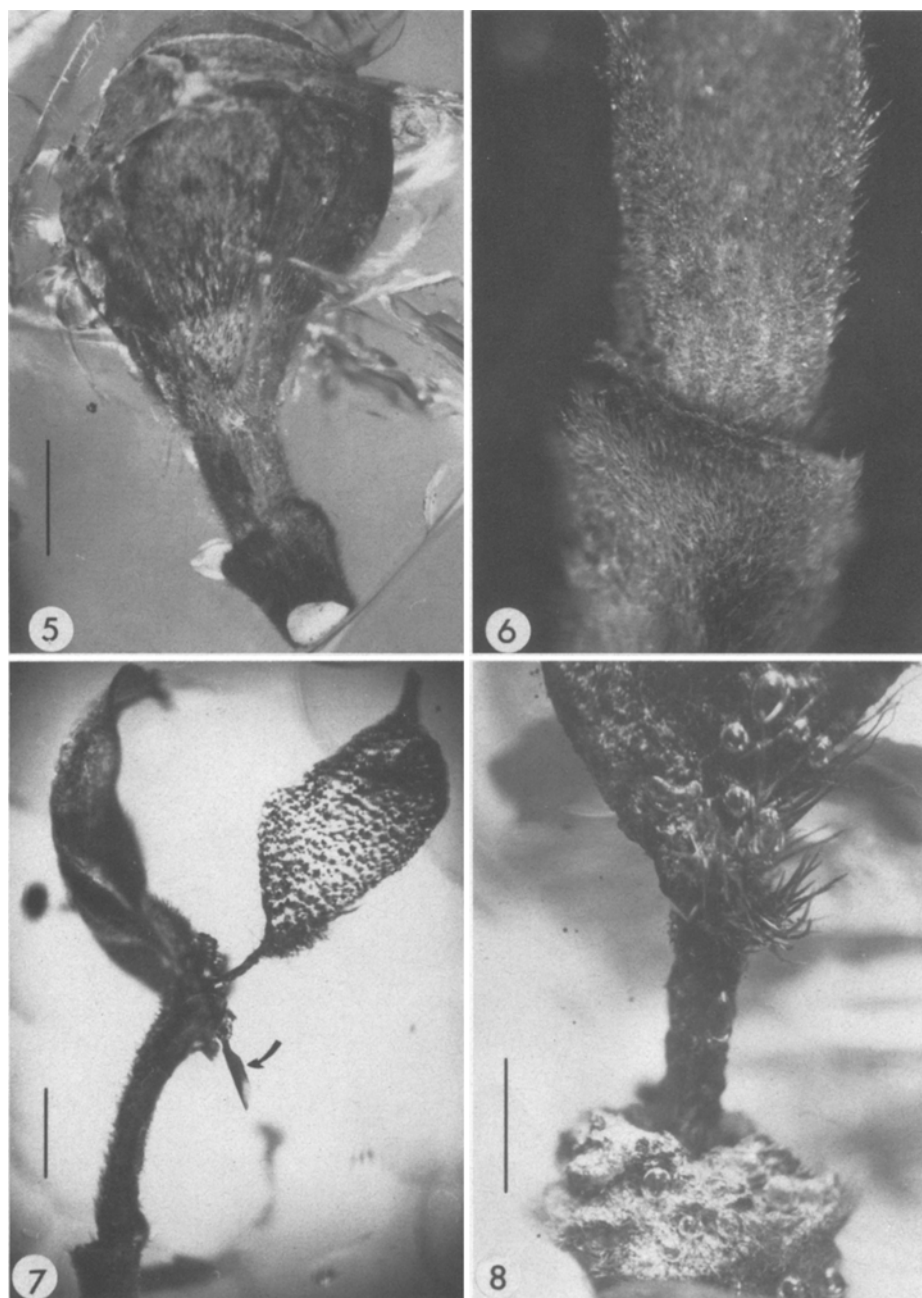
Figures 1–4. *Hymenaea protera*. (1) Dorsal view of leaflet (tip gone) (specimen H-L-1) (bar = 5 mm). (2) Detail of petiole and petiolule (specimen H-L-2) (bar = 2 mm). (3) Stipules separating along their common

margin (specimen H-st-1) (bar = 2.1 mm). (4) Detail of venation of leaf blade shown in fig. 1 (specimen H-L-1).

Leaflets (figs 1, 2, 4, 15). The leaflets were petiolulate. The twisted petiolules occurred only on the adaxial side of the leaflet and ranged from 1.5 to 3.0 mm (av. = 2.3 mm; N = 4) in length and from 0.6 to 1.2 mm (av. = 0.9 mm; N = 4) in width. The abaxial side of the leaflet was sessile. The petiolules bore some tan-colored hairs. The leaflets were broadly falcate in outline; the laminae were inequilateral (distinctly unequal at the base) and were rounded more on the outside than on the inside. The laminae were glabrous and the venation

was closely reticulate near the margin. The leaflets ranged from 23 to 51 mm (av. = 31 mm; N = 4) in length and from 9 to 22 mm (av. = 13 mm; N = 4) in width.

Stipules (fig. 3). The stipules were paired and in most cases they were still partially interlocked to each other along the medial line. They were narrowly elliptical in outline, truncate at their bases and obtuse at their apices. The inner surface was glabrous while the dorsal surface was covered with scattered, straight, tan-colored hairs.



Figures 5–8. *Hymenaea protera*. (5) Flower bud (specimen H-B-1) (bar = 2.1 mm). (6) Detail of pubescence on peduncle (Holotype specimen H-O-2). (7) Developing pistil attached to receptacle; arrow shows a scale-like petal at base of disc (specimen H-34) (bar = 1.7 mm). (8) Detail

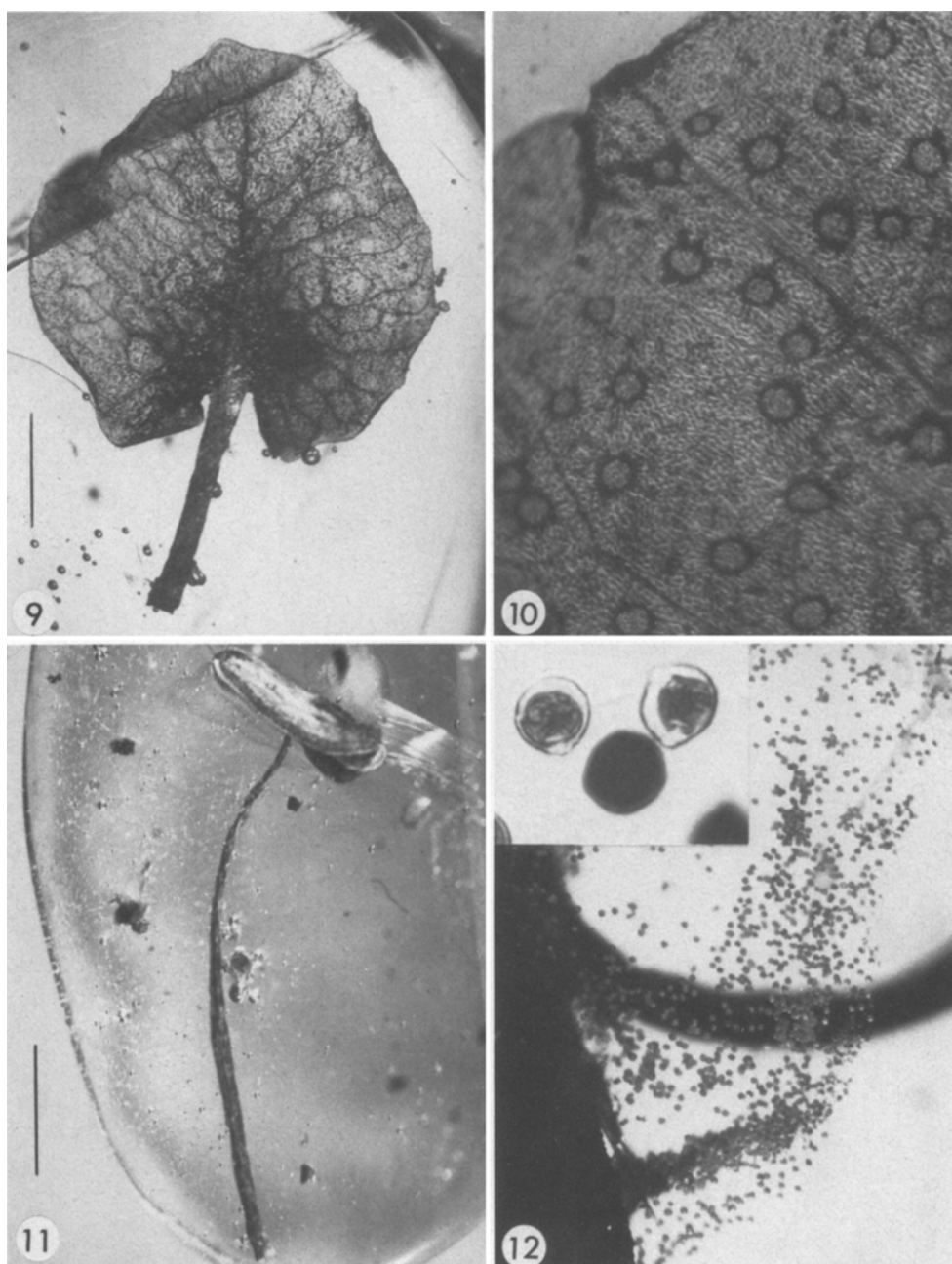
of disc of receptacle, stipe and basal portion of ovary. Note hirsute pubescence at top of stipe and base of ovary (specimen H-O-1) (bar = 1 mm).

The margins were tomentose, especially the border that connected the two stipules together in what appeared to be similar to a velcro-like adhesion. They ranged from tan to dark brown in color and their surfaces were covered with pellucid glands. Both stipules appeared to be similar in size and shape and each ranged from 11 to 20 mm (av. = 14 mm; N = 9) in length and from 2.5 to 5.3 mm (av. = 3.9 mm; N = 9) in width.

Petiole (figs 2, 15). The one available petiole was covered with dense, tan-colored hairs. It bore inconspicuous resin

pockets and lenticels and was 5.9 mm long and 0.6 mm wide.

Floral structures. Bracteoles (fig. 14). The bracteoles were probably early caducous since many were found free in the amber but were rarely found associated with buds or later stages of the flower. Two bracteoles subtended each bud. They were unequal in length and width, the outer one being longer than wide (ca 6 by 5 mm) and the inner shorter than wide (ca 5 by 6 mm). They were concave, ranged from broadly ovate to orbicular in outline and



Figures 9–12. *Hymenaea protera*. (9) Ventral view of petal (specimen H-P-1B) (bar = 2.5 mm). (10) Detail of petal surface showing circular resin glands (specimen H-Pet-1). (11) Lateral view of stamen (specimen

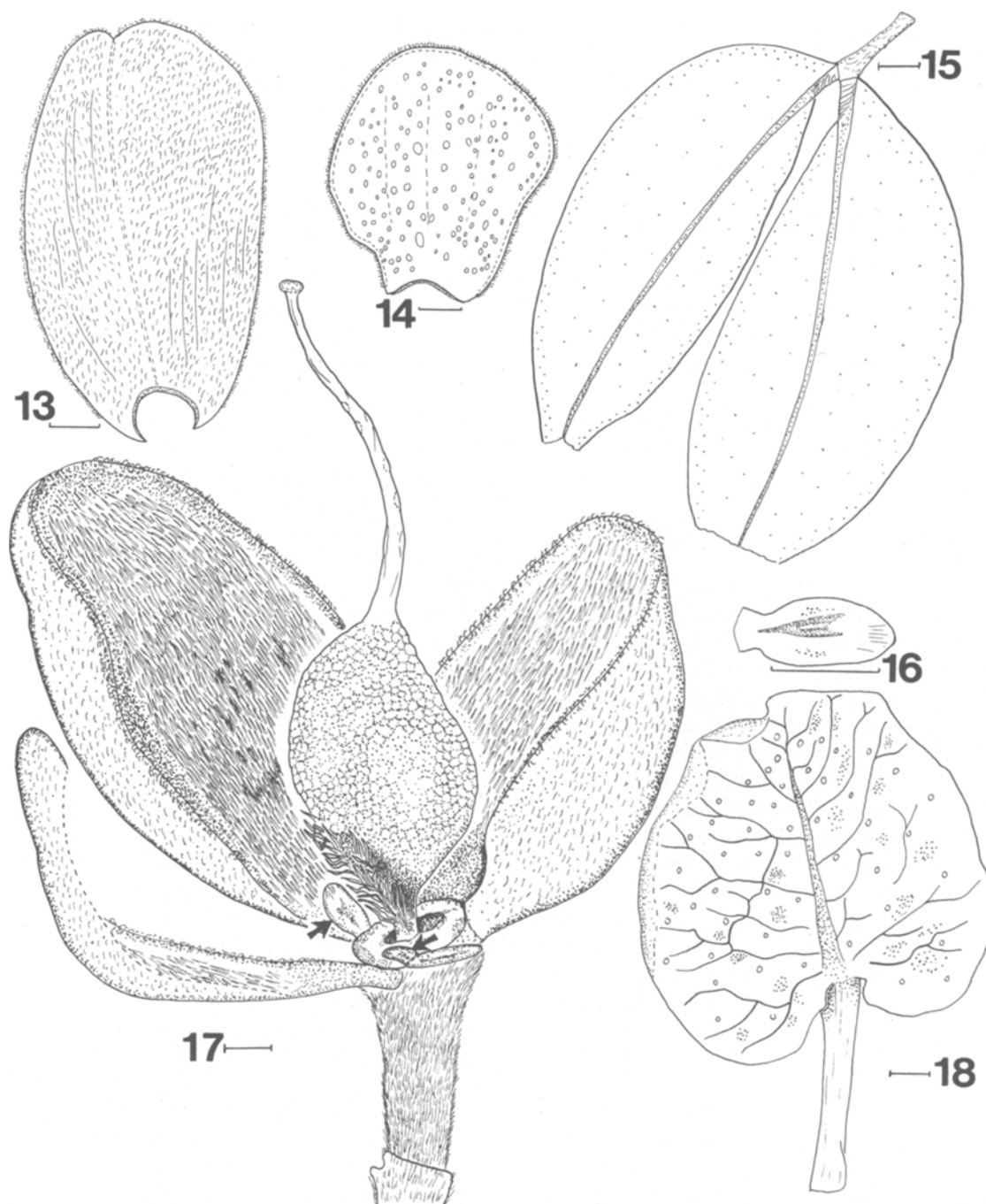
H-8) (bar = 2 mm). (12) Pollen grains that have issued from the adjacent anther; insert shows detail of several pollen grains in the amber (specimen H-Pol-1).

possessed truncate bases and obtuse-truncate apices. The inner surfaces were glabrous and dotted with numerous pellucid resin glands. The margins were fimbriate and lacked glands. The dorsal (outer) surfaces were covered with straw-colored hairs.

Buds (fig. 5). The buds ranged from 5.0 to 9.6 mm (av. = 7.4 mm; N = 4) in length and from 4.0 to 6.5 mm (av. = 5.4 mm; N = 4) in greatest width. They were dark brown and pubescent throughout.

Sepals (figs 13, 17). The calyx was urn-shaped, coriaceous and more persistent than the bracteoles. The calyx

was composed of four sepals which were arranged spirally on the flower. Beginning with the lowest and rising in a counterclockwise direction, the third sepal was wider than the others and was normally bifid at the tip, suggesting that it represented a fusion of two separate sepals (this condition occurs in extant species). The bifid sepal was wider than the other three and ranged from 6 to 10 mm (av. = 7 mm; N = 9) in length and from 6 to 8 mm (av. = 7 mm; N = 9) in width. The other sepals were similar in size and ranged from 7 to 11 mm (av. = 9 mm; N = 9) in length and from 5 to 9 mm



Figures 13–18. *Hymenaea protera*. (13) Dorsal view of sepal; bifid tip may represent incomplete fusion of two calyx lobes; only four lobes are present (specimen H-C-2). (14) Ventral view of bracteole showing glandular areas on the glabrous surface (specimen H-Br-1). (15) Dorsal view of leaf with petiole and paired leaflets (specimen H-L-2). (16) Dorsal view

of reduced scale-like petal (specimen H-34). (17) Flower showing peduncle, hypanthium, disc, pistil, two reduced scale-like petals (arrows) and two entire and one partial sepals (Holotype specimen H-O-2). (18) Ventral view of petal showing distinct claw and reniform blade (specimen H-P-1A). All bars represent 1 mm.

(av. = 7 mm; N = 9) in width. All sepals were elliptical in outline, truncate at the base and obtuse at the tip. A layer of dense, tan-colored, sericeous hairs covered the dorsal surface and extended to the margin of the ventral (inner) surface. There were two rows of long, spinelike hairs which originated from the base of the inner surface and coalesced in the center area. The periphery of the ventral surface contained a border of tomentose hairs

similar to those found on the dorsal surface. On the dorsal surface of the bifid-tipped sepals, there was a 'midrib' area that contained no pubescence.

Petals (figs 7, 9, 10, 16–18). There were two types of petals present. The common ones found loose in the amber were showy and obviously early caducous. Reduced, scale-like petals were persistent. The showy petals were unguiculate (clawed) and the laminar portion was

expanded on either side of the apex of the claw, producing a cordate to reniform base. The blade was orbicular in shape with a broadly obtuse tip. These petals were tan-colored, completely glabrous, possessed a central midrib and several parallel lateral veins, and were spotted with pellucid glands. They ranged from 10 to 15 mm (av. = 13 mm; N = 19) in length, the total length of the lamina ranged from 6 to 11 mm (av. = 8 mm; N = 19), the length of the claw ranged from 4 to 7 mm (av. = 5 mm; N = 19) and the width of the claw at the base ranged from 0.3 to 0.8 mm (av. = 0.6 mm; N = 19). The reduced petals were 1.3–1.4 mm long, 0.6 mm wide and elliptical in outline with a constriction just above the base. They were also glabrous, darker in color than the showy petals, possessed a diffuse brownish area along the center and the sides were dotted with minute pellucid glands.

Stamens (fig. 11). The anthers were tan-colored, linear, bilocular, glabrous, dorsifixed, and longitudinally dehiscent. They ranged from 3 to 5 mm (av. = 4 mm; N = 14) in length and from 0.4 to 1.4 mm (av. = 0.9 mm; N = 17) in width. They were crenulated on the end nearest the point of insertion of the filament. The filaments were dark brown, glabrous, free, broadest at the base and narrowed at the apex and inserted slightly off center of the anthers. They ranged from 8 to 17 mm (av. = 12 mm; N = 17) in length and from 0.2 to 0.5 mm (av. = 0.4 mm; N = 17) in width at the base.

Pollen (fig. 12). Pollen issuing from stamens in anthesis was examined under the light microscope. The pollen grains were spherical to subprolate, ranged from 27 to 34 μ m in a diameter and were triplicate. The area adjacent to some of the pores was swollen and in some grains, the bicellular condition could be observed, including the spindle-shaped generative cell and tube cell nuclei.

Receptacles (figs 6–8, 17). The peduncle, ranging from 2 to 4 mm (av. = 3 mm; N = 16) in length and from 0.8 to 1.5 mm (av. = 1.0 mm; N = 16) in width, was short and thick. It was covered with a tan woolly pubescence. The peduncle expanded at its apex into a disc-bearing hypanthium which ranged from 1.7 to 3.0 mm (av. = 2.2 mm; N = 16) in length and from 2.0 to 3.0 mm (av. = 2.5 mm; N = 16) in width. The campanulate hypanthium was densely covered with tan-colored hairs similar to those of the peduncle. A stipe emerged from the center of the hypanthium. The base of the stipe was normally inserted in a circular depression in the center of the hypanthium. The stipe ranged from 1 to 3 mm (av. = 2 mm; N = 8) in length and from 0.4 to 0.8 mm (av. = 0.6 mm; N = 8) in thickness. The basal and mid-portion of the stalk was glabrous but the upper portion was covered with elongate, straw-colored hairs. These elongate hairs extended up one side of the ovary, rarely reaching half the length of the ovary.

Pistil (figs 7, 8, 17). The ovary was rhomboidal to oblong in outline and was completely glabrous except for elongate hairs that were restricted to the base and along one

margin. The surface of the larger ovaries was dark brown and verrucose. The ovary ranged from 3 to 8 mm (av. = 6 mm; N = 14) in length and from 1.3 to 5.0 mm (av. = 3.4 mm; N = 13) in greatest width. The style was rolled up in the young flower and slightly curved in the mature flower. It was filiform and glabrous and the surface bore expanded resin ducts. The style ranged from 7 to 9 mm (av. = 8 mm; N = 4) in length and from 0.4 to 0.7 mm (av. = 0.5 mm; N = 4) in width at the base. The stigma was capitate, 0.1 mm long and 0.2 mm wide. The surfaces of some of the stigmas contained pollen grains.

Type specimen. The holotype is a piece of La Toca amber (specimen H-O-2) (fig. 17) containing a peduncle, hypanthium, disc, pistil, two reduced petals and two entire and one partial sepals. The holotype piece weighs 3.9 gram and measures 30 mm long by 21 mm wide by 13 mm thick. The holotype is deposited in the Poinar collection of Dominican amber maintained at the University of California, Berkeley.

Diagnosis. The vegetative and floral parts described above for *H. protera* are very similar to those of the extant members of *Hymenaea* as defined by Lee and Langenheim⁴. The fossil species can be separated from all the new world extant species of *Hymenaea* by the presence of reduced scale-like petals. It shares this trait with the single African representative of the genus, *H. verrucosa* Gaertner⁵. The fossil specimen differs from all extant species in the genus by the possession of stalked, cordate petals. Using the key to the extant species of *Hymenaea* provided by Lee and Langenheim⁴, the fossil species would fall into the section *Trachylobium* on the basis of its small flowers and the densely hirsute basal portion of the ovary. Of the three species in this group, *H. protera* is closest to *H. verrucosa* on the basis of the verrucose-rugose surface of the mature ovary and the type of pubescence.

The other two species in section *Trachylobium* (*H. parvifolia* Huber and *H. oblongifolia* Huber) each have a smooth fruit and the ovary is pubescent throughout. The other members of the genus have been placed into section *Hymenaea* and are all characterized by large flowers (buds 12–35 mm \times 6–18 mm) and the absence of scale-like petals. However, some of these species do share petal and pistil characteristics with *H. protera*. *H. torrei* León from Cuba has a verrucose fruit, but can be distinguished from the fossil species by its pubescent anthers and sessile petals. *Hymenaea oblongifolia* may also have clawed petals, but they range from oblanceolate to broadly spatulate in shape. Also the calyx lobes are subequally tomentose on both surfaces (not silvery-sericeous inside) and the ovary is pubescent throughout. From the closely related *H. verrucosa*, the fossil form can be distinguished by the reniform shape of its petals (spatulate in *H. verrucosa*), the type of hirsute pubescence on the ovary (along the entire base in *H. verrucosa*, but on only one side in *H. protera*) and the centrally placed stipe (excentric in *H. verrucosa*).

Quantitative differences between *H. verrucosa* and *H. protera* include the length of the petiole (8–18 mm in *H. verrucosa* and 6 mm in *H. protera*), the length of the petiolule (3–5 mm in *H. verrucosa* and 1–3 mm in *H. protera*), the length of the petals (15–20 mm in *H. verrucosa* and 10–15 mm in *H. protera*), the length of the petal claw (7–10 mm in *H. verrucosa* and 4.0–6.5 mm in *H. protera*) and the length of the stamens (25 mm in *H. verrucosa* and 8–17 mm in *H. protera*).

Discussion

In describing this fossil, the author has followed the recommendation of Collinson⁶ regarding the decision of placing the species in an extant genus rather than creating a fossil genus. Collinson concluded that when overwhelming evidence was present indicating that a fossil plant belonged to an extant genus, then that genus should be used in the description.

Hymenaea protera is the first described fossil species of the genus *Hymenaea*. It also possesses the smallest known flowers of the genus. It is not known whether all the flowers of *H. protera* had three showy petals and two scale-like petals or just some because Brennan⁷ showed that in Malagasy and Mauritius, the flowers of *H. verrucosa* may have either three or five showy petals.

Small to large flowers was one of the possible morphological trends of development in the evolutionary history of *Hymenaeae* noted by Lee and Langenheim⁴. Another primitive trait noted by them and substantiated by the present study was clawed petals. The authors also considered a pubescent ovary to be primitive, however, this could not be substantiated in the present study.

Although *H. protera* is now considered extinct, there are a few specimens of *H. courbaril* L. presently in the Dominican Republic. However, no *Hymenaeae* parts found in amber during the present study fit the description of this species. It is unknown when *H. courbaril* arrived in Hispaniola and whether it can be considered indigenous to the area or became naturalized within the past several hundred years.

Morphological studies reported here showing a close relationship between *H. protera* and the African species *H. verrucosa* substantiates the study by Cunningham et al.⁸ on analyses of *Hymenaea* trunk resins. Their results indicated a close relationship between Dominican amber and recent *H. verrucosa* resin.

As an explanation for the origin of the genus and the amphi-Atlantic distribution pattern, Lee and Langenheim⁴ and Langenheim and Lee⁵ assumed a common ancestral stock from the West African rain forest. They suggested that oceanic dispersal from that stock to the New World could have occurred during the early Tertiary.

The present author offers an alternative explanation based on plate tectonics. The genus could have originated during the period when the South American and African continents formed a common land mass (middle

to late Cretaceous). Thus, the precursor of *H. protera* sp.n. could have been distributed from what is now Central America to what is now the East Coast of Africa. As the continents separated in the late Cretaceous⁹, the distribution of *Hymenaea* became disjunct with populations remaining on both continents. Climatic changes or biological factors on both continents eradicated *H. protera* from the New World and its direct descendents from most areas in Africa except for ecological refugia on the East Coast of Africa, Malagasy and the islands of the Seychelles and Mauritius. Thus the center of origin for the genus was the combined South American-African continent during the Cretaceous. For some reason, *Hymenaea* found conditions for speciation more favorable in the New World than in Africa since there are presently 13 neotropical species and only a single species in Africa⁴. The present distribution of the related resin-producing genus, *Copaifera* (Leguminosae; Caesalpinioideae) with 30 neotropical and 4 African species¹¹ may have evolved similarly.

The discovery of pollen of the tropical caesalpinoid genera *Crudia* from the Paleocene and *Sindora* from the upper Cretaceous¹², together with caesalpinoid remains in the Green River Eocene formations¹⁰ provides evidence that the Caesalpinioideae was established by the upper Cretaceous and early Tertiary.

Biological factors may also have influenced the paleodistribution of *Hymenaea*. Many of the vegetative and floral parts of *H. protera* show signs of insect damage. The tips of some of the leaves, portions of petals and calyx lobes show evidence of chewing insect damage and calyx lobes contain small holes typical of those made by insects depositing eggs in flower buds. The long, stiff, forward-pointing hairs lining the inner sides of the calyx lobes could have evolved as a defense against insects attempting to reach the unexposed floral parts.

It is assumed that at least the great majority, if not all, of the amber recovered from the La Toca mine and other mines in the region with roughly similar-aged deposits originated from resin produced by *H. protera*. This assumption is based on the presence of only *H. protera* inclusions in the amber, the knowledge that extant *Hymenaea* trees produce large amounts of resin and nuclear magnetic resonance and infrared studies showing a strong resemblance of Dominican amber to present day *Hymenaea* resin, especially that of *H. verrucosa*⁸.

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Chemical defense in the three European species of *Crematogaster* ants

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Abstract. The composition of the Dufour gland of the ant *C. scutellaris* has been reinvestigated by gas chromatography/mass spectrometry. The major components of the gland are (2E,5E,12Z)-4-oxoheneicosa-2,5,12-trien-1-ol acetate (**1a**) its Δ^{14} and Δ^{16} double bond isomers (**1b** and **1c**), and the corresponding (Z,Z)-dienes **5a** and **5b**, all containing an acetylated C₂₁ chain. The previously proposed structures **1d**, **1e**, and **5c**, which are based on an homologous acetylated C₂₃ chain, correspond to minor derivatives present in the gland. Traces of acetylated C₁₉ homologs, tentatively identified as **1g**–**1i**, have also been found. The Dufour gland contents of the two other European *Crematogaster* species have also been studied. *C. auberti* is very similar to *C. scutellaris* in producing mainly **1a**, **1b** and **1c**, together with the same higher and lower homologs, but it lacks the dienic derivatives **5**, whereas *C. sordidula* contains essentially the acetylated C₁₉ compounds **1g**, **1h**, and **1i**, accompanied by acetylated C₁₇ homologs.

Key words. Ants; *Crematogaster*; Dufour gland; chemical defense; electrophilic contact poisons.

Crematogaster ants are characterized by a peculiar defense strategy. Instead of injecting their venom as most primitive ant species do, they use their spatulate sting to apply their venom topically to the integument of attacking insects. In a previous paper¹, we reported that the venom of *C. scutellaris*, collected on bits of filter paper and stored in hexane, was an exceedingly complex mixture of unstable compounds. The latter were only partially separated by Sephadex LH-20 chromatography, affording five major fractions named CS1 to CS5 in order of increasing polarity. The compounds of one fraction differed from those of the other fractions by the nature of the functional group at the end of the chain: aldehyde (CS1), acetate (CS2), and carboxylic acid (CS5). In all compounds, a cross-conjugated dienone was linked to the terminal functional group. The minor fraction CS3 polymerised immediately after its isolation, whereas CS4 was an artifact¹. Each fraction was still a mixture of compounds differing by the number or position of the central double bond(s) in the carbon chain. The most stable acetate fraction, CS2, was shown by HPLC¹ to consist of at least six components. Two of the major compounds of this fraction were assigned the molecular formula C₂₅H₄₂O₃ and structures **1d** and **1e** (fig. 1),

differing only by the position of the central double bond in the chain. A third major derivative was shown by ¹H NMR to contain a Z,Z-diene and was assigned the molecular formula C₂₅H₄₀O₃ and, tentatively, structure **5c**¹ (fig. 1). Further work² led us to discover that only the acetates (fraction CS2) were stored in the Dufour gland of *C. scutellaris*. During venom emission, the acetates were transformed into the corresponding aldehydes by two enzymes, an esterase and an oxygen-dependent alcohol oxidase, which are present in the poison gland. The aldehydes, for which structures **3d**, **3e** and **7c** (fig. 1) were proposed, are powerful electrophiles and thus responsible, at least in part, for the toxicity of the venom².

We now report on a reinvestigation of the venom constituents of *C. scutellaris*, demonstrating that the Dufour gland content of this ant is more complex than was originally found¹. Indeed, gas chromatography-mass spectrometry analyses (GC-MS) and chemical degradations have shown that the major constituents are acetates **1a**–**1c** and **5a**, **5b**, containing an acetylated C₂₁ chain. These compounds are accompanied by small amounts (less than 10%) of acetylated C₂₃ homologs for which we propose structures **1d**, **1e**, **1f**, **5c** and **5d** and by traces of