

LASIAMBIX DOMINICENSIS GEN. AND SP. NOV., A EUDICOT FLOWER IN
DOMINICAN AMBER SHOWING AFFINITIES WITH
FABACEAE SUBFAMILY CAESALPINIOIDEAE

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ABSTRACT

Lasiambix dominicensis gen. & sp. nov., represented by six floral specimens at different stages of development, is described from Tertiary Dominican amber. The genus is characterized by small, perigynous, bilaterally-symmetrical flowers possessing a cup-shaped hypanthium, 5 ovate-deltate sepals, 5 equal, early-deciduous petals, 3 short, incurved stamens, each attached to the hypanthial cup opposite a sepal, and a superior, simple pistil attached basally within the hypanthium, the style positioned excentrically opposite the stamens and between 2 of the sepals. Immature fruits are obovoid, with a short, thick stipe and rugose surface. The combination of floral traits suggests a position in Fabaceae subfamily Caesalpinioideae, but with uncertain tribal affinity.

KEY WORDS: amber, Dominican Republic, Caesalpinioideae, eudicot flower, Fabaceae, Greater Antilles, Tertiary

RESUMEN

Se describe **Lasiambix dominicensis** gen. & sp. nov., representado por seis especímenes florales en diferente estado de desarrollo, del ámbar terciario dominicano. El género se caracteriza por sus flores pequeñas, periginas, con simetría bilateral, con un hipanto en forma de copa, 5 sépalos ovado-deltados, 5 pétalos iguales, tempranamente caducos, 3 estambre cortos, incurvados, adheridos a la copa del hipanto opuestos a los sépalos, y un pistilo súpero, simple unido basalmente al hipanto. El estilo excéntrico opuesto a los estambres y entre dos de los sépalos. Los frutos inmaduros son obovoides, con un estipe corto y grueso, y superficie rugosa. La combinación de trazos florales sugiere una posición en las Fabaceae subfamilia Caesalpinioideae, pero con una afinidad tribal incierta.

INTRODUCTION

Amber is well known for its preservative qualities of both animal and plant remains (Poinar 1992, Poinar & Poinar 1999). Amber flowers, maintained in three-dimensional form, are often preserved with such detail that they can be assigned to extant genera (Spahr 1993). Such fossils can be useful in paleontological reconstructions (Poinar & Poinar 1999).

The majority of described amber flowers originate from Baltic deposits (Spahr 1993); however legume (Dilcher et al. 1992; Poinar 1991) and palm (Poinar 2002a, 2002b) flowers have been described from Dominican amber, and there are also descriptions of Early Cretaceous flowers in Burmese amber (Poinar & Chambers 2005; Poinar et al. 2007).

During an ongoing investigation of floral remains in Dominican amber, 6 flowers in 5 separate pieces of amber were discovered, which could be linked through the possession of an identical cup-shaped, puberulent hypanthium with deltate-ovate, spreading-recurved sepals. One flower, with petals present, is probably at a pre-anthesis stage; 3 flowers, with petals absent, are at or near anthesis; and 2 flowers show early fruit development, with the stipe of the pod still held in the hypanthium. The exceptional preservation of the flowers and clarity of the amber allow description and photographic documentation of their unique features. These flowers, which are described below as a new genus, possess a combination of characters that favors an assignment to Fabaceae subfamily Caesalpinioideae.

MATERIALS AND METHODS

All 5 pieces of amber containing the fossil flowers originated from mines in the northern mountain range (Cordillera Septentrional) of the Dominican Republic, between the cities of Puerto Plata and Santiago. Dating of Dominican amber is controversial, with the youngest proposed age of 20–15 mya based on foraminifera (Iturralde-Vincent & MacPhee 1996) and the oldest as 45–30 mya based on coccoliths (C  pek in Schlee 1999). Most of the amber is secondarily deposited in turbiditic sandstones of the Upper Eocene to Lower Miocene Mamey Group (Draper et al. 1994).

The 6 flowers are similar in the morphology of their floral cup (hypanthium) and are assumed to have originated from the same plant species. The amber piece containing the flower assigned to catalogue number Sd-9-154A (Holotype) is circular in outline, measures 13 mm in diameter, 9 mm in greatest thickness and weighs 6 grams. The amber piece containing specimen Sd-9-154B is roughly triangular in shape, measures 12 mm along the sides, 7 mm at the base, is 3 mm thick and weighs 3 grams. The third amber piece (Sd-9-154C) is rectangular, measures 8 mm by 7 mm along the sides, 2 mm in thickness and weighs 2 grams. The fourth amber piece (Sd-9-154D), which contains the specimen with the petals, is semicircular in outline, measures 17 mm in greatest length, 9 mm in greatest width, 7 mm in greatest thickness and weighs 1 gram. The fifth amber piece (Sd-9-154E), which contains the specimen with the fruits, is trapezoidal in outline, measures 17 mm in greatest length, 12 mm in greatest width, 8 mm in greatest thickness and weighs 1 gram. All specimens are deposited in the Poinar amber collection maintained at Oregon State University.

DESCRIPTION

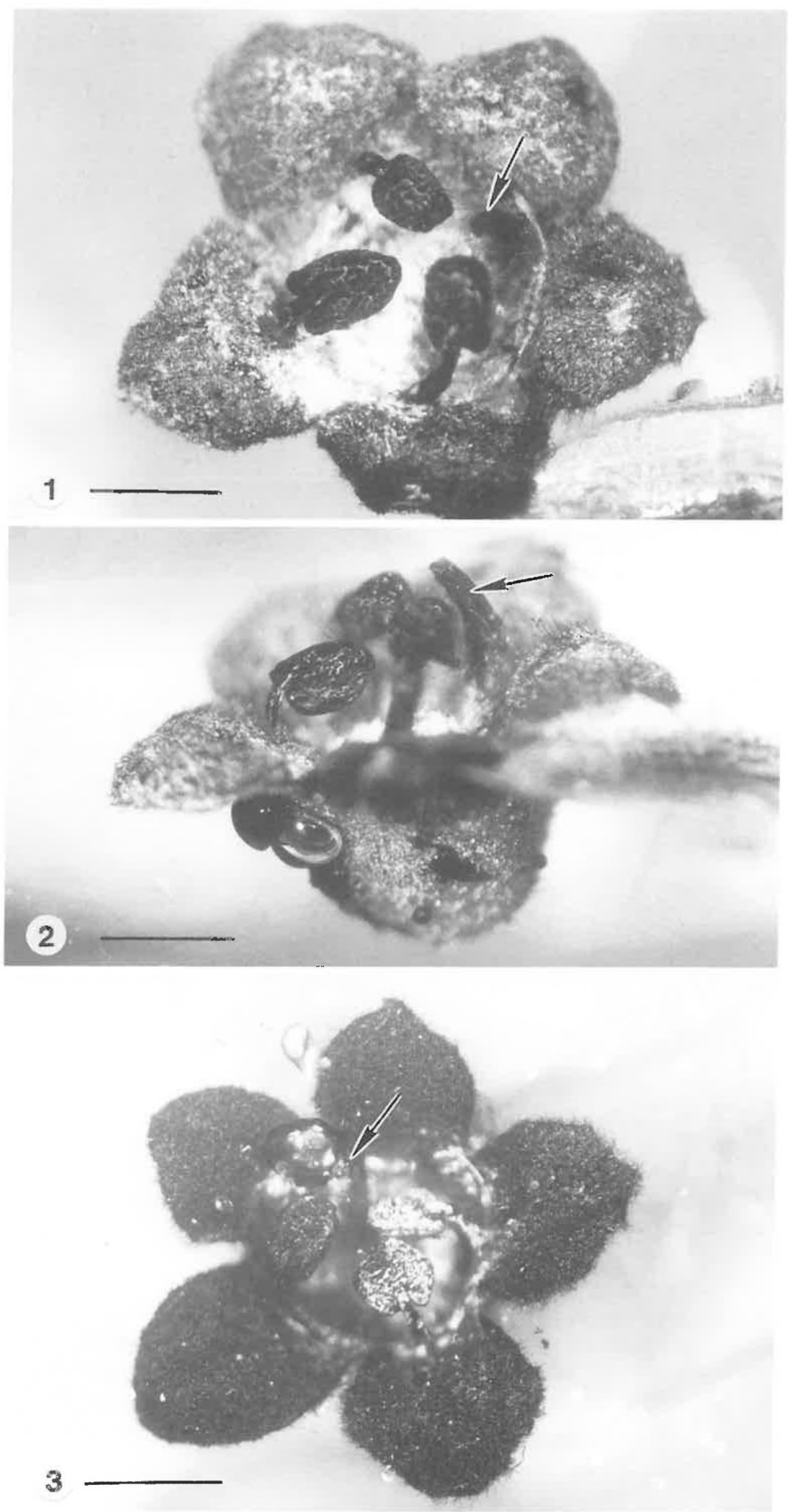
Lasiambix Poinar, Chambers & Brown, gen. nov. TYPE SPECIES: *Lasiambix dominicensis* Poinar, Chambers & Brown sp. nov.

Flowers small, bilaterally symmetrical, perfect (bisexual), with a cup-shaped hypanthium; calyx isosepalous, sepals 5, deltate-ovate, free, imbricate or valvate; corolla isopetalous, petals 5, free, early-deciduous; stamens 3, arising from rim of hypanthium opposite 3 adjacent sepals, filaments short, linear, strongly incurved, anthers bilocular, dorsifixed, introrse; ovary superior, sessile at base of hypanthial cup; style single, barely exceeding stamens, positioned excentrically opposite the stamens and between the two sepals that lack stamens; stigma simple, not enlarged; fruit (immature) obovoid, tapered to a short, thick stipe, style deciduous.

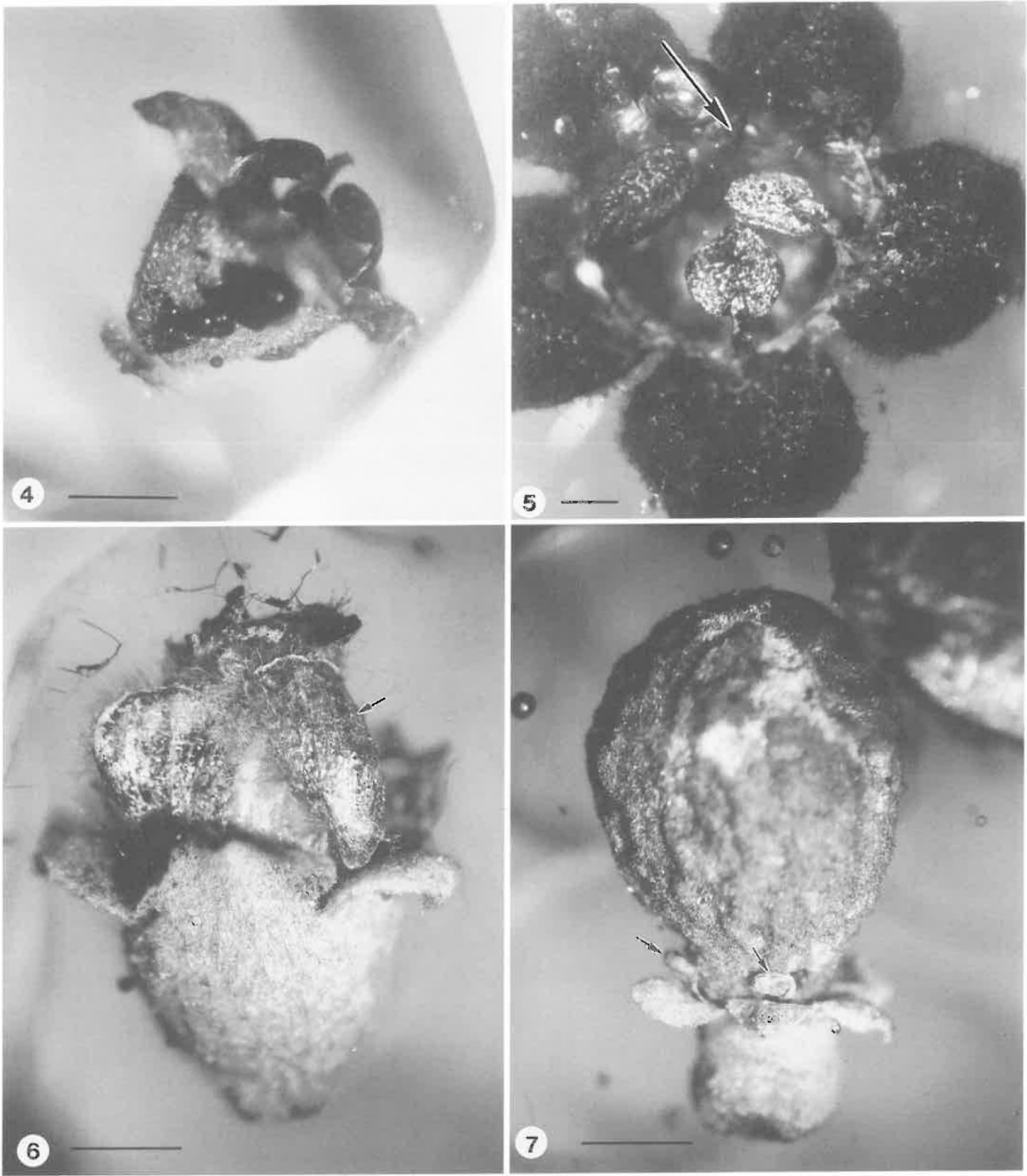
Lasiambix dominicensis Poinar, Chambers & Brown, sp. nov. (Figs. 1–9). TYPE: HISPANIOLA, DOMINICAN REPUBLIC: amber mine in the northern mountain ranges (Cordillera Septentrional), between Puerto Plata and Santiago, 2003, collector unknown (HOLOTYPE: OSC-cat. no. Sd-9-154A, Poinar amber collection).

Flowers 3.6–3.7 mm in diameter, bilateral, pedicel none; hypanthium cup-shaped, densely tomentulose externally, pubescent within, 1.7–2.1 mm long, the opening 1.4–2.2 mm wide, bearing a distinct rim to which stamens and petals are attached; disc none; sepals deltate-ovate, densely tomentulose on both surfaces, spreading with reflexed tip, 0.9–1.6 mm long, 1.0–1.6 mm at widest point; petals erect, early-deciduous, 1.3–1.9 mm long, 0.8–1.1 mm wide, oblanceolate, bluntly rounded at tip, thick-textured, margins ciliate; stamens short, incurved, slightly exerted from hypanthium, the filaments attached to hypanthial rim, linear, thickened at point of insertion, glabrous, the anthers positioned horizontally over the mouth of hypanthium, bilocular, slightly dorsifixed, ovate, blunt-tipped, cordate at base, 0.4–0.7 mm long, glabrous, dehiscence introrse by lengthwise slits; ovary sessile in hypanthial cup, lightly pubescent, style linear, 0.6–1.0 mm long, pubescent proximally, stigma terminal, undivided, not enlarged; fruit (immature) obovoid, probably 1-few-seeded, 4.8–4.9 mm long, 3.7–3.9 mm wide, the short, thick stipe mostly enclosed in the hypanthium, surface thick-textured and rugose (as preserved), style not persistent.

Etymology.—Genus name from the Greek “lasios,” woolly, and “ambix,” cup, referring to the tomentulose hypanthium that unifies the 6 specimens. Species name derived from the Dominican Republic, the country where the fossils were found.



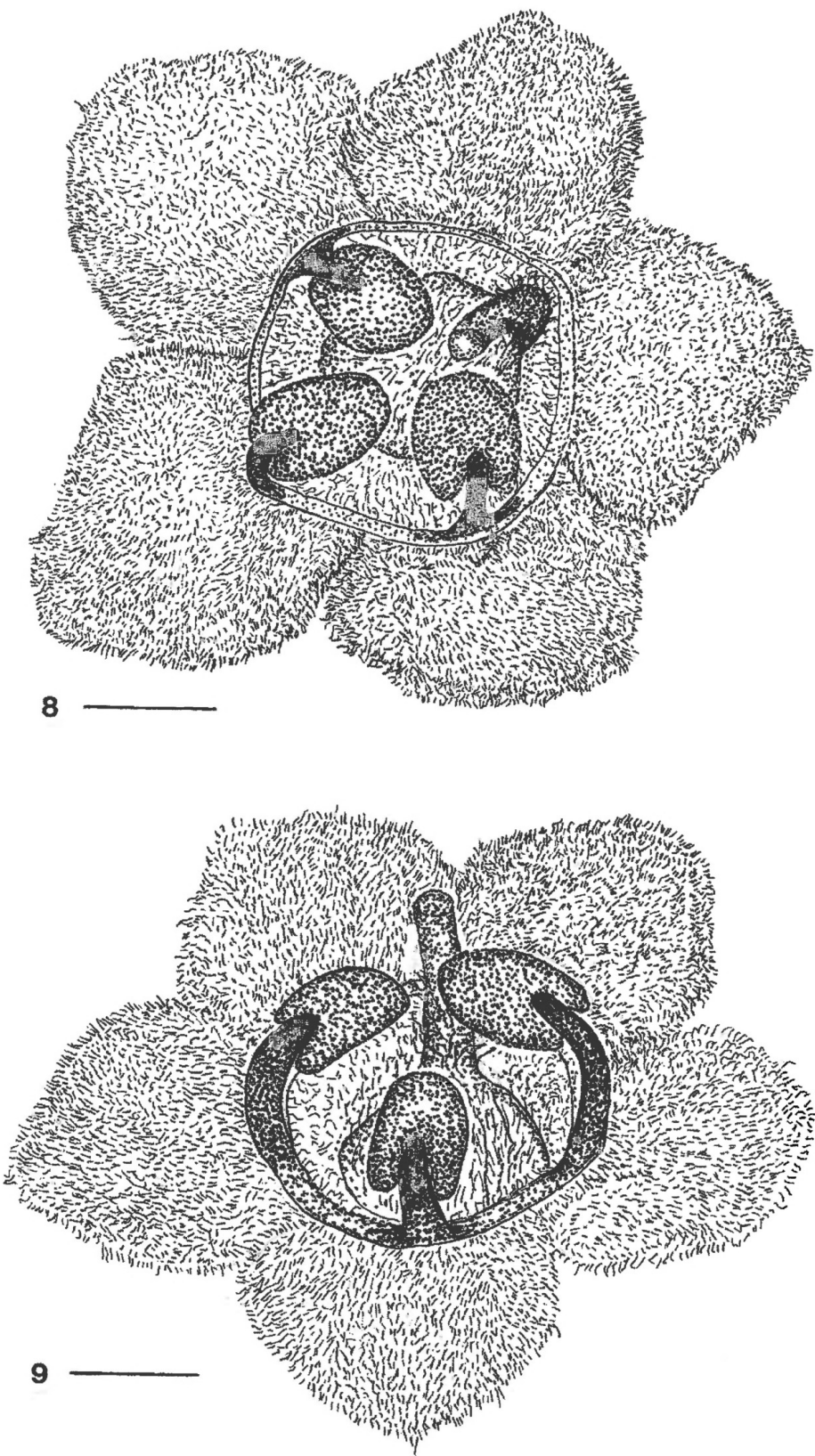
FIGS. 1–3. *Lasiambix dominicensis* gen. and sp. nov. 1. Top view of holotype (accession # Sd-9-154A); arrow points to style. Scale bar = 0.82 mm. 2. Oblique view of holotype (accession # Sd-9-154A); arrow points to style. Scale bar = 0.82 mm. 3. Top view of specimen Sd-9-154C; arrow points to style. Scale bar = 0.82 mm.



FIGS. 4–7. *Lasiambix dominicensis* gen. and sp. nov. 4. Side view of holotype (accession # Sd-9-154A). Scale bar = 0.84 mm. 5. Detail of stamens in specimen Sd-9-154C; arrow points to style. Scale bar = 0.28 mm. 6. Side view of specimen Sd-9-154D; arrow points to loose petal. Scale bar = 0.77 mm. 7. Side view of specimen Sd-9-154E showing developing fruit; note stamens at base (arrows). Scale bar = 0.57 mm.

DISCUSSION

The floral features that we believe unite these 6 specimens into a single taxon are evident in the photographic illustrations (Figs. 1–7). Although at different stages of development, the flowers have a remarkably similar hypanthium, with respect to shape, calyx lobes, and pubescence. All have a truncate base where they broke off of their inflorescences. One specimen with an immature fruit (Fig. 7) retains a pair of stamens attached



FIGS. 8–9. Holotype of *Lasiambix dominicensis* gen. and sp. nov. (accession # Sd-9-154A). 8. Top view. Scale bar = 0.57 mm. 9. Oblique view. Scale bar = 0.57 mm.

opposite the calyx lobes. The specimen in early flower (Sd-9-154D, Fig. 6) has all 5 petals visible, and one is detached at the base, illustrative of what we term an early-deciduous corolla. The petals are clearly seen when the specimen is viewed from the top as well as the sides. The center of this flower is unsuitable for study due to an accumulation there of apparent insect remains and frass. The sharp hypanthial rim on the 3 flowers at or near anthesis shows where the petals presumably were attached, alternate with the sepals. It remains ambiguous whether the sepal lobes were imbricate or valvate in the bud, perhaps because of different degrees of spreading and separation in the samples at hand. Because no slits or pores are evident on the back, sides, or tips of the anthers, we suggest an introrse dehiscence, which is supported by observations of the adaxial side of one strongly inflexed stamen. The nature of the mature fruit is uncertain, although from the shape and thick-textured exocarp of the 2 specimens here (Fig. 7), a non-compressed, 1- or few-seeded drupaceous fruit is suggested. Although atypical for members of the Fabaceae, several extant genera of the Cassieae have similar indehiscent, drupaceous fruits. *Dialium* s.l. is characterized by small fruits consisting of one seed surrounded by a soft, but somewhat dry, edible aril (Gentry 1993). Few-seeded, ovoid, fleshy- or thick-walled fruits are not unusual in Fabaceae subfamily Caesalpinioideae (e.g. Lewis et al. 2005). This fruit-type, together with a well-developed hypanthium, a superior simple pistil, regular corolla, reduced stamen number, and a zygomorphy of androecium and pistil, are what lead us to suggest assigning the fossil to this family and subfamily.

The caesalpinoid legumes are extremely diverse in floral characteristics, including numbers of stamens, presence or absence of a hypanthium, numbers and form of petals, length of filaments, form of anthers and stigmas, shape and structure of fruits, floral symmetry, modification to unisexuality, etc. The compendium by Polhill and Raven (1981), with its taxonomic treatments of the relevant tribes (Cowan & Polhill 1981; Irwin & Barneby 1981; Polhill & Vidal 1981), was consulted in a search for modern genera with the particular combination of features seen in the fossils. Illustrations and descriptions of genera were examined in Taubert (1894), Hutchinson (1964), and Lewis et al. (2005). No examples have been found that correspond in all respects with *Lasiambix*, but its described traits are present separately in numerous caesalpinoid genera.

A cup-shaped, externally puberulent hypanthium occurs frequently in the subfamily. Bilateral symmetry (zygomorphy) is also common, and this accompanies a reduction to three stamens in such genera as *Tamarindus*, *Macrolobium*, *Gilbertiodendron*, *Elizabetha*, *Apuleia*, *Dialium*, etc. As discussed by Tucker (1998, 2002) there are parallel evolutionary trends towards reduction of stamen number in groups of related genera in separate tribes (her examples were Detarieae-Amherstieae and Daliinae). From the basic number 10, stamens may be reduced to as few as 1 (some *Dialium* spp.), and during development, some of the stamen primordia that form early may cease their growth and become rudimentary or staminodial (e.g. *Gilbertiodendron*, *Macrolobium*; Tucker 2002). Except for *Dialium* and *Apuleia*, the 3-stamen genera mentioned fall into the Amherstieae (including Macrolobieae) clade, as defined by analysis of the chloroplast *trnL* intron (Bruneau et al. 2001). This group is also recognizable in the *rbcL* analyses by Doyle et al. (1997) and Kajita et al. (2001). However, the corolla evolution in these particular genera leading to loss of all but one petal to form an adaxial vexillum (e.g. Cowan 1953), the 2-many-seeded, mostly dehiscent pods, plus the usual absence of a hypanthium, argue against a relationship to *Lasiambix*. *Cynometra*, also in this clade, is discussed below.

Dialium and *Apuleia*, of subtribe Daliinae, show some resemblance to *Lasiambix* in their zygomorphic, few-stamened flowers and their few-seeded, indehiscent fruits. According to Irwin and Barneby (1981, p. 101) *Dialium* "can be defined accurately and rigorously by its pod, a sort of indehiscent, 1- or 2-seeded nut, sometimes strongly, sometimes scarcely compressed laterally, consisting of a crustaceous exocarp and a pulpy, when ripe mealy endocarp enveloping the seeds." In their key (p. 100) the fruit is termed "drupaceous." The flowers of *Dialium*, a pantropical genus, are hypogynous and have only 1 or 2 petals and usually 2 stamens. The related *Apuleia*, of South America, possesses a hypanthium and 3 stamens, but its pistil is exserted, not sessile, its perianth is 3-merous, and its pod is compressed and coriaceous, not ovoid. Despite

their few-seeded, indehiscent pods, neither of these few-stamen genera of Daliinae suggests a close affinity to *Lasiambix*.

Other possible relationships of the fossils are with genera having regular flowers and more numerous stamens but with a similar type of few-seeded fleshy fruit. One such example is *Vouacapoua* of tribe Caesalpinieae (Lewis et al. 2005). This genus possesses regular flowers with 10 short stamens, but its hypanthium, sepals, and short petals much resemble *Lasiambix*, and its fruits are round, thick-walled, 1-seeded, and dehisce by a single furrow (Lewis et al. 2005, p. 161; Polhill & Vidal 1981, p. 89). The genus is presumed to have affinity to the *Peltophorum* group of tribe Caesalpinieae (Bruneau et al. 2001; Haston et al. 2003), but as yet the DNA support for this connection is weak.

A similar type of fruit occurs in the large genus *Cynometra* of tribe Detarieae (Lewis et al. 2005, p. 89). Its pod is described as thick, turgid, rugose to verrucose (rarely smooth), 1-seeded, and regularly indehiscent with a spongy pericarp (Hutchinson 1964, p. 235; Dwyer 1958); it lacks a floral disc, its ovary is usually hairy, and its style may be eccentric in the hypanthium (Dwyer 1958, p. 322). However, it has 10 long-exserted stamens, a shorter hypanthium, and a usually showier perianth than in *Lasiambix* (Dwyer 1958). Other differences, besides these, are that its sepals are glabrous adaxially (except *C. cubensis* Rich.) and its filaments are united very briefly at the base. Modern-day *Arcoa*, of Hispaniola, has turgid, 1-seeded, indehiscent fruits (Lewis et al. 2005, p. 132), but its flowers differ considerably from *Lasiambix* in being unisexual, bearing ca. 12 stamens, and having an exserted pistil with capitate stigma (Herendeen et al. 2003). Another Caribbean genus, *Stahlia* (tribe Caesalpinieae), has fleshy, 2-seeded, indehiscent fruits, regular 5-merous perianth, imbricate sepals, and well-developed, dorsally puberulent petals (Hutchinson 1964, p. 235; Lewis et al. 2005, p. 145). It differs from *Lasiambix* principally in having 10 erect, connivent stamens with filaments densely woolly in the lower half. Placement of *Stahlia* near the large genus *Caesalpinia* and its segregates was established by the molecular and morphological studies of Simpson et al. (2003).

The examples mentioned, falling into several distinct clades within the subfamily, illustrate the parallelisms in floral and fruit morphology that make it difficult to suggest a specific, definitive placement of *Lasiambix*. A large amount of recent phylogenetic research, both morphological and molecular, was reviewed by Lavin et al. (2005), to estimate the time frame of early diversification of this and other subfamilies of Leguminosae. Earlier estimates of a Late Cretaceous origin of the family and a "basal" position for Caesalpinioideae (e.g. Polhill et al. 1981; Herendeen et al. 1992), are no longer accepted as "conventional wisdom." Rather, the fossil record supports an origination in the Paleocene, allowing some 60 my for diversification within the family (Lavin et al. 2005). In molecular phylogenetic studies, with best resolution provided by the *matK* chloroplast gene, divergence of 6 early-formed lineages of caesalpinoids was found, along with the similarly old crown nodes of many papilionoid and mimosoid clades. Caesalpinoids are viewed as a paraphyletic grade from which stem the mimosoids and papilionoids, but because of the very early, rapid branching of the ancestors of modern clades, the caesalpinoid grade "harbor(s) neither the oldest diversification nor some other quality of legume antiquity" (Lavin et al. 2005).

If our suggested placement of *Lasiambix* is correct, it offers a well-preserved example of several specialized floral characteristics of Tertiary-age caesalpinoid legumes. These include the loss of all but 3 stamens and accompanying bilateral symmetry of the flowers, an absence of petals at anthesis, and presence of few-seeded, fleshy, probably indehiscent fruits. What pollination syndrome is represented by flowers with short, incurved stamens and no apparent nectar disc, is difficult to say. Perhaps nectar was produced at the base of the ovary, which was not visible to us. In this case small bees might have been able to enter the flowers and remove pollen from the arched, introrse anthers. The ecology of the plants is likewise unknown, other than that they grew in proximity to *Hymenaea* in moist tropical forests such as those described by Poinar and Poinar (1999). Such habitats are typical for many genera of modern-day Caesalpinioideae.

Note: In the illustrations, because the orientation of the flowers is unknown, we have not tried to suggest a placement of the stamens as either abaxial, as in *Macrobium* et al. (Cowan 1953) or adaxial as in *Dialium* et al. (Tucker 1998).

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