

TROCHANThERA LEPIDOTA GEN. AND SP. NOV., A FOSSIL ANGIOSPERM INFLORESCENCE IN DOMINICAN AMBER

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ABSTRACT

Trochanthera lepidota gen. & sp. nov., represented by a capitate male inflorescence at anthesis, is described from Tertiary Dominican amber. The genus is characterized by small, staminate flowers arising from between persistent flat-topped bracts on a spherical receptacle. Each flower is composed of 3–4 stamens, with distally connivent filaments and bilocular anthers showing longitudinal extrorse dehiscence. The perianth is represented by a short, appressed, truncate sheath around the filament column. The remaining fragment of stem below the head is leafless and minutely puberulent. The fossil, although of uncertain affinity, shows similarities to the families Balanophoraceae and Moraceae.

KEY WORDS: amber, Balanophoraceae, Dominican Republic, fossil flower, Greater Antilles, Moraceae, Tertiary

RESUMEN

Trochanthera lepidota gen. & sp. nov., representada por una inflorescencia masculina capitada en antesis, es descrita del ámbar terciario dominicano. El género se caracteriza por tener flores estaminadas pequeñas que surgen de entre brácteas persistentes de ápice plano en un receptáculo esférico. Cada flor se compone de 3–4 estambres, con filamentos conniventes distalmente y anteras biloculares con dehiscencia longitudinal extrorsa. El perianto está representado por una vaina corta, truncada y apresada alrededor de la columna de filamentos. Es resto de fragmento de tallo debajo de la cabezuela no tiene hojas y es ligeramente puberulento. El fósil, aunque de afinidad incierta, muestra semejanzas con las familias Balanophoraceae y Moraceae.

INTRODUCTION

Dominican amber is well known as a preservative agent of both animal and plant remains. Flowers may retain their structural details so clearly that they often can be assigned to extant genera (Poinar 1992) and can be used in paleontological reconstructions (Poinar & Poinar 1999).

During an investigation of floral remains in Dominican amber, we discovered a complete, globose male inflorescence of uncertain affinity. Its morphology is compared with the families Balanophoraceae and Moraceae, with which it shares many essential characteristics. The fossil's exceptional preservation allows microscopic study of the flowers, which are here illustrated. Due to its unique combination of features, the plant is described below as a new genus and species.

MATERIALS AND METHODS

The fossil 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 (Cêpek 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 amber piece containing the fossil is rectangular in outline, measuring 15 mm in length, 10 mm in width and 8 mm in depth. The holotype is deposited in the Poinar amber collection maintained at Oregon State University.

DESCRIPTION

Trochanthera G.O. Poinar, K.L. Chambers & A.E. Brown, gen. nov. TYPE SPECIES: *Trochanthera lepidota* G.O. Poinar, K.L. Chambers & A.E. Brown, sp. nov.

Diagnosis.—Stem leafless and minutely puberulent, total length unknown. Head depressed-globose, completely covered with persistent glabrous, flat-topped, closely connivent bracts in \pm a hexagonal pattern. Staminate flowers numerous, emerging over the entire head from between the edges of the bracts, each consisting of a column of distally connivent filaments and 3–4 anthers; anthers connivent, not fused, each with 2 ovate, unilocular thecae dehiscing extrorsely by longitudinal slits. Perianth represented by a short, truncate, erose sheath enclosing base of emergent filament column. Pistillate flowers unknown, absent from the described head or hidden beneath the bracts.

Trochanthera lepidota G.O. Poinar, K.L. Chambers & A.E. Brown, sp. nov. (**Figs. 1–6**). TYPE: HISPANIOLA. DOMINICAN REPUBLIC: amber mine in the northern mountain ranges (Cordillera Septentrional), 1995, unknown amber miner s.n. (HOLOTYPE: catalogue number Sd-9-148A, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

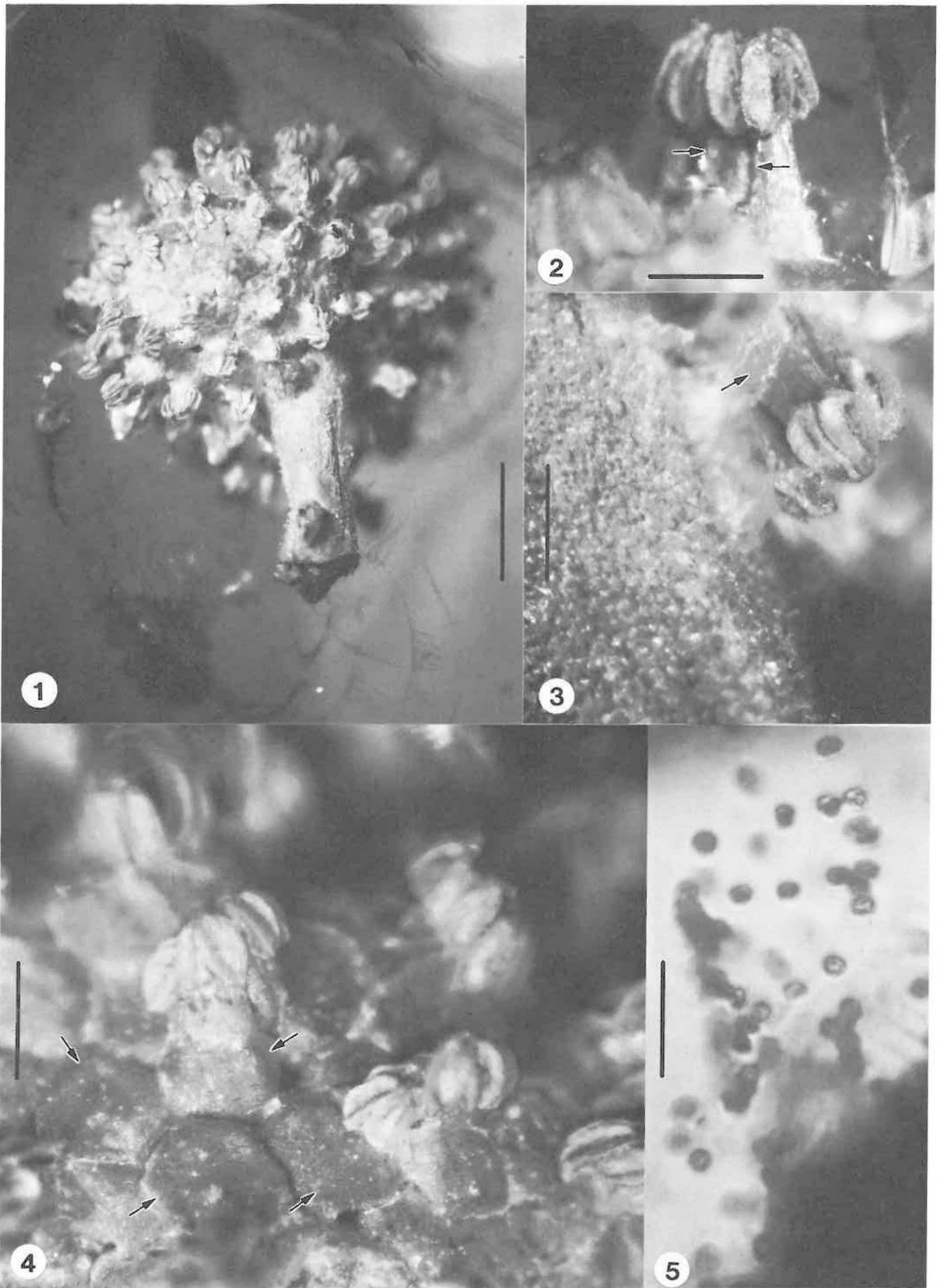
Description.—**Staminate flower head:** width 7.3 mm, length 5.3 mm; attached stem piece 2.6 mm long, 1.2 mm thick; peltate bracts of inflorescence 408(371–468) μm in diameter, anthers of emergent stamens 280(226–323) μm long, 113(96–145) μm wide; length of exposed filaments 0–193 μm ; perianth a short (up to 60 μm) sheath enclosing base of filament column; pollen grains spherical, 5–12 μm in diameter, out of position for detailed view of exine morphology.

Etymology.—Genus name from Greek “trochos” ball, and “antheros” flowery. Species name from Greek “lepidotos” scaly.

DISCUSSION

We consider the fossil’s distinctive unisexual inflorescence, consisting of a small, globose receptacle completely covered with flat-topped (presumably peltate) bracts, between which project numerous simple staminate flowers, to have its closest analogs in two modern angiosperm groups—family Balanophoraceae and family Moraceae, tribe Dorstenieae (formerly Brosimeae). Both these groups have modern representatives in the Caribbean region. We have not been able to identify a modern genus to which the fossil can confidently be assigned, although it shares characteristics with both families. The following discussion, where *Trochanthera* is compared with each of these putative relatives, calls attention to the striking parallelisms in inflorescence morphology between the two taxa, which otherwise differ markedly in habit—small holoparasitic herbs versus tall tropical forest trees.

Balanophoraceae are a morphologically distinctive group of holoparasitic angiosperms occurring in tropical and subtropical regions of the Old and New Worlds (Hooker 1856; Engler 1889; Harms 1935, Nevling 1960; Kuijt 1969; Hansen 1976, 1980; Nickrent 1997 onwards; Stevens 2001 onwards; Gonzáles 2004). They are obligate subterranean parasites, usually forming a tuberous attachment to host roots from which naked or bracteate inflorescence-bearing stems arise. By upward growth of the stem, the flowering portion is exposed at the soil surface or elevated on a fleshy, usually upright stalk, the plants at this stage often being described as “mushroom-like.” Inflorescences are variously shaped, forming a loose or compact (tightly branched) raceme in some genera and a flat-topped or club-shaped to spherical head in others (Kuijt 1969, p. 125). The flowers are unisexual, the plants being dioecious or monoecious with the two sexes, in the latter case, either mixed or in separate parts of the inflorescence (or on separate heads from the same tuber). Pistillate flowers, in particular, are often minute and extremely numerous, while the usually synangial anthers of staminate flowers take a great diversity of forms (Kuijt 1969, pp. 128, 130). A 3–6-lobed perianth is most often present in staminate flowers and may act as a protective covering over the anthers as the young inflorescence pushes through the soil. A different kind protection for such inflorescences, occurring, for example, in the New World genera *Helosis* and *Corynea*, is a complete covering of peltate bracts, fitting tightly edge-to-edge in a geometric pattern and giving the capitulum a somewhat pineapple-like appearance



FIGS. 1–5, *Trochanthera lepidota*. 1. Entire flowering head. Scale bar = 1.4 mm. 2. Group of stamens showing edges of connivent filaments (arrows). Scale bar = 150 μ m. 3. Stamens at base of head adjacent to minutely puberulent stem, showing perianth sheath surrounding the filament column (arrow). Scale bar = 180 μ m. 4. Portion of head showing peltate bracts (arrows) with anthers emerging between their margins. Scale bar = 360 μ m. 5. Pollen grains adjacent to anther. Scale bar = 50 μ m.

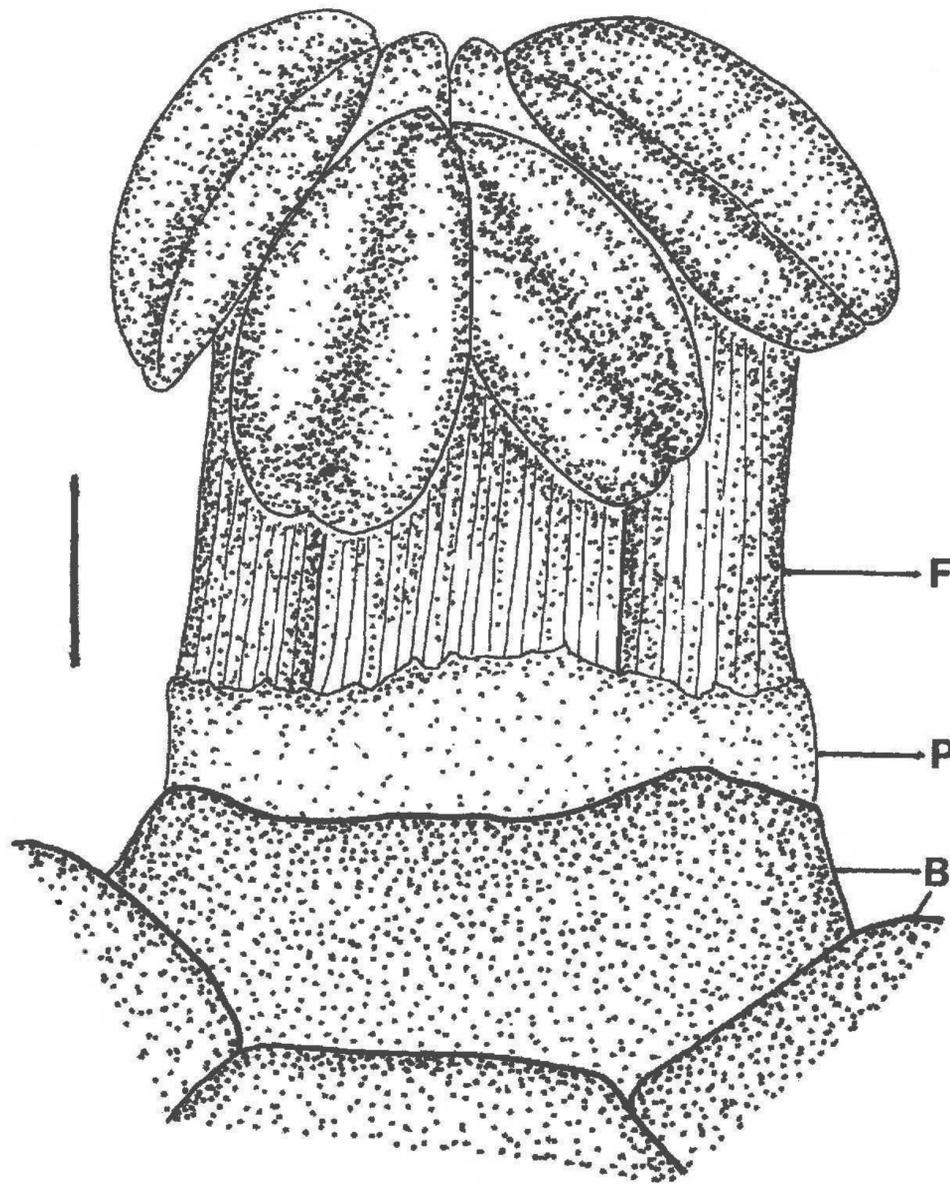


FIG. 6. *Trochanthera lepidota*. Individual flower showing dehiscent anther thecae, connivent filament column (F), delicate perianth sheath (P), and portions of peltate bracts (B). Scale bar = 130 μ m.

(Hooker 1856, pls. XIII, XV; Hansen 1980, fig. 11). The development and function of these bracts is well described by Hansen (1978). In the two genera mentioned above, the peltate bracts are deciduous following emergence of the capitulum, and the small staminate flowers then become evident as they emerge from a dense, mat-like covering of clavate hairs (Hooker 1856, pl. XIII). The tiny pistillate flowers remain embedded in these hairs with only the styles and stigmas exposed.

Trochanthera differs from the condition described for *Helosis* and *Corynea*, among others (see Hansen 1978, 1980), in that a covering of tight-fitting bracts persists at anthesis, and the staminate flowers force their way out between the connivent edges of the bracts (Figs. 1–4, 6). In the process, some flowers elongate farther than others, and occasional anthers are broken and left behind, as it were. It seems remarkable that the delicate tubular perianth (Figs. 3, 6) is also able to emerge, at least in some flowers, in the process of the staminal column forcing itself between the bracts. A similar system for the emergence of staminate flowers from between protective bracts occurs in the monoecious species *Balanophora wrightii*, illustrated by Nickrent (1997 onwards), but in it the male flowers are fewer on the head, they possess a broadly 3-lobed perianth, and the anthers form a synandrium with transverse dehiscence, as in some other *Balanophora* taxa. In his discussion of inflorescence structure in the related Asian *Balanophora* species *B. harlandii* and *B. wilderi*, Hansen (1978) refers to the clavate bracts covering the pistillate portion of the heads as “spadicles,” although this usage may be inappropriate (R.K. Eberwein pers. comm.). These intergrade with the broader sub-peltate type in the staminate part of the heads. We cannot be sure to what extent Hansen’s term spadicles applies to *Trochanthera*, and we prefer the term peltate bracts even though their 3-dimensional form cannot be determined from the fossil.

The stamens of Balanophoraceae are extremely diverse, especially in the construction of the anthers.

Anthers similar to those of *Trochanthera* are found in the South African genus *Mystropetalon*; that is, they are of an unspecialized, bithecal type, dehiscent extrorsely through two longitudinal slits. *Mystropetalon* happens also to be characterized by the putatively plesiomorphic trait of male and female flowers each with vestigial organs of the opposite sex (Nickrent et al. 2005; Kuijt 1969, p. 127), whereas pistillodes are not present in male flowers of *Trochanthera*. Compared with *Helosis* and *Corynea*, and with the Asian *Balanophora* taxa mentioned above (Hansen 1972), *Trochanthera*'s anthers are notably larger than in the 2 New World genera (see illustrations in Hooker 1856; Hansen 1980) and are extrorse rather than introrse (Figs. 1–4, 6). The anthers are not fused into a synandrium that releases pollen through horseshoe-shaped or transverse slits, pores, etc., as is common in *Balanophora* (Hansen 1972). The filaments of the fossil may be proximally fused, as in these other genera, but are only closely connivent distally (Figs. 2–4, 6).

The short, tubular, sheathing, unlobed perianth of *Trochanthera* most resembles that of *Corynea crassa* Hook. f. var. *crassa* (Hooker 1856, pl. XIII; Hansen 1980, fig. 11). On the other hand, a prominently 3-lobed type is characteristic of staminate flowers in *C. crassa* var. *sprucei* and also of *Helosis*, while in *Mystropetalon* and *Balanophora* species the perianth is well developed and 3–6-lobed. An unlobed, sheathing perianth is present in staminate flowers of the Asian *Rhopalocnemis* (Harms 1935, fig. 163), but its anthers form a single multichambered syngonium.

The stalk or stem of *Trochanthera* is leafless, at least distally (Fig. 1). This is comparable to various genera of Balanophoraceae (Hooker 1856; Kuijt 1969; Hansen 1980; Nickrent 1997 onwards). More or less bracteate stems are also common in the family.

A remarkably similar form of staminate inflorescence to the above occurs in the *Brosimum* alliance of Moraceae, tribe Dorstenieae (Berg 1989; Rohwer 1993; Datwyler & Weiblen 2004; Zerega et al. 2005; formerly Brosimeae of Engler 1889; Hutchinson 1967; Berg 1972). Congested, often globose flowering heads are frequent in Moraceae, as for example the members of tribes Castilleae (Olmedieae) and Dorstenieae (Brosimeae) described and illustrated by Berg (1972). Heads may be bisexual (one or more pistillate flowers mixed with the staminate ones) or unisexual (staminate or pistillate only, Berg 1989, fig. 11.3). These are borne on short, axillary peduncles, one to several per node (Woodson 1960; Berg 1972) and are in the same size range as *Trochanthera*. Because of the covering of peltate bracts in *Trochanthera*, between which the staminate flowers emerge, the most promising comparisons are with similarly bracteate *Brosimum* species. Other genera having small, globose heads of male flowers, such as *Coussapoa* (Woodson 1960, now in family Cecropiaceae; Rohwer 1993; Datwyler & Weiblen 2004), *Helicostylis* of tribe Dorstenieae (Olmedieae of Berg 1972), or *Poulsenia* (Woodson 1960, assignable to tribe Castilleae per Datwyler & Weiblen 2004) lack peltate bracts and have flowers with a 3–4-parted perianth and stamens either free and more numerous or 1–2 and often connate.

The *Trochanthera* inflorescence appears completely staminate, whereas species of *Brosimum* often, but not always, have bisexual heads with a single, deeply embedded pistillate flower accompanying numerous staminate ones. However, the style of this female flower may wither early, and the head may then appear staminate. Woodson (1960, p. 130) quotes Standley as to the difficulty of finding “with ordinary herbarium specimens...even one pistillate flower.” We could not find an exposed style in the fossil.

Flowers with 2–4 stamens occur in *Brosimum* species of section *Brosimopsis* (genus *Brosimopsis* of Hutchinson 1967, p. 172), but a well developed, 4-lobed, pubescent perianth is present, and stamens are clearly separate with slender filaments (Berg 1972, p. 178). In section *Piratinera* (Berg 1972, p. 181) a perianth is absent in the staminate flowers and may be replaced by an enclosing bract (e.g., *B. gaudichaudii*, p. 185). However, there is only 1 stamen, which has a broad anther connective unlike *Trochanthera*. Other *Brosimum* species with a reduced or absent perianth and only 1 stamen are found in section *Brosimum* (Berg 1972, p. 169); they differ from *Trochanthera* in having either a peltate anther (*B. alicastrum*) or a tiny one only 0.2 mm in length and breadth (*B. acutifolium*). The peltate bracts of these and other *Brosimum* taxa differ from *Trochanthera* in being circular in outline, rather than closely connivent and more or less hexagonal (Woodson 1960, pp 131–133; Berg 1972, figs. 62, 66, 71, 73). In *Brosimum* subgenus *Ferolia* (Berg 1972, p. 188) the

stamens, if more than 1, are divergent with slender filaments. The sheathing perianth, if present, is minutely ciliate apically. The peltate bracts are usually puberulent. The stamen, if 1, usually has the anther bent at 90°, with a thickened connective (all data from Berg 1972). In this comparison, therefore, the fossil cannot be accommodated in the genus *Brosimum*, and its description as a separate taxon is supported.

Recognition of *Trochanthera* as a distinct genus will assist in future comparison of this unique fossil with extant members of Balanophoraceae and Moraceae, both of which are diverse in floral morphology and inflorescence structure. In Balanophoraceae, we prefer not to assign the plant to a variable modern genus like *Balanophora* (Hansen 1972), since taxonomic circumscriptions may change in the future, especially when DNA methods are applied to the family. A principal authority on the family, Bertel Hansen, was admittedly conservative in his taxonomic approach (Friis 2006), and he merged 9 later synonyms into the single genus *Balanophora*. Additionally, other generic unions have recently been proposed (Eberwein & Weber 2004), which strengthen Old and New World taxonomic affinities in the family. Further, when comparing *Trochanthera* with representatives of Moraceae, it is again unclear that a close relationship exists between it and particular modern genera, including *Brosimum* and allied taxa.

Molecular studies of the phylogenetic relationships of parasitic angiosperm families have advanced rapidly in recent years (summarized in Barkman et al. 2007). Based on such work, the Balanophoraceae have been firmly assigned to order Santalales (Nickrent & Franchina 1990; Nickrent 1997 onwards; Stevens 2001 onwards), but their exact position was uncertain until the work of Nickrent et al. (2005). Based on 4 loci from the plastid, nuclear, and mitochondrial genomes, this study clearly placed 3 selected members of this family within a clade containing 3 genera representative of Santalaceae, Olacaceae, and Loranthaceae.

Knowledge of the relationships of Moraceae with allied families, and of generic groups within the family, has been clarified by recent molecular studies (Sytsma et al. 2002; Datwyler & Weiblen 2004; Zerega et al. 2005). Changes in the familial and tribal assignments of certain genera mentioned above are based on Datwyler and Weiblen (2004) and Zerega et al. (2005). The latter paper involved a combined phylogenetic analysis of 26S and *ndhF* gene sequences and included proposals for phylogeography and divergence times of the higher taxa. For Moraceae tribe Dorstenieae, a stem group age of 48 mybp was estimated, while for *Brosimum* and its 2 closest relatives, the crown group age was placed at 28 mybp. Because the family placement of *Trochanthera* is uncertain, and our analysis may not have exhausted all possibilities, we can only point out that the fossil falls within an age of interest for presumed evolutionary diversification in both of the families discussed above. Morphological parallelisms abound in the angiosperms, and in this case, a similar form of inflorescence in quite different families prevents us from proposing a more exact assignment for this distinctive Tertiary fossil.

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REFERENCES

- BARKMAN, T.J., J.R. McNEAL, S-H. LIM, G. COAT, H.B. CROOM, N.D. YOUNG, AND C.W. DEPAMPHILIS. 2007. Mitochondrial DNA suggests at least 11 origins of parasitism in angiosperms and reveals genomic chimerism in parasitic plants. *BMC Evol. Biol.* 7:248.
- BERG, C.C. 1972. Olmedieae, Brosimeae (Moraceae). *Fl. Neotropica* 7:1–228.
- BERG, C.C. 1989. Systematics and phylogeny of the Urticales. In: P.R. Crane and S. Blackmore, eds. *Evolution, systematics and fossil history of the Hamamelidae*. Vol. 2. Clarendon Press, Oxford. Pp. 193–220.
- DATWYLER, S.L. AND G.D. WEIBLEN. 2004. On the origin of the fig: phylogenetic relationships of Moraceae from *ndhF* sequences. *Amer. J. Bot.* 91:767–777.

- DRAPER, G., P. MANN, AND J.F. LEWIS. 1994. Hispaniola. In: S. Donovan and T.A. Jackson, eds. Caribbean geology: an introduction. The University of the West Indies Publishers' Association, Kingston, Jamaica. Pp. 129–150.
- EBERWEIN, R.K. AND A. WEBER. 2004. *Exorhopala ruficeps* (Balanophoraceae): morphology and transfer to *Helosis*. Bot. J. Linn. Soc. 146:513–517.
- ENGLER, A. 1889. Balanophoraceae. In: A. Engler and K. Prantl, eds. Die Natürlichen Pflanzenfamilien III. 1. Verlag Wilhelm Engelmann, Leipzig. Pp. 243–263.
- ENGLER, A. 1894. Moraceae. In: A. Engler and K. Prantl, eds. Die Natürlichen Pflanzenfamilien III. 1. Verlag Wilhelm Engelmann, Leipzig. Pp. 66–98.
- FRIIS, I. 2006. Bertel Hansen (1932–2005). Taxon 55:1055–1056.
- GONZÁLEZ, F. 2004. Balanophoraceae. In: N. Smith, S.I. Mori, A. Henderson, D.W. Stevenson, and S.V. Heald, eds. Flowering plants of the Neotropics. Princeton University Press, Princeton, NJ. Pp. 41–43.
- HANSEN, B. 1972. The genus *Balanophora* J.R. and G. Forster. A taxonomic monograph. Dansk Bot. Arkiv. 28: 1–188.
- HANSEN, B. 1976. Balanophoraceae. Fl. Malesiana 7:783–805.
- HANSEN, B. 1980. Balanophoraceae. Fl. Neotropica 23:1–80.
- HANSEN, B. AND K. ENGELL. 1978. Inflorescences in Balanophoroideae, Lophophytoideae and Scybalioideae (Balanophoraceae). Bot. Tidsskr. 72:177–187.
- HARMS, H. 1935. Balanophoraceae. In: A. Engler and H. Harms, eds. Die Natürlichen Pflanzenfamilien 16b. Verlag Wilhelm Engelmann, Leipzig, pp. 296–339.
- HOOKE, J.D. 1856. On the structure and affinities of Balanophoreae. Trans. Linn. Soc. London 22:1–68.
- HUTCHINSON, J. 1967. The genera of flowering plants (Angiospermae). Clarendon Press, Oxford.
- ITURRALDE-VINCENT, M.A. AND R.D.E. MACPHEE. 1996. Age and paleogeographic origin of Dominican amber. Science 273:1850–1852.
- KUIJT, J. 1969. The biology of parasitic flowering plants. University of California Press, Berkeley.
- NEVLING, L.I. 1960. Flora of Panama: Balanophoraceae. Ann. Missouri Bot. Gard. 47:303–308.
- NICKRENT, D.I. 1997 onwards. The parasitic plant connection. <www.parasiticplants.siu.edu>
- NICKRENT, D.I. AND C.R. FRANCHINA. 1990. Phylogenetic relationships of the Santalales and relatives. J. Molec. Evol. 31:294–301.
- NICKRENT, D.I., J.P. DER, AND F.E. ANDERSON. 2005. Discovery of the photosynthetic relatives of the “Maltese mushroom” *Cynomorium*. BMC Evol. Biol. 5:38
- POINAR, JR., G.O. 1992. Life in amber. Stanford University Press, Stanford.
- POINAR, JR., G.O. AND R. POINAR. 1999. The amber forest. Princeton University Press, Princeton, NJ.
- ROHWER, J.G. 1993. Moraceae. In: K. Kubitzki, J.G. Rohwer, and V. Bittrich, eds. The families and genera of vascular plants. Springer-Verlag, Berlin. Pp. 438–453.
- SCHLEE, D. 1999. Das Bernstein-Kabinett. Stuttgarter Beitr. Naturk., Ser. C, 28.
- STEVENS, P.F. 2001 onwards. Angiosperm Phylogeny Website. Version 8, June 2007 [and more or less continuously updated since]. <http://www.mobot.org/MOBOT/research/APweb>
- SYTSMA, K.J., J. MORAWETZ, J.C. PIRES, M. NEPOKROEFF, E. CONTI, M. ZJHRA, J.C. HALL, AND M.W. CHASE. 2002. Urticalean rosids: circumscription, rosid ancestry, and phylogenetics based on *rbcl*, *trnL-F*, and *ndhF* sequences. Amer. J. Bot. 89:1531–1546.
- WOODSON, R.E. 1960. Flora of Panama. Moraceae. Ann. Missouri Bot. Gard. 47:114–178.
- ZEREGA, N.J.C., W.L. CLEMENT, S.L. DATWYLER, AND G.D. WEIBLEN. 2005. Biogeography and divergence times in the mulberry family (Moraceae). Molec. Phylogen. Evol. 37:402–416.