Comparative Wood Anatomy of *Ruptiliocarpon caracolito* (Lepidobotryaceae)

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ABSTRACT. Wood anatomy of *Ruptiliocarpon caracolito* is described and compared in general to Sapindales, and specifically to *Trichilia* (Meliaceae) and the monotypic, African *Lepidobotrys* (Lepidobotryaceae). It is aberrant in all groups compared for having vestured pits. Otherwise, it is most similar to both *Trichilia* and *Lepidobotrys*. Wood anatomy does not conflict with the recognition of *Ruptiliocarpon* as a second genus of Lepidobotryaceae; however, the question of affinities of that family needs further investigation.

Analysis of wood anatomy is often crucial for the elucidation of relationships of taxa problematic at the generic or higher levels (cf. Hayden & Brandt, 1984; Mennega, 1984; Pennington & Styles, 1975). During the course of an investigation (Hammel & Zamora, 1993) into the affinities of a Costa Rican tree that could not be placed to family, an analysis of its wood anatomy became essential.

MATERIALS AND METHODS

Microtome sections and macerations of wood of *Ruptiliocarpon caracolito* Hammel & N. Zamora from the trunk (*Hammel & Chavarría 17965*, bole ca. 17 cm diam.; MO) and from a branch (*Hammel 17983*, 4.5 cm diam.; MO) both from near Rincón de Osa on the Osa Peninsula of Costa Rica, of *Lepidobotrys staudtii* Engler (*Breteler 2087*, Cameroon near village Zendé, tree 15 m; Uw, WAGw), and of *Trichilia lepidota* C. Martius subsp. *leucastera* (Sandwith) Pennington (*Maas 10841*, Suriname, Maratakka, tree 13 cm diam.; Uw) were prepared according to standard methods (Mennega, 1982). Descriptions, counts, and measurements follow recommendations of the International Association of Wood Anatomists Committee (IAWA, 1989).

WOOD ANATOMY OF *RUPTILIOCARPON CARACOLITO*

GENERAL ASPECT

A straight-grained wood apparently without differentiation in sapwood and heartwood, color uniformly light, pinkish cream; moderately light, volume weight ca. 0.40.

MICROSCOPIC CHARACTERS (FIG. 1)

Growth rings faint, formed by a narrow zone of flattened fibers and occasionally by a 1- or 2-celled band of parenchyma. *Vessels* solitary for about 45%, the remainder in radial multiples of 2 or 3(–8) and a few clusters, the latter mainly on the border of the growth ring; number 5(0–12) per sq. mm, distribution somewhat irregular; perforations simple, perforation plates oblique; cross section oval to round, diameter (70–)100–140 μm, average vessel member length 860(600–1,300) μm, mostly with long, narrow tails; intervascular pits alternate, crowded, vestured, diameter 5–6.5 μm, the slits enclosed or locally confluent; vessel/ray pitting similar; resinous contents occasionally present. *Fibers* regularly distributed, angular in cross section, thin-walled, diameter 22–28 μm, the walls 2.5–3.5 μm wide; nonseptate; minute bordered pits restricted to the radial walls; length 1,000(750–1,290) μm. Fiber/vessel ratio 1.16. *Rays* uniseriate, homogeneous or nearly so, cells procumbent, except for a marginal row of slightly higher and shorter cells, which resemble square cells; number 5–7 per mm; width 15 μm, height 130–500 μm, up to 21 cells high; no contents. *Parenchyma* as scattered strands and in fine, often interrupted, rather straight bands 1 or 2 cells wide, also paratracheal, narrow vasicentric, occasionally aliform; terminal parenchyma as a band 1 or 2(–4) cells wide. Number of bands 6–8 per mm; strands of (2–)4–8 cells. Rhombic crystals numerous in subdivided cells of the isolated strands.

DISCUSSION

Preliminary analysis of wood samples of *Ruptiliocarpon* suggested a relationship to Meliaceae by way of a very close match to the genus *Trichilia*. This was in agreement with Hammel and Zamora's independent conclusion that *Ruptiliocarpon* seemed to belong to Sapindales. Although they found that

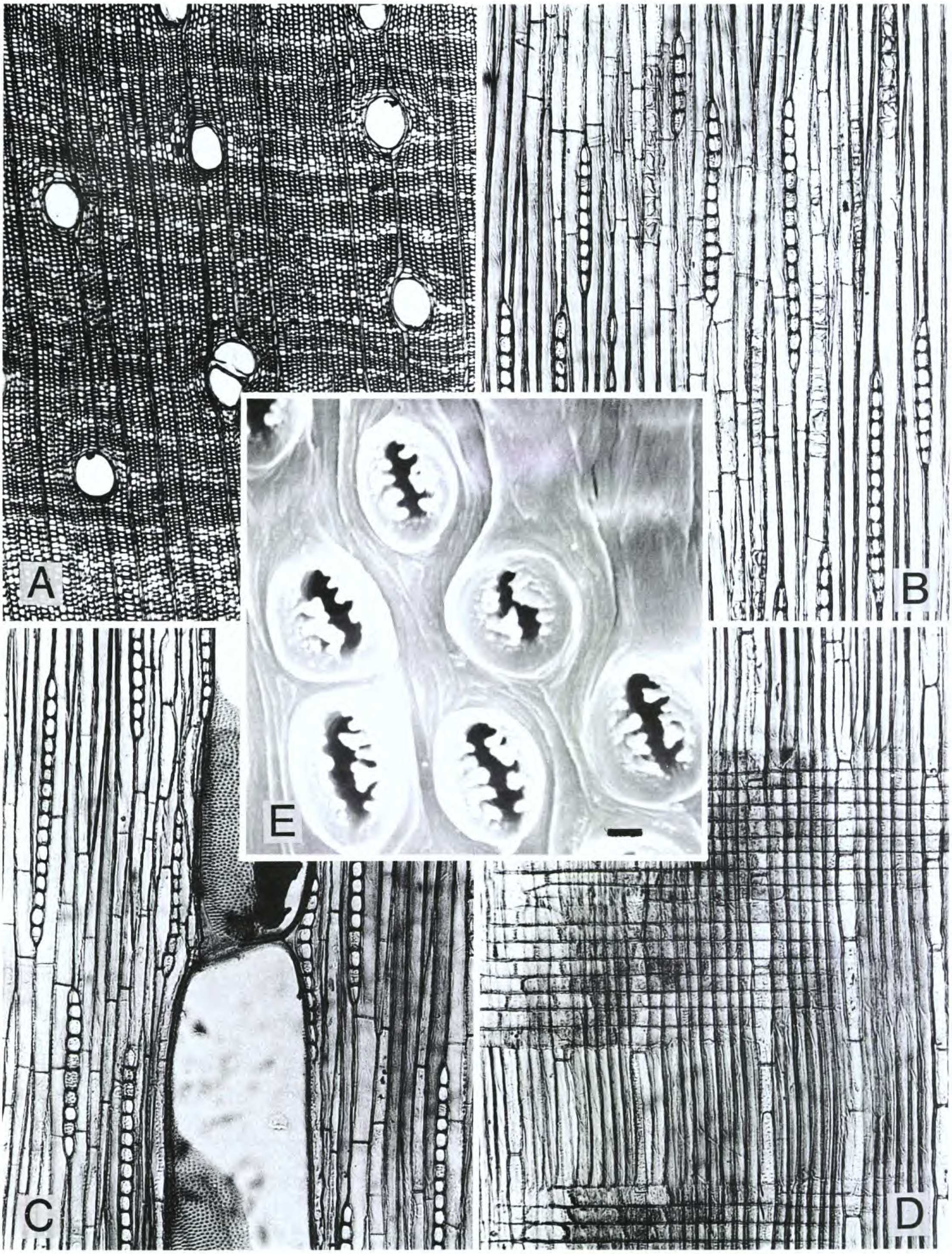

Figure 1. *Ruptiliocarpon caracolito* Hammel & N. Zamora. —A. Transverse section, ×45. Vessel and parenchyma distribution. —B. Tangential longitudinal section, ×112. Uniseriate rays and parenchyma strands, partly with crystals. —C. Tangential longitudinal section, ×112. A vessel member with a lump of gum. —D. Radial longitudinal section, ×112. Homogeneous to weakly heterogeneous rays. All from *Hammel & Chavarría 17965.* —E. Vestured intervascular pitting; *Hammel 17983.*

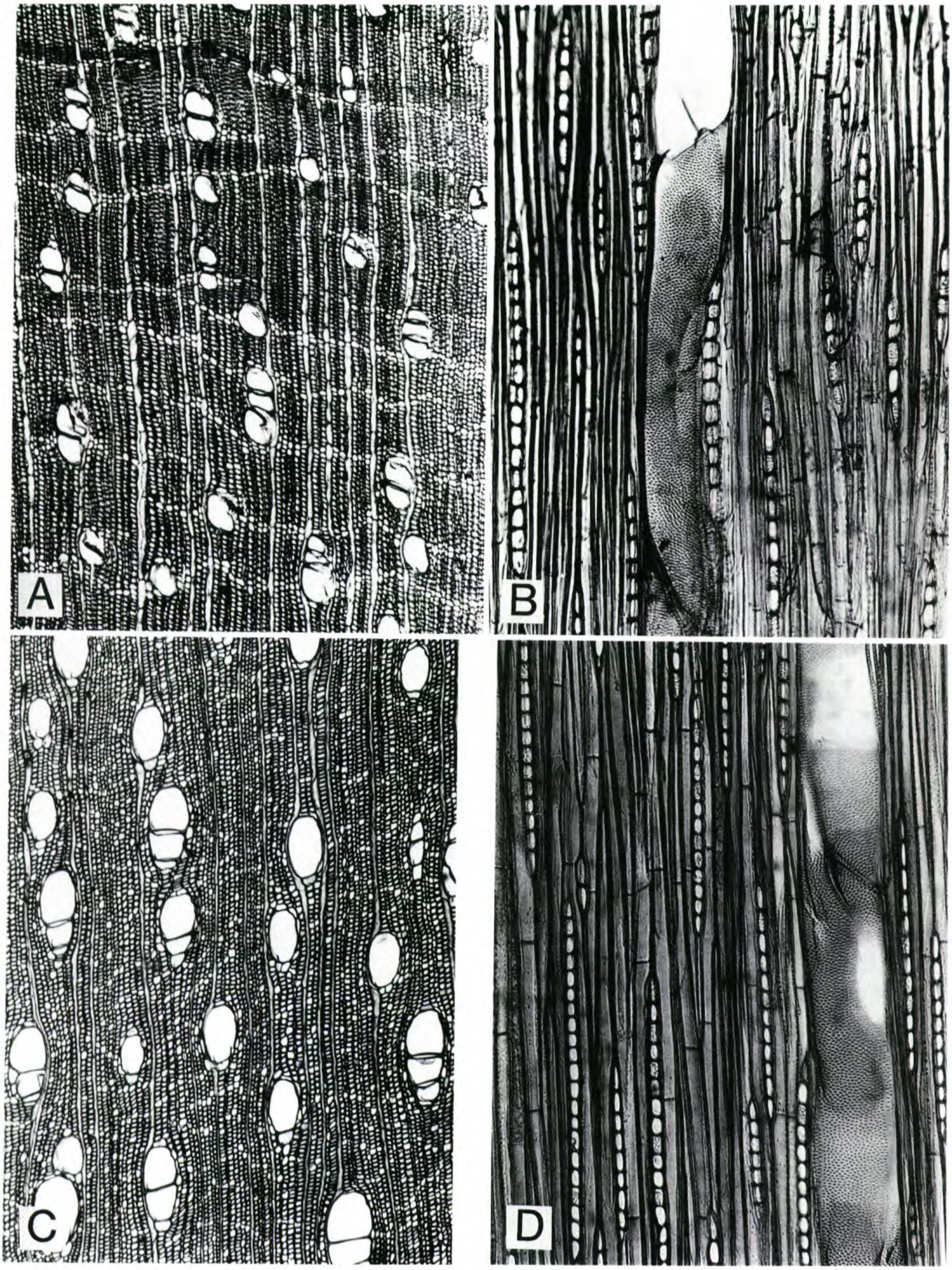

Figure 2. A, B. *Trichilia lepidota* C. Martius subsp. *leucastera* (Sandwith) Pennington. —A. Transverse section, ×45. Vessel and parenchyma distribution. —B. Tangential longitudinal section, ×112. Intervascular pitting and uniseriate rays. Both from *Maas 10841*. C, D. *Lepidobotrys staudtii* Engler. —C. Transverse section, ×47. Vessel and parenchyma distribution. —D. Tangential longitudinal section, × 120. Uniseriate rays, intervascular pitting, crystal-bearing parenchyma strand (left side). Both from *Breteler 2087*.

certain features of the fruits of Burseraceae resemble those of *Ruptiliocarpon*, vessels with large pits, septate fibers, and scarce parenchyma are salient features of Burseraceae that characterize their difference from *Ruptiliocarpon* and eliminate that family from consideration as a close relative. Three Sapindalean families, Sapindaceae, Hippocastanaceae, and Meliaceae, have members with wood that superficially resembles that of *Ruptiliocarpon*. In Sapindaceae, which like Meliaceae has great diversity in wood structure, the genus *Talisia* shows a remarkable similarity to *Trichilia* (Mennega, 1972) and therefore with *Ruptiliocarpon* (see below). The main difference is the occurrence of septate fibers in *Talisia*, in particular in the species with thin-walled fibers. *Billia* (Hippocastanaceae) is comparable to *Ruptiliocarpon* but here more numerous dissimilarities occur; these include a different parenchyma distribution with mainly rather wide conspicuous terminal bands and hardly any diffuse strands, random occurrence of septate fibers, and shorter vessel members.

Among Sapindales, the closest match to *Ruptiliocarpon* is *Trichilia* of the Meliaceae. Superficial examination of the branch sample suggested a similarity to *Trichilia* (Fig. 2A, B), and that impression was confirmed in detail on closer study of cross sections. Wood characteristics of *Ruptiliocarpon* such as nonseptate fibers, small intervascular pits, uniseriate wood rays that are weakly heterogeneous and not over 20 cells high, parenchyma in narrow wavy bands and partly aliform-confluent, several strands with rhombic crystals, and normal strands of 4–8 cells are features present in *Trichilia* according to older and more recent literature (e.g., Pennington & Styles, 1975). In a study of wood samples from the Guianas, Klaassen (1988) confirmed the above features for nine species of *Trichilia* and also recorded a vessel member length of 550–760 μm, fiber length of 870–1,300 μm, very similar to those for *Ruptiliocarpon*.

One important feature, vesturement of the vessel pits, that was discovered later in this analysis and reconfirmed with SEM (Fig. 1E) does not coincide with *Trichilia* or with any other Meliaceae (Kribs, 1930; Record & Hess, 1943; Metcalfe & Chalk, 1950). A reference in Metcalfe & Chalk (1983) to a report of vestured pits in Meliaceae is an error; the original paper (Kanazawa, 1968) does not make that claim. It is remarkable, here, that just as overall vegetative appearances of *Ruptiliocarpon* suggest Leguminosae (see discussion in Hammel & Zamora, 1993), many of the wood characters, including vestured pits, are also in accordance with that family. In fact, in Record's (1944) key one is led to a choice between *Trichilia* with vascular pits less than 4 μm wide and Leguminosae with pits more than 4 μm; *Ruptiliocarpon*, with pits 5–6.5 μm in diameter, should key to Leguminosae. On the other hand, vessel members in legumes are seldom over 500 μm (Baretta-Kuipers, 1981; Metcalfe & Chalk, 1950; Reinders-Gouwentak & Rijsdijk, 1968), whereas in *Ruptiliocarpon* the length ranges from 600 to 1,300 μm. In any case, floral and fruit characters of *Ruptiliocarpon* must eliminate Leguminosae from consideration (Hammel & Zamora, 1993; Tobe & Hammel, 1993).

Ruptiliocarpon differs from *Trichilia* on the basis of wood anatomy primarily because of the vesturing of the vascular pits, a feature not reported for Meliaceae (nor any other Sapindales). Presence or absence of this feature has long been considered constant for a given family or genus. The few exceptions include the tribe Bauhinieae in Leguminosae, which lacks vestured pits, otherwise present in the family; *Bridelia*, the only Euphorbiaceae with vestured pits (Mennega, 1987); and certain species of *Prunus* from China (Zhang & Baas, 1992), a genus that otherwise lacks vestured pits. It may be that the exceptions are too many and that we should no longer attribute such great value to this feature as a condition *sine qua non* in assigning a given taxon to a family or genus, but it does add, importantly, to the list of characters suggesting that *Ruptiliocarpon* does not belong in *Trichilia* or even in Meliaceae.

On the eve of describing *Ruptiliocarpon* as a monotypic genus in its own family within Sapindales, congruence in a majority of vegetative, floral, and fruit characters with *Lepidobotrys*, an African monotypic genus in its own family, was discovered (Hammel & Zamora, 1993; Hammel, pers. comm.). Examination of wood of *Lepidobotrys staudtii* Engler (Fig. 2C, D) also revealed a close conformity to the wood of *Ruptiliocarpon*. Apart from the absence of vestured pits in *Lepidobotrys*, the main difference is found in the more diffuse parenchyma in the latter species. In wood anatomy *Trichilia* and *Lepidobotrys* appear to differ and agree with *Ruptiliocarpon* in similar ways, but the preponderance of other evidence favors a relationship with *Lepidobotrys* (Hammel & Zamora, 1993). The question of where the affinities of Lepidobotryaceae (*Lepidobotrys* and *Ruptiliocarpon*) lie remains open. The historical alignment of Lepidobotryaceae in the Linaceae complex or in Oxalidaceae was discussed by Van Welzen & Baas (1984) based on a leaf anatomical study. Since leaf anatomy proved neutral with respect to the question, they saw no reason to differ from the generally accepted preference for its placement in Oxalidaceae. However, the wood structure of *Lepidobotrys*, poorly known at the time Van Welzen & Baas published their analysis (cf. Metcalfe & Chalk, 1950: 272), is in several respects entirely different from that of *Averrhoa*, one of the few woody members of Oxalidaceae. The Linaceae complex comprises several mainly woody families with a rather great diversity of structure. From literature and personal knowledge of the wood structure of genera belonging to these families, a close relationship of Lepidobotryaceae with that complex seems improbable. For a well-founded statement, comparative research of a much broader scope than this paper would be necessary. The present study, along with accumulated knowledge (cf. Mennega, 1987), suggests that a relationship to the Sapindales or to Euphorbiaceae, as proposed by Hammel & Zamora (1993), should also be considered. Wood anatomy alone does not support or eliminate the possibility that Lepidobotryaceae may lie close to Euphorbiaceae. Although most of the wood anatomical characters present in Lepidobotryaceae are manifested among the genera of Euphorbiaceae in subfamily Phyllanthoideae, they are not found together in any one genus. Also, rays in Phyllanthoideae woods are decidedly heterogeneous, whereas those of Lepidobotryaceae are homogeneous or nearly so.

Acknowledgments. It was a great pleasure to have the opportunity to discuss the problematic wood of *Ruptiliocarpon* with Regis B. Miller during his recent brief visit to Utrecht. I am also greatly indebted to him for the kind offer to have the SEM photographs made in Madison at the U.S. Forestry Products Laboratory. I thank my colleagues J. Koek-Noorman, L. Y. Th. Westra and B. J. H. ter Welle for critical remarks and for technical advice and assistance. Thanks are also due to B. Hammel for his much appreciated suggestions for textual improvements. To D. Makhan I am indebted for the preparation of slides.

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