
Ruptiliocarpon (Lepidobotryaceae): A New Arborescent Genus and Tropical American Link to Africa, with a Reconsideration of the Family¹

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ABSTRACT. A new genus and species of trees from Costa Rica and northern South America, *Ruptiliocarpon caracolito*, is described and compared to the African *Lepidobotrys*. It is distinguished from *Lepidobotrys* primarily by its much shorter filaments, basifixed rather than versatile anthers, its lack of styles, its two-rather than three-locular ovary, and by its irregularly dehiscent fruits with a woody exocarp and cartilaginous endocarp. In wood anatomy, apart from the presence of vestured pits in *Ruptiliocarpon*, the two genera are remarkably similar. They match in important floral and fruit characteristics (dioecious; 5 + 5 stamens of unequal length with filaments fused at base; two apical, collateral ovules per locule; one-seeded fruit; black seed with a large red aril and no endosperm), and both have unifoliate leaves with very fugaceous stipules and stipels, and leaf-opposed inflorescences. The familial placement of *Lepidobotrys* has been controversial: the genus was placed first in the Linaceae by Engler, then in the Oxalidaceae by Hallier, then in its own family (between Linaceae and Erythroxylaceae) by Léonard, and then again in the Oxalidaceae by Cronquist. Reviewing evidence, old and new, we maintain *Ruptiliocarpon* and *Lepidobotrys* (only) in the Lepidobotryaceae and suggest that they relate more to Sapindales or possibly Euphorbiaceae than to Oxalidaceae.

Populations of Cedro caracolito, a local name for the new taxon described below, lay hidden and protected in Costa Rica's Osa Peninsula until recently built roads exposed the area to easy access for botanical exploration and the process of deforestation.

There, caracolito is a large, locally common tree with light wood having good qualities for cabinet work, but it is not generally known or sought by wood harvesters. Ongoing investigations of bark extract show that it has promise as a biocide (natural-product agricultural pesticide, Arnason, pers. comm.). Several earlier collections of *Ruptiliocarpon* from South America (most of them filed among the Fabaceae) have come to light since its discovery in Costa Rica. Study of the flowers led us to search among the Sapindales (Cronquist, 1981) and, following submission of an earlier draft of this paper, we distributed numerous Costa Rican collections (including the type) with the new name but placed in Meliaceae. Bringing together information on wood anatomy, floral anatomy, embryology, and pollen morphology, we were later convinced to describe it as a new family. Finally, we saw it to its proper home as a distinct new genus of the hitherto monotypic Lepidobotryaceae, itself of controversial relationships. The novelty, problematic placement, and economic potential of *Ruptiliocarpon* underscore the urgency of continued exploration, study, and protection of tropical floras.

Ruptiliocarpon caracolito Hammel & N. Zamora, gen. et sp. nov. TYPE: Costa Rica. Limón: Cordillera de Talamanca, Cantón de Matina, cuenca media del Río Barbilla, margen izquierda, sendero entre Cerro Amú siguiendo la fila hacia el este hasta estribaciones del Cerro Tigre, 200 m, 9 Nov. 1988 (fr), Herrera & Martínez 2310 (holotype, CR; isotypes, AAU, BM, CAS, COL, DUKE, F, G, GB, K, KYO, LE, MEXU, MICH, MO, NY, PMA, QCA, QCNE, RSA, S, TEX, UC, US, USJ, VEN, WIS).

Lepidobotrys similis sed inflorescentiis et floribus masculinis femineis similibus, antheris basifixis antiseptis ses-

¹The usual editorial policy of *Novon* only to allow papers that present new taxa has been relaxed for the two following papers (Mennega, Tobe & Hammel); each was written in concert with and designed to be published with the core paper in which a new genus is described.

silibus, antipetalis in filamentis parvis, ovario biloculari, stylis quasi nullis, stigmatibus 2, capsulis exocarpio lignoso ruptili differt.

Dioecious, evergreen trees 20–30(–40) m tall, (20–)50–90 cm DBH; bole straight, smooth and branch-free for the lower ca. 15 m, light gray with large scattered lighter and darker patches; bark with very shallow, narrowly lanceolate, longitudinal fissures, bitter; wood pinkish white, porous and lightweight. Leaves unifoliolate; leaflets elliptic, (5–)6.5–16 cm long, (2.7–)4–7.5 cm wide, entire, without pellucid lines or dots, without obvious fragrance, chartaceous, sparsely appressed-pubescent at the base with small simple trichomes, obtuse at the base, the apex acute to acuminate, the acumen ca. 1 cm long; lateral veins 5–7 pairs; reticulate venation obvious on the lower leaf surface; petiolule pulvinate (thickened) for its entire length, 2–4 mm long with a distinct articulation at juncture with petiole and on emerging leaves, subtended by a slender clasping, deciduous stipel 4–5 mm long; petiole (0.4–)0.6–1.5 cm long, pulvinate at the base; stipules paired, ensiform, 1–1.5 mm long, soon deciduous, visible on emerging leaves and leaving minute, scarcely visible scars on the twigs. Inflorescence a lax, mostly leaf-opposed (terminal) panicle of spikes; peduncle 1–2 cm long; 1–3(–4) branches 2.3–8(–10) cm long, each with a small bracteole at the base; rachis puberulous. Flowers cryptically unisexual (the staminate with pistil but only rudimentary ovules, the pistillate with stamens but no pollen), globose to ovoid, 4–4.5 mm long, 3.5–4 mm wide, at anthesis opening only slightly, green, subtended by 3 rounded, abaxially sparsely puberulous, ciliate bracts 0.5–0.8 mm long; sepals 5, free, imbricate, ciliate, 1.6–2 mm long and wide; petals 5, free, imbricate, apically ciliate, 3–4 mm long, 2.5 mm wide. Stamens ca. 3 mm long (including filament tube), slightly shorter in female flowers than in male; filaments fused into a tube/nectary ca. 0.5 mm long; anthers 10, narrowly cordate, ca. 1(–1.2) mm long, inserted in 2 alternating series, the antipetalous at apex of filaments (ca. 0.5 mm long), the antisepalous \pm sessile on the margin of the tube, rarely with a small, simple appendage produced on the margin of the tube between the anthers; connective produced to form a small pubescent appendage. Pollen tricolporate with no thickenings at apertures, subspheroidal, 10.5–15 μ m (polar axis) \times 11–16 μ m (equatorial axis); exine variable (di- or polymorphous?), psilate or verrucate to fossulate/foveolate; amb triangular; colpi rather short with thin costae ca. 0.8–1.0 μ m thick; pores sometimes slightly protruding, elongated along polar axis, ca. 2.5–4.0 μ m; exine

0.8–1.0 μ m thick, tectate, columellae hardly visible. Intrastaminal or gynophoreal nectary lacking. Ovary \pm ovoid, ca. 1.5–4 mm, smaller in the male flowers than in the female, glabrous, 2-locular; each locule with 2 collateral ovules, pendulous from near the summit of the partition; obturator from funicular tissue present. Style essentially lacking, the summit of the ovary \pm directly produced into an obscurely 2-lobed stigma. Fruit an ovoid 1(rarely 2)-seeded capsule, 2.5–3.5 cm long, 1.5–2.5 cm wide; exocarp coriaceous to woody, irregularly rupturing and falling away to expose 2 horny endocarps, one nearly completely surrounding the seed, the other usually empty and smaller, these also falling away, the larger taking on the shape of a snail shell. Seed globose, shiny black, $\frac{1}{3}$ covered with a red-orange aril, pendulous (by the aril) at the end of a coriaceous strip (the partition) attached to the pedicel. Figures 1–3.

Paratypes. COSTA RICA. **Puntarenas:** Cantón de Golfito, steep forested slopes above Golfito Airstrip, 1–200 m, 19 Jan. 1984 (st), *Pennington et al. 11398* (CR); Reserva Nacional de Vida Silvestre Golfito, en fila entre Golfito y Villa Briceño, 200 m, 27 Jan. 1992 (fr), *U. Chavarría et al. 511* (CR, F, MO); Cantón de Osa, Reserva Forestal Golfo Dulce, entre Chacarita & Rincón, ca. 15 km de Chacarita, Alto los Mogos, 100 m, 27 Mar. 1991 (fl), *Aguilar & Hammel 101* (AAU, BM, CAS, COL, CR, DUKE, F, G, GB, K, KYO, LE, MEXU, MICH, MO, NY, PMA, QCA, QCNE, RSA, S, TEX, UC, US, USJ, VEN, WIS); ca. 4 km de Rincón, 230 m, 9 Nov. 1990 (st), *Hammel & M. M. Chavarría 17965* (CR, MO); antiguo campo de aterrizaje de Rincón, en fila al N de la Estación Agua Buena de Boscosa, 300 m, 28 Nov. 1990 (fr), *Hammel 17983* (CAS, CR, F, MO, NY, K, US, USJ, WIS); entre Rancho Quemado—por camino nuevo—y Drake, 50 m, 29 Mar. 1991 (imm fr), *Aguilar et al. 103* (CR, F, MO); 300 m, 20 Mar. 1991 (fl), *Hammel et al. 18154* (CR, F, MO); 300 m, 17 June 1990 (fr), *Herrera 4198* (CR, F, MO); 21 Mar. 1989 (fl), *Jiménez et al. 672* (CR); Fila Ganado, between Rancho Quemado—along old road—and Drake, 400 m, 5 June 1988 (fr), *Hammel et al. 17034* (CR, F, MO); entre Rancho Quemado—por camino nuevo de madereros—y Guerra, 300 m, 28 Mar. 1991 (fl), *Hammel et al. 18166* (CR, F, MO); Finca de Juan Marín, cerca a Guerra, 250 m, 6 Aug. 1991 (fr), *Marín 87* (CR, MO); Reserva Indígena Guaymí, ca. 2 km noreste de la unión del Río Pavón con Río Rincón, 100 m, 20 Oct. 1990 (fr), *Hammel et al. 17911* (CR, F, MO); San Pedrillo, Playa Campanario, 10 m, 27 Mar. 1991 (fl), *Harmon 210* (CR, F, MO). COLOMBIA. **Valle:** Bajo Calima, 15 km N of Buenaventura, 50 m, 26 Mar. 1986 (fr), *Gentry et al. 53632* (MO).

Etymology. The essence of caracolito's most characteristic feature is captured by combination of the Latin "ruptilis," irregularly splitting, with the Greek "carpon," fruit. We explicitly choose this hybrid word "Ruptiliocarpon," against recommendation of the *Code*, because we consider the purely Greek or Latin options decidedly inelegant (e.g.,

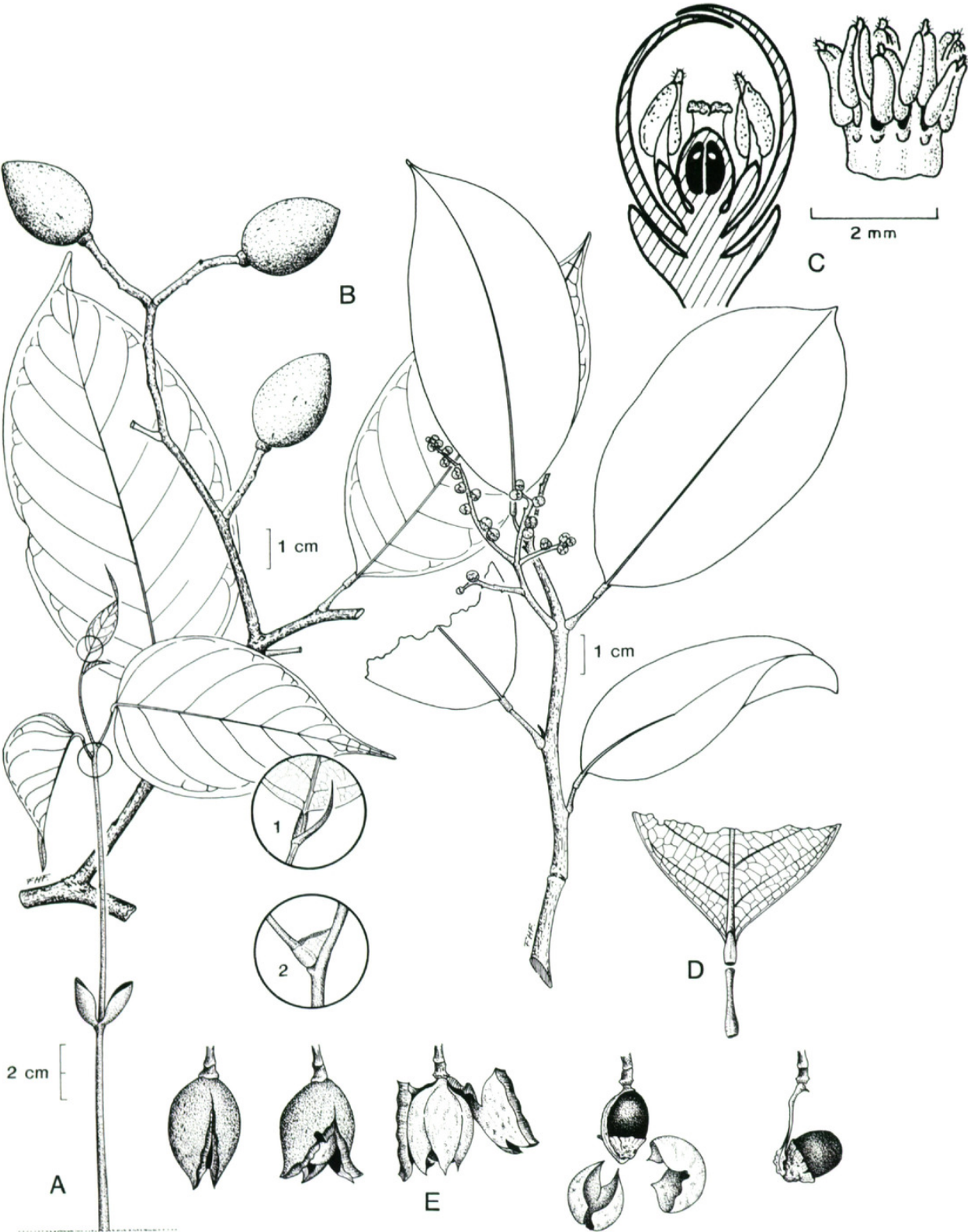
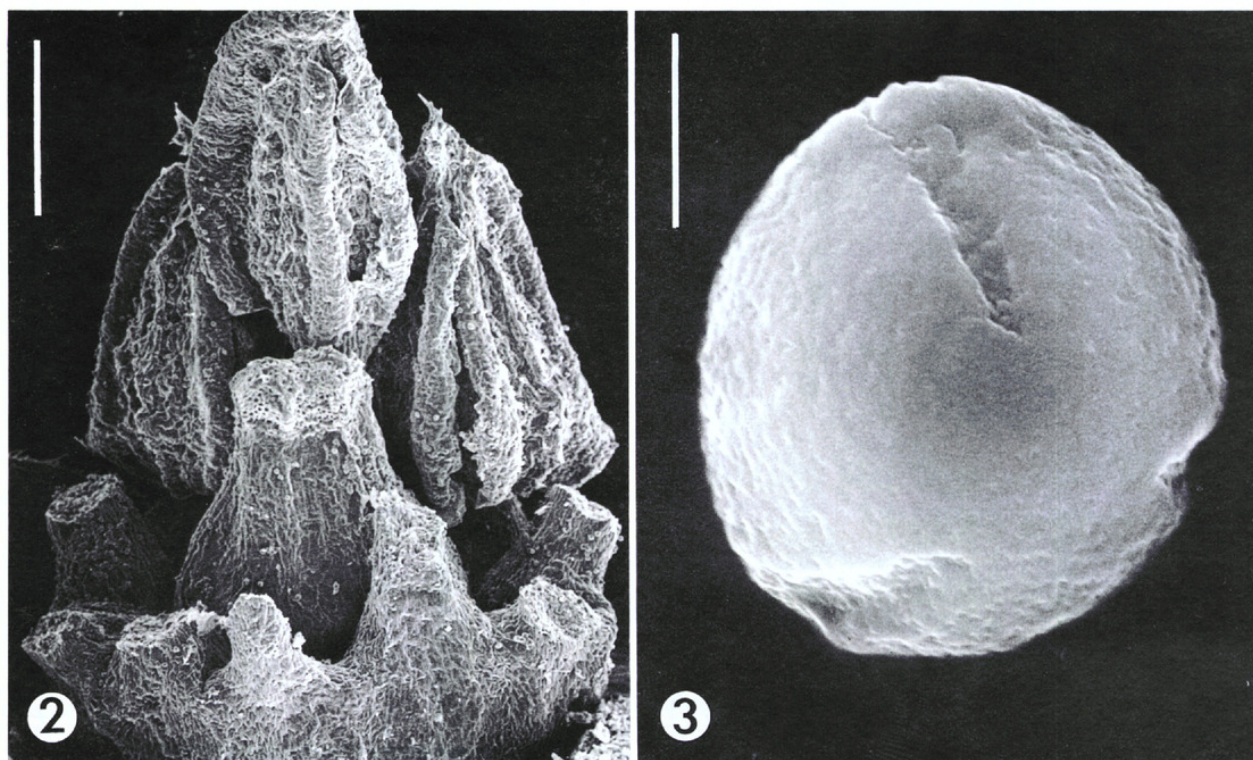


Figure 1. *Ruptiliocarpon caracolito* Hammel & N. Zamora. —A. Seedling with insets: 1-stipel, 2-stipule. —B. Fruiting and flowering branches. —C. Flower showing longitudinal section and androecium. —D. Articulation of leaflet. —E. Fruit dehiscence series. Flowering material from *Aguilar & Hammel 101*, other material from *Hammel 17983*.

“Ruptilifructum” or “Klastocarpum”) by comparison. Likewise, we intentionally take “io” as the combining form rather than either “i” or “o” alone because it effectively and smoothly bridges the Latin/

Greek chasm. The epithet “caracolito,” meaning small snail, as in the shape of shell macaroni (also called “caracolino” in Spanish), is in reference to the shape of the fallen, horny endocarp and is taken



Figures 2, 3. Flower and pollen of *Ruptiliocarpon caracolito*. —2. Mature flower bud with perianth and seven anthers removed, showing staminal tube and ovary. Bar = 0.5 mm; *Hammel 18154*. —3. Pollen. Bar = 5 μ m; *Harmon 210*.

directly from the common name (*Cedro caracolito*). As such, it assumes the gender of its genus, in this case neuter, without change. We clarify these origins so that well-meaning Latinists will resist correcting our spellings. In Costa Rica the common name “cedro” is used mostly—often in combination with a clarifying epithet—for species of *Cedrela*, *Carapa* (Meliaceae), *Calophyllum* (Clusiaceae), and *Tapirira* (Anacardiaceae). A common name for *Ruptiliocarpon* in Peru is *Cedro masha* (R. Vásquez, pers. comm.).

Phenology. In Costa Rica, *Ruptiliocarpon caracolito* flowers in late March to early April, directly following a flush of new leaves. The fruits are nearly mature by late December and last into February. By the time flowering begins, the previous year’s crop of fallen seeds has germinated and grown to the third or fourth leaf. Apparently not all mature individuals flower in a particular year. However, we have found flowering individuals that had obviously flowered and fruited the previous season.

Germination. Seeds fallen below trees germinate readily *in situ*, and those taken from ripe fruits also germinate readily in pots; the radicle begins to emerge within ca. 2 weeks of planting. Germination is epigeal; the thick cotyledons are green and the first leaves are opposite. The first few seedling leaves are often reddish below and, in general aspect, are strik-

ingly similar to those of *Protium aracouchini* (Aubl.) Marchand (Burseraceae) and *Pterocarpus* spp. (Fabaceae).

Habitat and Distribution. In Costa Rica this often large tree is common on slopes and hills of the Osa Peninsula and nearby Golfito. We have found it near sea level but most often between 100 and 400 m elevation and always in well-drained primary forest, typically with red clay soils. It has also been collected from near Barbilla (the type locality) on the Atlantic slope. This transmontane, distribution between the Caribbean lowlands and the Osa Peninsula on the Pacific slope, is exhibited in Costa Rica by numerous other wet forest, basically South American taxa such as *Dendrobangia boliviana* Rusby (Icacaceae), *Hirtella tubiflora* Prance (Chrysobalanaceae), *Humiriastrum diguense* Cuatrecasas (Humiriaceae), *Pleurothyrium trianae* (Mez) Rohrer (Lauraceae), *Qualea paraensis* Ducke (Vochysiaceae), and *Thoracocarpus bissectus* (Vellozo) Harling (Cyclanthaceae). On the basis of that pattern we had predicted the presence of the genus in South America. Now that it is known from Colombia, Peru, and Suriname, *Ruptiliocarpon* seems conspicuously absent from Panama and Ecuador.

In addition to the Colombian specimen, included among the paratypes, numerous other South American, mostly Peruvian, collections have also come

TABLE 1. Characters shared by *Ruptiliocarpon* and *Lepidobotrys*.

Leaves	unifoliolate with stipules, stipels and disarticulation at upper pulvinus
Inflorescences	leaf opposed
Flowers	unisexual; 5 imbricate, free sepals; 5 imbricate, free petals; 10 stamens with 5 longer and 5 shorter filaments; filaments fused at base into nectary/tube
Ovules	apical axial placentation, 2 collateral ovules per locule; placental obturator
Fruits	exocarp and endocarp separate; dehiscence septicial
Seeds	black, one per fruit; orange aril at apex of fruit attached to tip of partition; endosperm lacking

to our attention. No flowering material from South America has been seen, but the observed variation suggests that more than one species may be involved. Therefore, we explicitly isolate the following South American collections of *Ruptiliocarpon* from those cited as *R. caracolito*: PERU. Loreto: 7 km SW of Iquitos, 31 July 1972 (fr), *Croat 18606* (MO); Maynas, Pucacuro, Río Chambira, 160 m, 20 Apr. 1986 (fr), *Vásquez et al. 7452* (MO); Maynas, Nauta, Carretera a Iquitos, 150 m, 8 Dec. 1986 (fr), *Vásquez & Jaramillo 8475* (MO); Maynas, Iquitos, Quebrada de Aucaya hasta Unión, 22 June 1976 (fr), *McDaniel & Rimachi Y. 20801* (MO); Maynas, Iquitos, Allpahuayo-IIAP, 150 m, Nov. 1990 (st), *Vásquez & Jaramillo 14820* (MO), Dec. 1990 (st), *Vásquez & Jaramillo 15543* (MO), (bud), *Vásquez & Jaramillo 15740* (MO), 22 May 1991 (fr), *Vásquez & Jaramillo 16314* (MO), 11 July 1991 (st), *Vásquez & Jaramillo 17366* (MO); Sapuena, Río Ucayali, 170 m, 2 July 1991 (fr), *Grández et al. 2732* (MO); Yanamono “Explorama Lodge,” 120 m, 19 May 1979 (fr), *Diaz et al. 1140* (MO); 130 m, 26 June 1983 (st), *Gentry et al. 42185* (MO), 10 July 1983 (st), *Gentry et al. 42866* (MO). SURINAME. Nassau Mts., 530 m, 23 Mar. 1949 (st), *Lanjouw & Lindeman 2877* (U), 1955 (st), *Lindeman & Cowan 7020* (U).

The fact that *Ruptiliocarpon* (in spite of the large population at Golfito) was neither reported by Allen (1956) nor apparently collected in Costa Rica before 1984 may result, in part, from the inconspicuous nature (small green flowers) of the species. However, as with *Ticodendron* (see Hammel & Burger, 1991) the discovery of *Ruptiliocarpon* surely has more

to do with a recent general upsurge in collecting efforts and, especially in Costa Rica, an intensive focus on collecting and classifying the large trees. We should also expect that more specimens from earlier collections, throughout the Neotropics, will now come to light.

Relationships. The section on relationships in earlier drafts of this paper focused on a search for a family for *Ruptiliocarpon* among the Sapindales. Due, in part, to a strong resemblance between the wood of *Ruptiliocarpon* and *Trichilia* (Mennega, 1993; R. Miller, pers. comm.; C. Morton, pers. comm.), but also because of floral similarities, most importantly, the filament tube, one earlier draft described *Ruptiliocarpon* as a new genus of Meliaceae. Another, bringing together information on wood anatomy, floral anatomy, embryology, and pollen morphology, presented it as a new family. Curiously, some 40 years earlier Léonard (1950) had come to this same conclusion after a similar, family-by-family, search (in part among Sapindales) focused on the African genus we now believe to be *Ruptiliocarpon*’s nearest relative.

The African (Gabon–Cameroon region) *Lepidobotrys* is a monotypic genus that has been variously compared or assigned to Linaceae (Engler, 1902), Oxalidaceae (Hallier, 1923; Cronquist, 1981), Lepidobotryaceae, Erythroxylaceae, and Sapindales (Léonard, 1950). *Ruptiliocarpon* and *Lepidobotrys* are nearly identical in their wood and leaves. Although floral and seed anatomy of *Lepidobotrys* have not been analyzed to the same detail as *Ruptiliocarpon*, the two genera coincide unambiguously in important floral and fruit characters, as well as in the unusual leaf-opposed position of inflorescences (Table 1). Specimens of them compared side by side immediately proclaim kinship from across the Atlantic Ocean. Here follows the history of why it took at least 40 years (after many millions) to make that comparison and get these two back together.

We first saw and recognized *Ruptiliocarpon* as problematic after collecting fruiting material in Costa Rica in 1988. As in nearly all examples of earlier collections and identifications from elsewhere that have come to light, the plant was soon determined to be a legume. Convergence among workers in identifying collections of *Ruptiliocarpon* as Fabaceae is remarkable. The earliest known collection (Suriname, 1949 (st), *Lanjouw & Lindeman 2877*) was placed provisionally at U in the “Papilionaceae” (Mennega, pers. comm.). The first known fertile collection (Peru, 1972 (fr), *Croat 18606*) was identified as *Swartzia simplex* (Swartz) Sprengel. Most other collections that have come to our attention had been identified as *Bocoa*, a papilionoid legume.

Although the fruits (immature) of our early collections, outwardly similar to those of species of *Cynometra*, were initially interpreted as drupaceous, the arillate seed was contradictory and suggested *Swartzia*. Furthermore, a scan through the Fabaceae material at MO revealed that the double pulvini, articulation of the leaflet, and overall appearance of leaf venation make caracolito look very much like a unifoliate legume such as *Bocoa prouacensis* Aublet (we now know that some specimens of this species at MO were actually sterile, misidentified collections of *Ruptiliocarpon*), *Dalbergia moneitaria* L.f., or *Swartzia hostmannii* Benth. The discovery of stipules and stipels on seedling leaves further supported Fabaceae. As noted below, many of the wood characters of *Ruptiliocarpon*, including vested pits, are also in accordance with that family.

However, once phenology and logistics finally coincided (in 1990), numerous flowering individuals were seen in the field, and flowers from five different collections were examined microscopically, it became clear that *Ruptiliocarpon* could not be a legume. The flowers, with a staminal tube/nectary, a compound, 2-locular ovary with 2 collateral ovules per locule and apical axial placentation, decisively eliminate the Fabaceae and would seem to place the new taxon within the Sapindales of Cronquist (1981). These and other floral characters give *Ruptiliocarpon* a resemblance to Meliaceae, although the secretory nature of the staminal tube would appear to be discordant in that family (Tobe & Hammel, 1993). Pollen morphology characters of *Ruptiliocarpon* are also discordant in Meliaceae because the characteristic (for Meliaceae) apertural thickenings are not present in *Ruptiliocarpon* (Hooghiemstra, pers. comm.).

Although the wood of *Ruptiliocarpon* is very similar to *Trichilia* (Mennega, 1993) one important feature, vestiturement of the vessel pits, which was discovered late in this analysis and reconfirmed with SEM, does not coincide with *Trichilia* nor with any other Sapindales and adds to the list of characters that isolate *Ruptiliocarpon* from Meliaceae. It is remarkable, here, that just as overall vegetative appearances of *Ruptiliocarpon* suggest Fabaceae, many of the wood characters, including vested pits, are also in accordance with that family (Mennega, 1993). In any case, as shown elsewhere in this paper, floral and fruit characters of *Ruptiliocarpon* must eliminate Fabaceae from consideration and suggest Sapindales.

Other families of Sapindales such as Rutaceae and Simaroubaceae are similar to *Ruptiliocarpon* in many reproductive characters, but none coincides

in convincing detail. In the Simaroubaceae stipules do occur (rarely) but arils are not known. Details of the flowers (free stamens, presence of a disk and usually only partially united carpels) tend to eliminate the family from consideration for *Ruptiliocarpon*. The capsular or follicular Rutaceae have fruits with similar loose, horny endocarps, but many other characters combine against placing caracolito in that family. In Rutaceae the exocarp remains with the infructescence rather than falling from the seed, the seeds lack arils, the flowers are bisexual, and stipules are wanting. Gland dots are present in the leaves of Rutaceae but lacking in *Ruptiliocarpon*. In Burseraceae (where stipules are rare but known) fruit dehiscence in certain genera (e.g., *Bursera*) is somewhat similar to caracolito in that the leathery exocarp falls away leaving the arillate diaspore attached to the pedicel, but the "aril" (pseudaril, fide Daly, 1989) is attached to the endocarp, which is stony and sealed until germination. In the genus *Dacryodes* the fruit is indehiscent with an oily and resinous mesocarp and an exarillate seed (Daley, pers. comm.), but the cartilaginous endocarp is very similar to that of *Ruptiliocarpon*. The endocarp is separable into two pieces, one smaller and empty with the margin folded over, the other larger and covering the seed, just as in *Ruptiliocarpon*. Nevertheless, in contrast to *Ruptiliocarpon*, the tribe Canarieae, which includes *Dacryodes*, is characterized by 3-merous flowers, fused sepals, and valvate petals. Furthermore, in contrast to typical Burseraceae, caracolito lacks resin ducts in the bark, lacks a floral disk, has two (rather than four or five) carpels and has the stamens fused in a single whorl rather than free in two whorls. The Burseraceae were eliminated early on in the wood anatomy analysis because, in distinction to Meliaceae, Sapindaceae, and Rutaceae, the Burseraceae are rather uniform in their anatomy and not at all like *Ruptiliocarpon* (Mennega, 1993). The Sapindaceae are known to have stipules in some of the lianas and agree with caracolito in many floral details, although they always have free stamens and, typically, a nectary disk and an ovary with one or two ovules in each of three locules. In fruit, the only similarity between caracolito and Sapindaceae (other than the presence of an aril) is that in certain genera (e.g., *Paullinia* and *Thouinia*) the mature carpels often fall away (entire) from the central axis, and in caracolito the exocarp and endocarp split off (in pieces) leaving the seed dangling by the central axis.

But for a casual glance at the excellent revised edition of Thonner's key to families (Geesink et al., 1981), we might have published *Ruptiliocarpon* in its own new family, leaving *Lepidobotrys* stranded

TABLE 2. Differences between *Ruptiliocarpon* and *Lepidobotrys*.

	<i>Ruptiliocarpon</i>	<i>Lepidobotrys</i>
Vestured pits	+	—
Dioecy	cryptic	+ obvious
Fibrous exotegmen	+	—
Gynoecium	2-merous	3-merous
Styles	—	+
Exocarp	woody	leathery
Endocarp	cartilaginous	chartaceous
Filaments	short	long
Anthers	basifixed	versatile
Connective	apiculate	truncate
Inflorescences	panicle of spikes	fasciculate spikes

in Africa a while longer. The cryptic dioecy of *Ruptiliocarpon*, which was only revealed in 1992 by anatomical studies (Tobe & Hammel, 1993), is perhaps the one major clue that led to this late success with Thonner. *Lepidobotrys staudtii* Engler has unifoliolate leaves with fugaceous stipules and stipels, and an articulation at the upper pulvinus. It has leaf-opposed inflorescences; small green flowers with five imbricate sepals and petals; ten stamens of two different lengths with the filaments fused at the base into a nectary-tube; two collateral, apical ovules per locule; obturators; capsular fruits splitting septically to reveal a single, black, exendospermous seed with a red aril attached to the tip of the partition, which is in turn attached to the pedicel (Table 1 and Fig. 1).

Rank. Although cedro caracolito is very similar to *Lepidobotrys*, we distinguish *Ruptiliocarpon* because the two are different in ways that can be regarded as generic: *Ruptiliocarpon* has vestured pits, *Lepidobotrys* does not (Mennega, 1993); *Ruptiliocarpon* has nearly identical male and female inflorescences and flowers, in *Lepidobotrys* dioecy is more obvious; pedicels are lacking in *Ruptiliocarpon*, 5–8 mm long (male flowers) in *Lepidobotrys*; anthers are basifixed and apiculate in *Ruptiliocarpon*, versatile and truncate in *Lepidobotrys*; the fused part of the filaments (nectary-tube) is much longer than the free part in *Ruptiliocarpon*, much shorter in *Lepidobotrys*; *Ruptiliocarpon* has a sessile, bilobed stigma and 2-locular ovary, *Lepidobotrys* has 3 styles and 3-locular ovary; the exocarp is woody and irregularly dehiscent with a cartilaginous endocarp in *Ruptiliocarpon* but leathery and 3-parted and with a papery endocarp in *Lepidobotrys*; the persistent partition is much narrower than the seed in *Ruptiliocarpon*, nearly as wide as or wider than the seed in *Lepidobotrys*; the mature seed of *Ruptiliocarpon* has a fibrous exotegmen

lacking in *Lepidobotrys* (Tobe & Hammel, 1993) (Table 2).

LEPIDOBOTRYACEAE RECONSIDERED

Although Léonard (1950) reviewed the literature concerning *Lepidobotrys* and described the family Lepidobotryaceae, the issue was not settled. Hutchinson (1959, 1967, 1973) included the primarily tropical Asian *Dapania* and *Sarcotheca* in Lepidobotryaceae. However, as pointed out by Veldkamp (1967) in his revision of these two genera and also by Willis (1973), *Dapania* and *Sarcotheca* are decidedly members of Oxalidaceae and closely related to *Averrhoa*, whereas their relationship to *Lepidobotrys* is questionable. Oltmann (1971) stated that the pollen of Lepidobotryaceae (including *Dapania* and *Sarcotheca*) stands next to Oxalidaceae but also shows affinity to the broadly circumscribed Linaceae complex where the floral morphology is more concordant, particularly with that of *Lepidobotrys* (e.g., presence of obturators). Huynh (1969) considered that the pollen of *Lepidobotrys* can be distinguished from all others of the family (Oxalidaceae) by its very long apertures. Oltmann (1971) also felt that *Lepidobotrys* has pollen distinct enough to support status as a separate family. Leaf anatomy (cf. discussion in Mennega, 1993) is uninformative on the question and wood anatomy, itself, does not presently resolve the issue.

The most striking similarities between *Lepidobotrys* and Oxalidaceae (i.e., *Dapania* and *Sarcotheca*) lie in the unifoliolate, articulate leaves and the woody habit. According to Léonard (1950), this similarity to leaves of Oxalidaceae, which generally have compound leaves with articulate leaflets, was Hallier's (1923) and later Knuth's (1931) principal reason for removing *Lepidobotrys* from Linaceae and placing it in Oxalidaceae. They might just as

well have placed it in the Fabaceae, where groups with not only compound leaves and articulated leaflets exist, but also with stipules and stipels, features lacking in Oxalidaceae including *Dapania* and *Sarcotheca*. The filaments of two lengths are also suggestive of Oxalidaceae, but that condition is present, as well, in some Sapindales, e.g., *Trichilia* spp. (Pennington, 1981).

The main new evidence presented here in support of Léonard's recognition of Lepidobotryaceae as a family distinct from Oxalidaceae has to do with obturators and endosperm. Engler (1902) described the ovules of *Lepidobotrys* as having the placenta dilated into a caruncle that covers the micropyle. As pointed out by Hallier (1923) and Oltmann (1971) this structure is an obturator, which presumably serves to guide pollen tubes to the micropyle (Cronquist, 1981). Placental obturators are also present in *Ruptiliocarpon* but lacking in Oxalidaceae. Both *Lepidobotrys* and *Ruptiliocarpon* lack endosperm in mature seeds (Tobe & Hammel, 1993). Although endosperm is often scanty or absent in some members of Cronquist's Geraniales (Geraniaceae and Balsaminaceae), it is nearly always copious in Oxalidaceae. Furthermore, Léonard did not point out that the petals are clawed in Oxalidaceae but unclawed in *Lepidobotrys* (and *Ruptiliocarpon*). Leaves and bark of *Ruptiliocarpon* have bitter substances while those of Oxalidaceae are sour or acidic. The Oxalidaceae are said to be tenuinucellate (Cronquist, 1981), whereas at least *Ruptiliocarpon* is crassinucellate. However, *Averrhoa* (Oxalidaceae) is also crassinucellate (Thathachar, 1942).

In addition to the above, and as pointed out by Léonard, Lepidobotryaceae differ importantly from Oxalidaceae in having septicidal (or irregular) rather than loculicidal (or no) dehiscence, collateral rather than superposed ovules, two or three carpels rather than five, and a disk (nectar-producing fused portion of filaments) (Table 3). With regard to the disk, a similarity to Oxalidaceae should be examined further; Cronquist stated that the outer filaments are often thickened nectariferous below in Oxalidaceae. Also the nature of the so-called disk in *Lepidobotrys* needs to be studied histologically. In contrast to published descriptions and drawings (e.g., Knuth, 1931; Tisserant, 1949; Léonard, 1950; Hutchinson, 1959; Badré, 1973), our examination of reconstituted dried male flowers of *L. staudtii* revealed no discontinuity (other than fusion) between free parts of filaments and the point where the androecial structure attaches to the base of the petals. The filaments simply expand gradually from tip to base and the "disk" seems quite obviously to be the fused basal portion of the filaments. We had this same

problem with *Ruptiliocarpon*, interpreting the structure first as a disk, then as a filament tube until finally it was shown, histologically, to be both, staminal tube and nectary (Tobe & Hammel, 1993).

All evidence considered, placing *Lepidobotrys* in Oxalidaceae seems no more defensible than placing *Ruptiliocarpon* in Fabaceae. The leaves, outwardly so similar to *Dapania* and *Sarcotheca* in the former and *Swartzia* and *Bocoa* in the latter, have been the principal culprit in both these errors and are homologous, we believe, only in the case of uniting *Ruptiliocarpon* with *Lepidobotrys*. Where, then, do the broader affinities of Lepidobotryaceae lie?

Léonard (1950) also compared *Lepidobotrys* with Linaceae and Erythroxylaceae, but none of the new evidence we have accumulated for *Ruptiliocarpon* suggests a particularly close relationship to either of those two families (Mennega, pers. comm.; Tobe, pers. comm.). Our preliminary studies of *Ruptiliocarpon* focused almost entirely on comparison with families of Sapindales, and that comparison, although discarded for *Lepidobotrys* by Léonard (1950), is still viable on the basis of floral, seed coat, and wood anatomy. *Ruptiliocarpon* seemed particularly close to Meliaceae, but its pollen, while similar to that of Sapindaceae (Hooghiemstra, pers. comm.; Pennington, pers. comm.), is not consistent with placement in the Meliaceae as it lacks the thickenings at the apertures, characteristic of that family (Hooghiemstra, pers. comm.).

Lepidobotryaceae, apparently, has never been compared to the Euphorbiaceae. However, its dioecy and obturators (both revealed very late in the investigation of *Ruptiliocarpon*) give credence to that possibility. The paired, apical, collateral ovules coincide directly with the primitive subfamily of euphorbs, Phyllanthoideae (Webster, 1975). Fibrous exotegmen, a character emphasized by Tobe & Hammel in comparing *Ruptiliocarpon* to Meliaceae, is also found among the Phyllanthoideae (Corner, 1976). Other important characters consistent with Euphorbiaceae include: two or three carpels; septicidal dehiscence; differentiation and separation of exocarp and endocarp; shape of the endocarp; and attachment of the seed via the aril (as in e.g., *Aporosa* and *Richeria*) to the persistent axis, which is suggestive of the characteristic euphorb columella (Cronquist, 1981). Although all of the wood anatomical characters manifested by Lepidobotryaceae may be found among the Phyllanthoideae, its particular set of characters is not found in any one genus (Mennega, pers. comm.) Furthermore, the androecium of Lepidobotryaceae, with its filament-tube disk, and the unifoliate, articulate leaves are discordant in Euphorbiaceae. If Lepidobotryaceae

TABLE 3. Comparison of Lepidobotryaceae to Meliaceae, Oxalidaceae, and Euphorbiaceae.

	Lepidobotryaceae	Meliaceae	Oxalidaceae	Euphorbiaceae
Leaves	unifoliolate	compound, rarely unifoliolate	compound, rarely unifoliolate	simple, rarely compound or unifoliolate (?)
Petiole	articulate with the petiolule	continuous	articulate with petiolule in unifoliolate spp.	continuous
Stipules	+	—	—	+
Wood (vestured pits)	±	—	—	— (+ in one genus)
Inflorescence	leaf-opposed	axillary, terminal or rarely extra- axillary	axillary	axillary, terminal or very rarely leaf-opposed
Flowers	unisexual	uni-bisexual	bisexual	unisexual
Stamens	10	10 (–25)	10	(1–)5–many
Filaments	fused, bicyclic	fused, sometimes bicyclic	fused, bicyclic	free-fused, not bicyclic
Nectary	staminal tube	separate or lacking	? (as scales) or lacking	separate or lacking
Carpels	2 or 3	(1–)2–5(–20)	5	2 or 3(–4–many)
Ovules/locule	2 collateral	(1–)2(–12) collateral or superposed	(1–)2–several superposed	1 or 2 collateral
Obturator	+	±	—	+
Placentation	apical-axial	axial (often apical)	axial	apical-axial
Fruit	septicidal capsule	septi-loculicidal capsule	loculicidal capsule	septicidal (schizocarp)- various
Seed	1	1–many	numerous	(1–)3–several
Seed coat (fibrous exotegmen)	±	±	—	±
Endosperm	—	+ (–)	+	+ (–)

were found to be a close outgroup to Euphorbiaceae, the generally accepted, simple-leaved origin of the Euphorbiaceae might be challenged. We have found a family for *Ruptiliocarpon* but the exact placement of Lepidobotryaceae among other Rosidae is not yet clear.

BIOGEOGRAPHY

Apparent sister genera separated by the Atlantic, *Ruptiliocarpon* and *Lepidobotrys* keep company with such taxa as *Cecropia–Musanga* and *Pour-*

ouma–Myrianthus (Cecropiaceae—Berg, 1978), *Duguetia–Pachypodanthium* (Annonaceae—Schatz, pers. comm.) and numerous others cited by Thorne (1973). These pairs, endemic to their respective continents, are examples suggesting that vicariance of the original population via plate tectonics resulted in the taxonomic structure we see. The substantial differentiation between *Ruptiliocarpon* and *Lepidobotrys*, as well as the wide distribution of *Ruptiliocarpon* within the Neotropics, is consistent with a division in the range of the ancestor population somewhere near or relatively

soon after the South American and African plates began to separate about, 100 million years ago (Raven & Axelrod, 1974). In contrast to the recently described *Nyssa* (Cornaceae) and *Ticodendron* (Ticodendraceae) from Costa Rica (cf. Hammel & Burger, 1991; Hammel & Zamora, 1990) we have no evidence here to support a boreotropical origin of *Ruptiliocarpon* (cf. Lavin & Luckow, 1993). Rather, the wide distribution and variability of *Ruptiliocarpon* in South America and its restriction to Costa Rica otherwise, suggest dispersal into Central America from a South American origin. Within this context, Lepidobotryaceae may be quite old, as is also suggested by its similarity to primitive members of various more or less disparate groups in the Rosidae.

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Note added in proof. We have now found flowering material from South America from among the family indets. at the Field Museum of Natural History: PERU. Loreto: Mishuyacu, near Iquitos, 100 m, Jan. 1930 (fl), *Klug* 749 (F). Annotations indicate that Erythroxylaceae, Meliaceae, and Burseraceae had been successively considered. The flowers are somewhat larger than those of the Costa Rican material.



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