

## *Micrandra inundata* (Euphorbiaceae), a New Species with Unusual Wood Anatomy from Black-water River Banks in Southern Venezuela

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**ABSTRACT.** *Micrandra inundata* is a distinctive new species adapted to seasonally flooded black-water river banks in southern Venezuela. Trees rarely exceed 10 m in height but have thick basal trunks composed of very lightweight wood. It has the smallest leaves and fruits of any known *Micrandra* species and appears to be most closely related to *M. minor* Benth. The botanical description is accompanied by habit photographs, line illustrations of morphological features, and photomicrographs and detailed descriptions of the wood anatomy.

*Micrandra* Benth. (including *Cunuria* Baill.) comprises about 15 species native to Amazonian South America and the Guayana Shield. It belongs to Euphorbiaceae sensu stricto (taxa with one ovule per carpel) in subfamily Crotonoideae, tribe Micrandreae, together with *Hevea* Aubl. (10 species) and *Micrandropsis* W. Rodr. (1 species), both of which are also restricted to the Guayanan and Amazon region (Webster 1994). Although species of *Micrandra* produce latex similar in appearance to that of *Hevea*, it has not been used commercially for rubber production. However, seeds of *M. spruceana* (Baill.) R. E. Schult. are cooked and eaten by indigenous tribes in the Vaupés region of Colombia (Baldwin and Schultes 1947; Schultes and Raffauf 1990), and the seeds of *Micrandra rossiana* R. E. Schult. are consumed by the Yanomami in southern Venezuela (C. Brewer-Carias, pers. comm., and *Brewer-Carias in Feb. 1991* at MO). Spruce (1854) described how the seeds of two different species of *Micrandra*, which he identified by its local name, "Cunuri," were used in the upper Río Negro and in the Río Casiquiare area of Venezuela in the mid-19th century to produce both a lamp oil and "cunuri cheese," similar in taste and texture to cream cheese. To produce this, the seeds were first boiled, then soaked for several days underwater, and later broken up by hand to form an edible paste.

In their initial revision of this group, Baldwin and Schultes (1947) recognized the genus *Cunuria*, with four species, as distinct from *Micrandra*. This was based on *Cunuria* having a higher number of stamens, more connate sepals, and no nectary disk in the staminate flowers compared to *Micrandra*. After additional field study and examination of new specimens, however, Schultes (1952a) reduced *Cunuria* to synonymy with *Micrandra*, based on several new species he described with combinations of characters supposedly unique to both genera. Despite Jablonski's support of Schultes' decision (Jablonski 1967), both

Webster (1994) and Radcliffe-Smith (2001) included *Cunuria* in their lists of valid genera of Euphorbiaceae, "not to affirm its generic distinctness . . . [from *Micrandra*, but] . . . to call attention to the problem" (Webster 1994, p. 99).

As part of an in-depth study of the basin of the Río Temi, a small black-water tributary of the Río Atabapo in southwestern Amazonas state in Venezuela (Berry and Aymard 1997), the senior author had the opportunity to collect intensively in the seasonally flooded forests along most of the length of this remote river. A surprising number of trees that are adapted to flooding up to 8 m above ground level during nearly nine months of the year showed very lightweight wood structure, at least in the lower portion of their stems (Berry et al. 2000; Wiedenhoef 2001). In the middle section of the river, especially upstream and downstream of the village of Yavita, a species of *Micrandra* was prominent along the riverbanks and showed broad, furrowed trunks with stiffly branched adventitious roots near the base when the river level was low (Fig. 1). When the Euphorbiaceae of this region were treated in the *Flora of the Venezuelan Guayana*, Berry (1999) treated this species as "*Micrandra* sp. A," since it did not fit into any previously described species. It was, however, included in the key to the species, where it grouped with two other species having faint or no basal laminar glands, inflorescences generally shorter than the leaves, and staminate flowers with five stamens. Of all known species of *Micrandra*, this is the only one adapted to seasonally flooded riverine forests, exclusively along black-water rivers. All other species grow mainly on "terra firme" and often in hilly or upland habitats (Baldwin and Schultes 1947; Schultes 1952a). Below we provide a botanical description of the new species as well as detailed anatomical data on its wood structure because it has remarkably lightweight wood for a tribe that otherwise has denser wood.

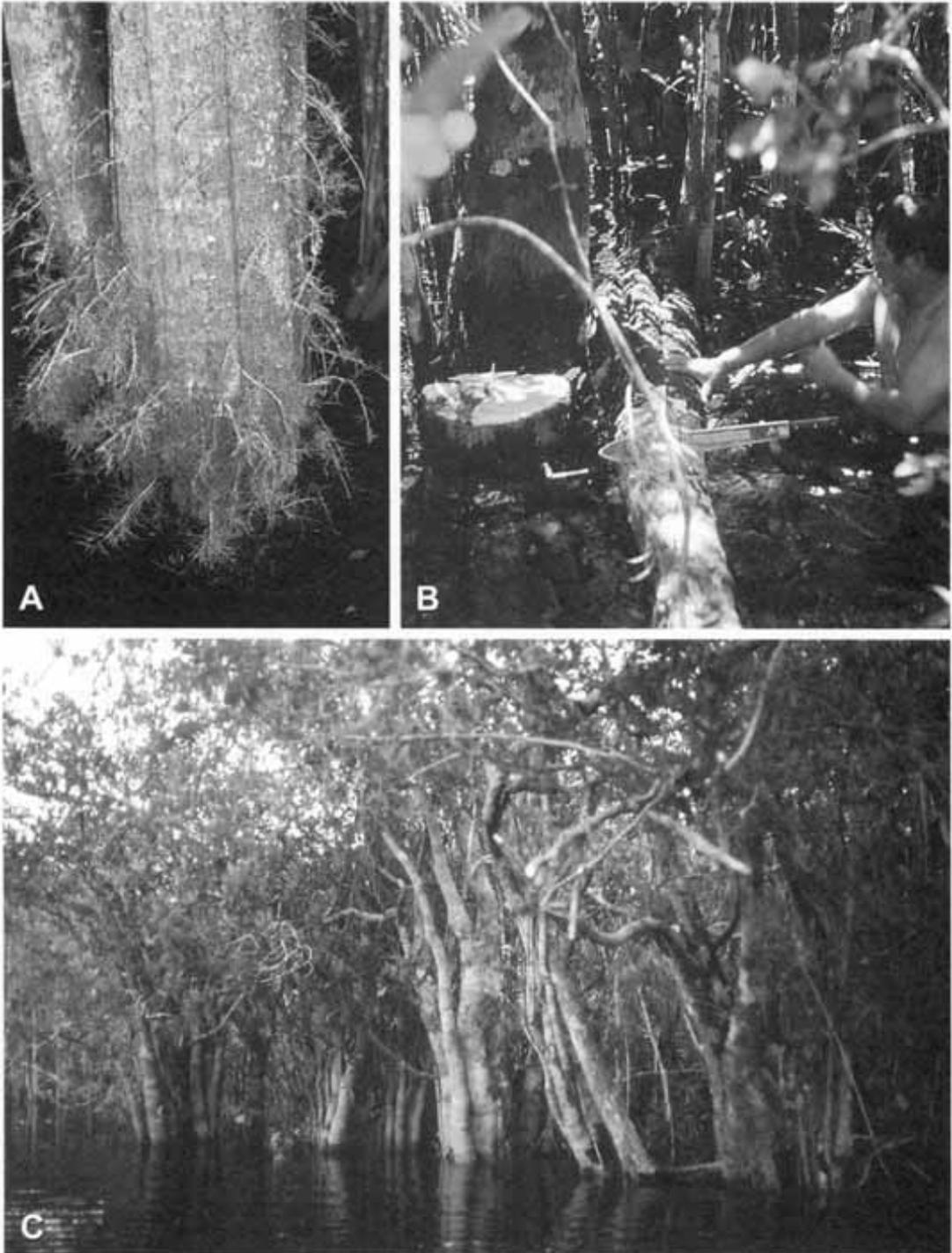


FIG. 1. A-C. Trunk and habitat features of *Micrandra inundata*. A. An exposed trunk at low water, showing the furrowed lower trunk with stiffly branched adventitious roots (diam of main trunk shown is ca. 30 cm). B. The trunk of wood specimen *Berry & Rosales* 6393 cut by machete showing its light weight and floatability. C. Dense colony of mostly multi-stemmed individuals, lining the banks of the Río Temi upstream of Yavita (type locality). The photograph was taken in November, about midway between the minimum and maximum river level; at peak flooding, water covers much of the tree canopies.

*Micrandra inundata* P. E. Berry & A. Wiedenhoef, sp. nov.—TYPE. VENEZUELA. Amazonas: seasonally flooded banks of black-water Río Temi 1–2 km above Yavita, 2°55'00"N, 67°24'28"W, 110 m, 18 Nov 1996, [f] and young fr, Berry & Rosales 6350 (holotype, MO!; isotypes DAV!, F!, GH!, MG!, K!, NY!, U!, US!, VEN!, WIS!). Figs. 14.

Arbor usque ad 12 m alta, in sylvis valde inundatis, tronco parum sulcato basin versus inde radicellas rigidas vulgo instructa, ligno inferiori levissimo, ramis superioribus aliquantim tortuosis; foliis obellipticis 3–10 × 1.5–5 cm; inflorescentiis 2–6 cm longis; staminibus 5 nectariis alternantibus; seminibus 10–12 × 7–8 mm.

Tree 5–12 m tall, the trunk either single or with two or more main trunks emerging from the base, each one 10–50 cm diam, typically lightly furrowed near the base and often with short, stiff, adventitious roots in the lowermost 1 to 2 m, noticeably tapering in diam upwards, wood very lightweight; bark light tan-gray and rugulose, but usually covered by crustose lichens, with white latex emerging when cut; young growth sericeous, with appressed simple trichomes 0.1–0.3 mm long, the pubescence sparser and erect on older growth. Stipules lateral, free, lanceolate, puberulent, 1.5–2 × 0.2–0.4 mm (not enveloping the terminal bud), semipersistent. Leaves coriaceous, 3–10(–11) × 1.5–5 cm, obelliptic, finely reticulate especially on abaxial side, rounded or retuse to occasionally acute at the tip, base cuneate, eglandular or with two faint glands 0.5–1 mm diam at the base of the blade on the adaxial surface, smaller glands sometimes present at junction of principal lateral veins and midvein on adaxial surface, abaxial midvein sparsely puberulent with erect simple trichomes 0.1–0.3 mm long, or glabrous (acridomatia lacking); secondary veins 6–9(–10) per side; petioles 7–15(–30) mm long, sparsely puberulent or glabrescent. Inflorescence a simple pedunculate cyme or a panicle of cymes in the upper leaf axils, 2–6 cm × 1–2(–3) cm, sometimes entirely staminate, but when pistillate flowers present, these terminal on the main branches, bisexual flowers lacking; bracts at base of side branches narrowly triangular, 1–2 mm long × 0.5–1 mm wide at the base, bracteoles of individual flowers slightly smaller, caducous. Pistillate flowers with pedicels 2–3 mm long (appearing longer after lower flowers on the secondary rachis dehisce); sepals 5, valvate in bud, shortly puberulent outside, glabrous inside, yellowish-green to cream-colored, lanceolate, 5–7 × 2 mm, connate and cupulate at the base for 1–1.5 mm, spreading-recurved at anthesis, falling off soon thereafter; ovary narrowly ovoid, shortly sericeous, 2–2.5 mm long, 2 mm wide at base, where surrounded by a thick nectary disc and antherless staminodes 1–2 mm long alternating with the sepals, the ovary nearly

confluent at the apex with the narrowly conical style, this solid and 2.5–3.5 mm long × 1.5 mm wide at the base; stigmas 3, bifurcate, recurved, 1 mm long, the branches divergent, smooth and receptive on the inner-facing surface; carpels 3, each with a single oblongoid ovule 1.2 mm long × 0.5 mm thick with a torus-like caruncle at the apex. Staminate flowers with pedicels 1–2.5 mm long; sepals 5, valvate in bud, shortly puberulent outside, glabrous inside, dull yellow to cream-colored, oblong-lanceolate, 3–4 mm × 1–2 mm, connate-cupulate at the base for 1 mm, spreading-recurved at anthesis; stamens 5, alternate with the sepals, filaments 2.54 mm long, incurved at anthesis, cream-colored; anthers basifixed, bilobed, 0.5–1 mm long and wide; thick nectary glands 1 mm wide and 0.8 mm deep situated opposite the sepals and between the stamens, with sparse hairs on the surface; pistilode shortly pyramidal, puberulent, ca. 1 mm high. Fruits capsular (explosive schizocarps), green and globose while maturing, slightly furrowed between the carpels at maturity, 15–20 × 13–15 mm when ripe, the thin mesocarp and exocarp drying yellowish or light brown at dehiscence and detaching from the woody cocci that open loculicidally from the apex, the style persistent for most of fruit development; mature seeds narrowly ovoid, 10–12 mm long, 7–8 mm wide (at widest axis transverse to the longitudinal raphe), apiculate, smooth and uniformly tan, with a persistent, short funicle ca. 1 mm long, but no caruncle evident at dehiscence.

**Ecology and Distribution.** *Micrandra inundata* is only known from the banks of black-water rivers in southwestern Venezuela that are seasonally flooded for over eight months of the year (Figs. 1–3). During the height of the dry season (between January and April), the trunks may be exposed to air down to ground level, but at the peak of the rainy season (between June and August), the river rises to the canopy level, a seasonal fluctuation in the river level of approximately 7–8 m. The known localities are all in Amazonas state, Venezuela, at elevations between 100 and 150 m. The main area of occurrence is the Río Atabapo basin, a black-water tributary of the Orinoco. The species is uncommon along the banks of the Río Atabapo itself but is more frequent in the Río Temi, its middle tributary. It is most common around the village of Yavita, about half way up from the river's mouth, where it is one of the dominant species in a narrow band along the main channel of the river. Given the proximity of the known localities to Colombia and Brazil, *M. inundata* should be expected in similar habitats in those countries as well.

The areas where *M. inundata* occurs have a very characteristic and partly endemic flora adapted to the flooded, black-water conditions. The main associated species include: *Heteropetalum brasiliense* Benth. [An-

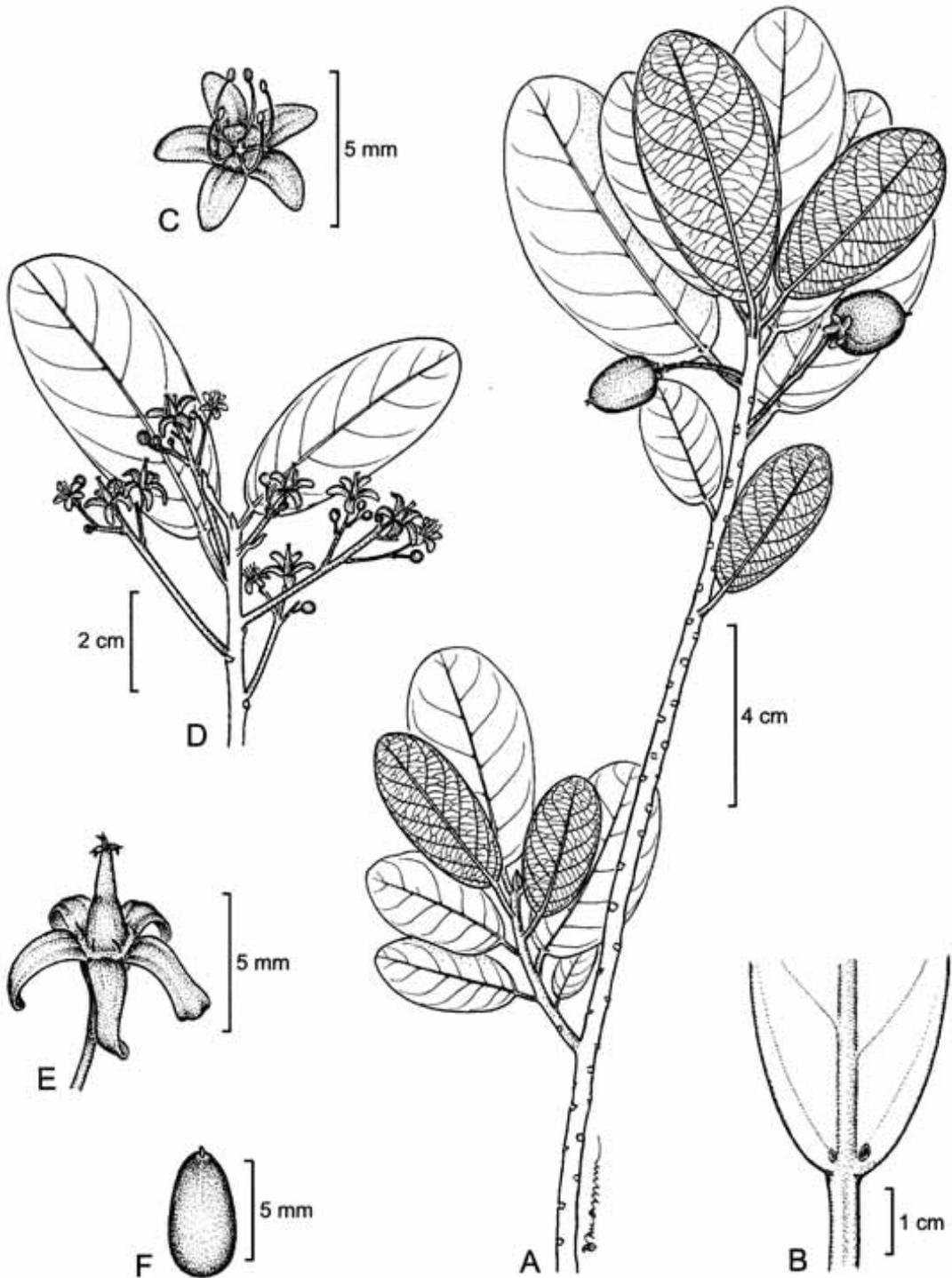


FIG. 2. *Micrandra inundata*. A. Fruiting branch habit, with some leaves drawn to show the venose texture on the undersides of the leaves. B. Adaxial side of leaf base, showing a faint pair of glands. C. Staminate flower. D. Flowering branch, showing inflorescence branches with both distal pistillate and more proximal staminate flowers. E. Pistillate flower. F. Immature seed (mature seed looks identical but reaches 10–12mm long). Based on the type, *Berry & Rosales 6350*.

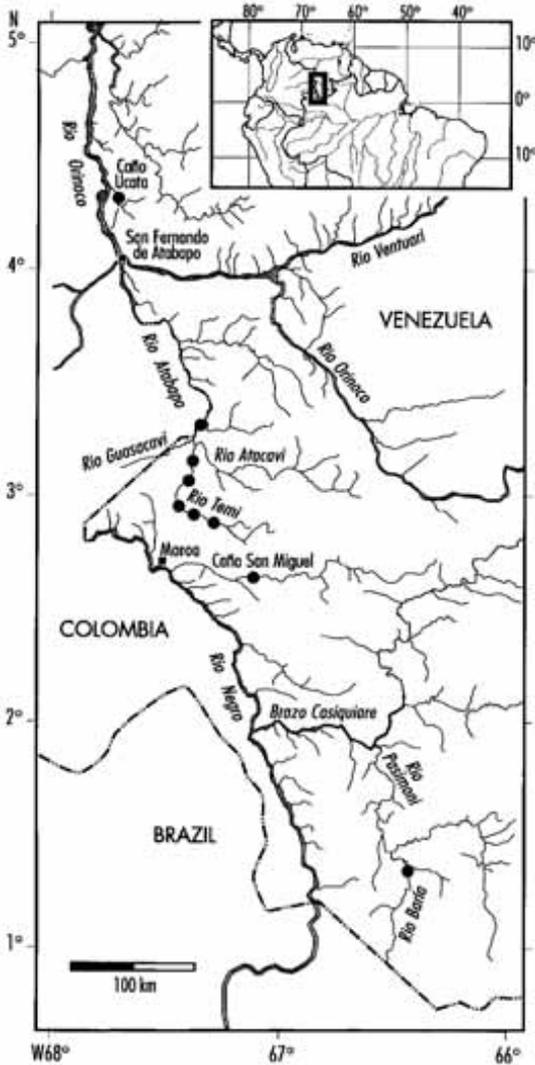


FIG 3. Map of known localities of *Micrandra inundata*. Note the proximity of the Río Temi and Caño San Miguel localities, even though the former drains north into the Río Orinoco and the latter south into the Río Negro.

nonaceae]; *Malouetia virescens* Spruce ex Mull. Arg., *Molongum laxum* (Benth.) Pichon, and *Parahancorniane-groensis* Monach. [Apocynaceae]; *Pachira aquatica* Aubl. [Bombacaceae]; *Archytaea angustifolia* Maguire [Bor-netiaceae]; *Calophyllum brasiliense* Cambess. and *Moron-obeia riparia* (Spruce) Planch. & Triana [Clusiaceae]; *Lis-socarpa benthamiana* Gürke [Ebenaceae]; *Amanoa almer-indae* Leal [Euphorbiaceae]; *Byrsonima bronweniana* W. R. Anderson [Malpighiaceae]; *Ouratea tkyrsoidea* Engl. and *Wallacea multiflora* Ducke [Ochnaceae]; and *Pouteria maguirei* (Aubrév.) T. D. Penn. and *Pouteriapimichinensis* T. D. Penn. [Sapotaceae]. Of these, the first five taxa have notably lightweight wood.

**Phenology.** The trees are evergreen, even when submerged for long periods. Flowering specimens

were collected in November, and fruiting specimens in March, which indicates that floral phenology may be timed to disperse fruits when water levels are low. Larger-seeded species of *Hevea* in similar habitats are known to be water-dispersed and heavily eaten by fish (Goulding 1989), but we are not sure if the same is true of *Micrandra inundata*. When the type specimen was collected, the male flowers produced small drops of nectar on the nectaries, but gave off no noticeable odor. Given their shape and size, the flowers are likely pollinated by small bees or wasps, as Schultes (1952a) reported for similar flowers of *Micrandra lopezii* R. E. Schult. in northern Brazil.

**Etymology and Common Name.** The specific epithet refers to the seasonally flooded forest habitat where this species occurs. This is one of several light-weight-wooded trees in flooded forests of southern Venezuela that are called 'Palo de boyá', or buoy wood. Due to the bearded appearance of the lower trunks, our guides coined the common name of 'Palo de boyá chivudo' (chivudo alludes to the dense, beard-like adventitious roots that emerge from the base of some trunks of *Micrandra inundata*).

**Affinities.** *Micrandra inundata* is highly distinctive in the genus, given its unusual habit and habitat. It is the shortest tree in the genus, rarely more than 10 m tall. Basally, the trunks may be as thick as some of the terra firme species, but the wood of *M. inundata* is almost balsa-like in consistency, and the diameter of the trunk tapers towards the upper branches. It also has the smallest leaves and fruits in the genus. Its inflorescence is among the shortest and fewest-flowered in the genus. Although *Micrandra lopezii* R. E. Schult. may have shorter inflorescences, they are more glomerate and much more floriferous than in *M. inundata* (Schultes 1952a). In terms of the prior distinction between *Micrandra* and *Cunuria*, the new species belongs to *Micrandra* sensu stricto, due to its 5 stamens, nectaries in staminate flowers, valvate sepals and open calyx. Most of the species formerly placed in *Cunuria*, such as *M. glabra* (R.E. Schult.) R.E. Schult. and *M. sprucei* (Mull. Arg.) R.E. Schult., have conspicuous connate stipules that envelop the terminal bud and subsequently leave a prominent scar. *Micrandra inundata* only has small, lateral stipules that leave tiny scars when they fall off.

The most closely allied species to *Micrandra inundata* appears to be *M. minor* Benth., which shares small, usually rounded leaves and similar flowers and inflorescences; however, *M. minor* can be readily distinguished by its larger fruits, longer pedicels, generally longer petioles, cylindrical trunks, denser wood, and mainly non-flooded habitats.

In the treatment of *Micrandra* for the *Botany of the Guayana Highland* by Jablonski (1967), the two Wurdack and Adderley collections cited below were treated under *Micrandra siphonoides* Benth., but that species has

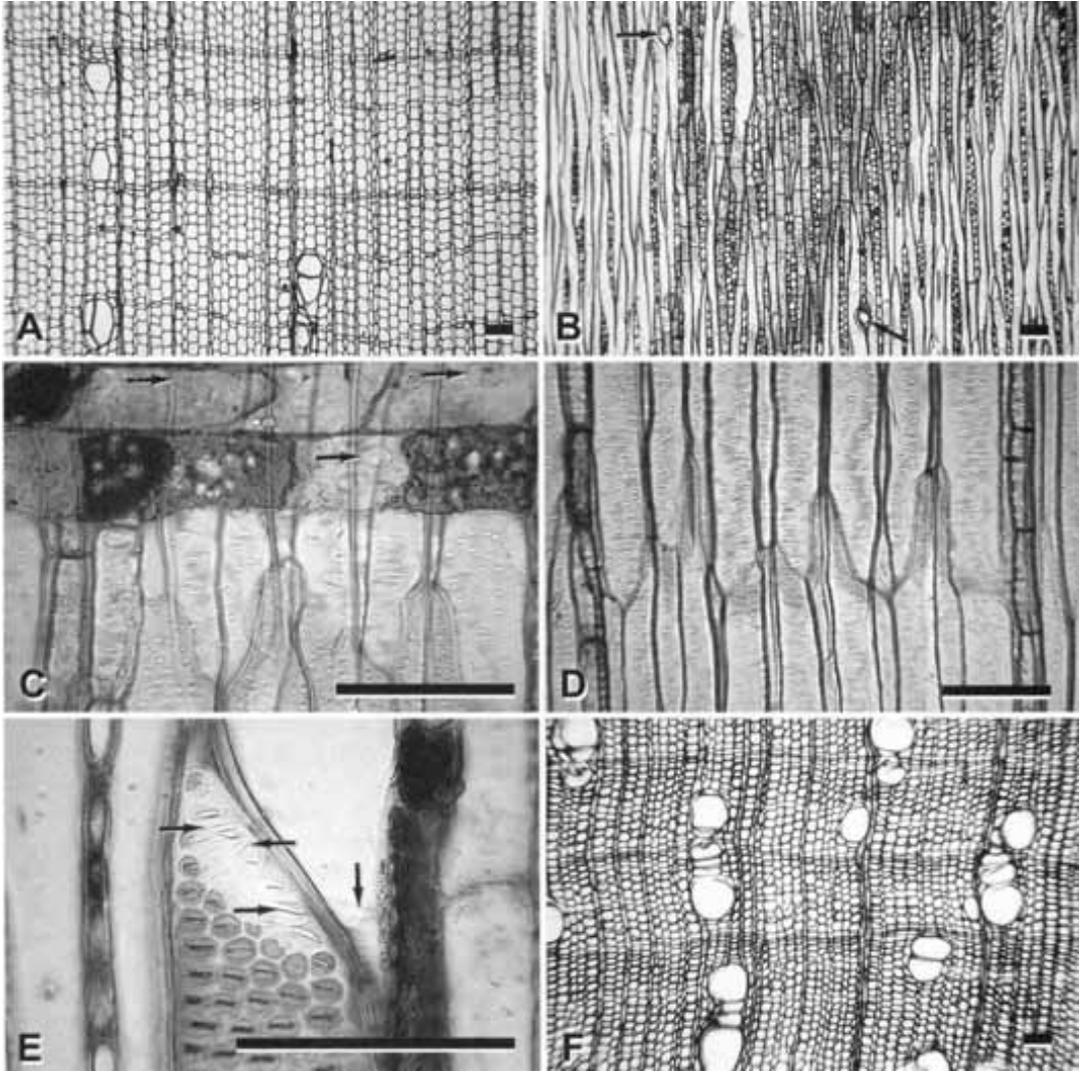


FIG. 4. A–F. Light photomicrographs of the wood of *Micrandra inundata*, from MADw 48857, corresponding to Berry & Rosales 6393. All scale bars represent 100  $\mu\text{m}$ . A. Transverse section from the bottom of the stem showing small, angular vessels, thin-walled polygonal fibers, narrow rays, and banded apotracheal parenchyma. B. Tangential section showing narrow rays, 8-celled axial parenchyma strands, thin-walled fibers and laticifers (arrows). C. Radial section showing large ray-fiber pits (arrows) and thin fiber walls. D. Radial section showing slight degree of intrusive growth in the fibers, and the large number of conspicuous fiber pits. E. Tangential section showing the ends of two vessel elements, each with faint but distinct helical thickenings (arrows). F. Transverse section from the top of the stem showing features typical for other *Micrandra* species: larger, rounded vessels and thicker-walled fibers.

larger leaves and is typical of well-drained soils on uneven terrain and on the lower slopes of tepuis. *Micrandra heterophylla* J. Poiss. was described from the "upper Orinoco" region of Venezuela (Poisson 1902), which could conceivably correspond to the area where *M. inundata* occurs. Poisson wrote that the material he received included a piece of root with an abundant mat of rootlets, which he took to indicate that the plant grew in water or in a very moist place. According to the (unnamed) collector of the plants, they had come from large colonies along the banks of the upper Ori-

noco. We examined the type material of *M. heterophylla* in Paris, and it is clearly distinct from *M. inundata*, with much larger, acuminate-tipped, long-petiolate leaves. These specimens were also seen by R. E. Schultes, who annotated them as *M. siphonoides* in 1950 and again in 1993. Whether or not these plants came from a habitat as strongly flooded as that of *M. inundata* is not clear, but the conspicuous, stiff rootlets of *M. inundata* occur on the lower trunk, not on the roots as in the description of *M. heterophylla*.

The two collections of *Micrandra inundata* from the

Río Negro drainage differ from those in the Orinoco drainage by having more elliptic leaves with an acute apex, longer petioles, and larger and laxer inflorescences. This may be an indication of significant genetic differentiation from the Orinoco basin populations, but they are included here under *M. inundata* because they share the species' short stature and inhabit similar flooded habitats along black-water rivers.

**Additional Specimens Examined.** VENEZUELA. Amazonas: Río Temi ca. 1 km above Yavita, 2°54'42"N, 67°24'12"W, ca. 110 m, 9 Mar 1996, *Berry, Romero & Brako* 6123 (F, GH, INPA, K, MO–2 sheets, NY, US, VEN, WIS); 2°55'04"N, 67°24'29"W, 110 m, 18 Nov 1996, *Berry & Rosales* 6393 (GH, MG, K, MO, NY, VEN, WIS); Río Temi 2 km NW of Yavita, 2°56'32"N, 67°48'44"W, 110 m, 3 Jun 1996, *Aymard, Berry & Melgueiro* 11291 (GH, INPA, K, MO, NY, PORT, TFAV, VEN, WIS); No Temi near Úquira, 3°07'50"N, 67°23'44"W, 110 m, 21 Nov 1996, *Berry & Rosales* 6472 (GH, MO, NY, TFAV, VEN, WIS); west side of Laguna de Úquira, west side of Río Temi, 6 km air distance S of mouth of river, 3°10'42"N, 67°23'02"W, ca. 100 m, 6–7 Mar 1996, *Berry, Romero & Brako* 6048 (MO, TFAV, VEN, WIS); Río Temi between Úquira and Cuya, 3°06'07"N, 67°23'22"W, ca. 100 m, 8 Mar 1996, *Berry, Romero & Brako* 6066 (DAV, F, GH, K, MG, MO, NY, TFAV, U, US, WIS); Río Temi between Budare and Yavita, 2°52'–55'N, 67°18'–27'W, ca. 110 m, 26 Nov 1995, *Berry, Duno & Romero* 5681 (GH, INPA, K, MO–2 sheets, NY, TFAV, VEN, WIS); lower Río Temi, 3°10'N, 67°22'W, 100 m, 9 Nov 1992, *Berry & Melgueiro* 5365 (GH, MO, TFAV, WIS, VEN); alrededores de Yavita (No Temi), 125 m, 6–19 July 1969, *Bunting, Akkermans & Van Rooden* 4037 (MY, U, VEN); lower part of the Río Baría, 1°27'–1°10'N, 66°32'–66°25'W, 80 m, 22–23 Jul 1984, *Davidse* 27669 (DAV, GH, NY, MO, WIS); area pantanosa abierta, seca temporalmente, a la orilla derecha del Alto Caño Yagua, 18 Feb 1979, *Huber* 3186 (DAV, VEN); riberas del Caño Ucata, arriba de San Juan, approx. 4°20'N, 67°49'W, 70 m, 19 Oct 1989, *Romero & Guánchez* 2105 (GH, MO, NY, TFAV); Caño San Miguel between Limoncito and Caño Ikebenie, 70 km above river mouth, 100–140m, 29 Jun 1959, *Wurdack & Adderley* 43250 (F, NY, VEN); Río Atabapo, 125–140m, 4 Jun 1959, *Wurdack & Adderley* 42933 (F, NY, US, VEN); Yavita, 128m, 1942, *Williams* 14041 (VEN).

#### WOOD ANATOMY

Four wood samples from near the bark of *Micrandra inundata* (*Berry & Rosales* 6393, base and top of stem; *Berry et al.* 6048, base and top of stem) were sectioned and macerated using standard microtechnique protocols for light microscopy. Slides and wood samples are housed at MADw. Sections and macerations were observed by light microscopy, and anatomical measurements were taken in part by a computer-assisted dig-

itizing tablet and in part by a calibrated ocular micrometer. Fifty fibers were measured for fiber data, 25 vessel elements for vessel data, and 50 rays for ray data. Element length data are expressed as (minimum value) average value (maximum value) standard deviation, in micrometers. Most frequent ranges were reported for intervessel pit sizes and ray widths. The IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee 1989) was used as a standard for description. Characters not mentioned are absent or not applicable.

Wood anatomical variation in this species is extreme due to a substantial change in wood specific gravity from the base to the top of the stem. The quantitative data for the description are reported as basal stem values [top stem average values] if the values differ. Qualitative features mentioned in the description are based on all four wood samples unless otherwise noted.

**Macroscopic Features.** Sapwood whitish to light orange in color grading to orange-brown heartwood. Wood darkens gradually upon exposure. Wood is low density, basic specific gravity (SG) approximately 0.20 [0.37].

**Microscopic Features.** Growth rings more or less distinct. Diffuse-porous, vessels solitary and occurring in radial multiples of 2–5 [2–10], rarely tangentially paired; less than 5/mm<sup>2</sup> (ave. 2.6/mm<sup>2</sup>) [14/mm<sup>2</sup>]. Vessel outline angular to slightly angular; tangential diam (41)100(179) st.dev. 13 µm [119 µm]. Vessel element length (551)754(1,110) st.dev. 141 µm [875 µm]; very fine helical thickenings occasionally present in tails and very rarely present in the body of the element at low stem heights. Perforation plates exclusively simple. Tyloses occasionally present, thin walled. Intervessel pits non-vestured, alternate, 8–10 µm with oval to angular outline. Vessel-ray pits with reduced borders, 8–10 µm, often angular in outline due to crowding. Fibers non-septate, very thin-walled, without helical thickenings, distinctly angular outline, (669)960(1,613) st.dev. 222 µm [1,157 µm] in length. Tangential fiber diam 35 µm [32 µm], radial fiber diam 50 µm [31 µm]. Fiber pits bordered, common in radial walls, occasionally present in tangential walls, 2–4 µm high and 2–6(max. 10) µm wide. Paratracheal parenchyma scanty to absent. Apotracheal parenchyma banded, wavy, 1 or (2) cells wide, often touching vessels. Marginal parenchyma present, 2 or 3 cells wide. Parenchyma strands typically 8-celled, without silica. Rays predominantly uniseriate, occasionally biseriate, mostly 8 per linear mm, intercellular spaces between the cell corners prominent, cells often slightly disorganized. Tall rays with 1–3 rows of square marginal cells, occasionally with square cells in the body of the ray, perhaps due to fusion of rays; rays (96)348(782) st.dev. 156 µm [272 µm] high, highest 10 rays average 573 µm [526 µm]. Upright cells rarely present at the margins of the ray.

Shortest rays composed solely of square cells or upright cells. Weakly disjunctive ray cell end walls sometimes present, typically more pronounced in the marginal cells. Wood not storied. Laticifers present, more common at top of stem. Silica bodies present in both upright and procumbent ray cells. Ray-fiber pits pronounced, occurring in two types: small, 2–6  $\mu\text{m}$ , half-bordered bottom and top of stem; large, 10–14  $\mu\text{m}$  in width, 10–12  $\mu\text{m}$  in height, half bordered, border much reduced, appearing like vessel-ray pits, often with 1 or 2 bars crossing the aperture appearing like unilaterally compound vessel-ray pits predominantly at the bottom of the stem. Crystals not observed.

**Comparative Wood Anatomy.** There is a paucity of wood anatomical literature for the tribe Micrandreae, except for *Hevea brasiliensis* (Willd. ex A. Juss.) Mull. Arg. which has been intensively studied (see Gregory 1994). *Cunuria* and *Hevea* were briefly described by Record (1938), and a macroscopic wood description was provided for the extremely dense-wooded *Micrandropsis scleroxylon* (W. Rodr.) W. Rodr. when it was first described (Rodrigues 1971). Otherwise, the group is only found in broad floristic studies focusing on the presence and absence of silica grains (Welle 1976; Espinoza de Pernia 1987). No general wood description was available for comparative work in *Micrandra*, so all comparisons are from the following species, samples of which came from MADw: *M. australis* (R. E. Schult.) R. E. Schult., *M. elata* Mull. Arg., *M. glabra* (R. E. Schult.) R. E. Schult., *M. rossiana* R. E. Schult., *M. siphonioides* Benth., *M. spruceana* (Baill.) R. E. Schult., and *M. sprucei* (Mull. Arg.) R. E. Schult.

At a macroscopic level, the wood of *Micrandra inundata* bears many similarities to the wood of other species in the genus. The general appearance of *M. inundata* on the transverse section is typical of Micrandreae, with pores solitary and in multiples occasionally with tyloses, parenchyma in apotracheal bands, and rays distinct with a hand lens. The single most distinctive feature of *M. inundata* is the very low specific gravity (SG) of the wood, being similar to balsa, which has a SG of 0.10–0.17 (Chudnoff 1984). *Micrandra inundata* has a SG of approximately 0.2 at the basal stem height, while Lorenzi (2002) reported a SG of 0.84 for *M. elata*.

At a microscopic level, the wood of *M. inundata* is distinct from that of other *Micrandra* species due to prominent differences in the vessels and the fibers. The vessels are narrower, thinner-walled, and tend to be more angular in outline in *M. inundata* than in other *Micrandra* species, imparting a distinct appearance on the transverse section (Fig. 4a). The ends of the vessel elements also bear fine helical or spiral thickenings (Fig. 4e). Fine spirals were observed in comparative material of *Micrandra* as well, and this is the first time this feature has been reported for the genus or tribe.

The fibers of *M. inundata* are very thin-walled, angular in outline, wide, short, and highly pitted (Fig. 4a, d). Other *Micrandra* taxa also have angular or rectangular fibers, but the walls are distinctly thicker, and the fibers are typically narrower in transverse section. This means that per unit area devoted to fibers, *M. inundata* has fewer fibers and thus less wall material, which contributes to its low specific gravity.

While terra firme species of *Micrandra* have fiber pits that are similar in size and shape to those in the seasonally flooded *M. inundata*, the abundance of fiber pits in *M. inundata* is distinctive within the genus (Fig. 4d). Also, the ray cells of *M. inundata* show distinct pitting within the fibers, which is uncommon in wood, and the large type often seen in *M. inundata* (Fig. 4c) is rare or absent in other species of *Micrandra*. The fibers of *M. inundata* actually resemble vessel elements, due to the extent of pitting between fibers, the presence of ray-fiber pits, and the relatively short element length and the nature of overlap on the end walls. The lack of perforations, however, clearly distinguishes them from true vessels. A term such as vascular tracheid (IAWA Committee 1989; Carlquist 1986a, 1986b, 1988) or fiber-tracheid (Baas 1983) may be appropriate for these cells, but we use the term fiber to reflect the fact that they form the ground mass of the wood, a conductive function for the cells is unknown, and at the top of the stem they are clearly fibers (Fig. 4f). In another lightweight-wooded species from the same flooded habitat as *M. inundata*, Berry et al. (2000) found cells with similar features in *Anaxagorea inundata* P. E. Berry & R. Miller (Annonaceae). In both these species, the differences with their congeners are related to the low density of the wood, with the lower stem wood resembling root wood that typically has thinner-walled fibers and fewer vessels than stem wood (Patel 1965). In the future, it would be very desirable to obtain root wood samples of both these species to compare with the stem wood.

Schultes (1952b) devoted a long article to describe the peculiarities of *Hevea microphylla* Ule, a species that occupies the same kind of heavily flooded, black-water or igapó habitats as *M. inundata*. Its fruits have coriaceous rather than woody valves that open slowly to drop the seeds below the tree rather than dehiscing explosively as in all other members of the tribe. Spending most of the year underwater, the trunk of this species is typically swollen at the base, narrows quickly to the top, and has a very sparse crown of leaves. Although Schultes reported this species as endemic to the upper Rio Negro region, we have since also found it growing sympatrically with *M. inundata* along the Rio Temi and Río Atabapo, which drain into the Orinoco basin (Berry et al. 1999). Wood specimens of *H. microphylla* from this area have an air dry density of 0.23  $\text{g/cm}^3$  for Berry 6430 and 0.26  $\text{g/cm}^3$  for Berry 6449

(values converted from Wiedenhoef 2001). This is a marked difference in air-dry density from the range reported for plantation-grown *H. brasiliensis* (0.56–0.64 g/cm<sup>3</sup>, BNS Wood Industry 2003).

The seasonally flooded habitat in which *Micrandra inundata* and *Hevea microphylla* grow is presumably the driving force behind the formation of low-density wood. Berry et al. (2000) postulated a potentially aerenchymatous role for the highly pitted, thin-walled fibers in *Anaxagorea inundata* from this habitat. Anatomically, however, no overtly delimited air-conduction system of intercellular spaces is present in the wood *M. inundata* or *A. inundata*, so that role seems unlikely. Worbes (1985) suggested that in the absence of a true air transport system, oxygen transport could not occur over the distance required by trees. Nonetheless, there is a striking convergence to lightweight-wooded species in the black-water habitats where *M. inundata* occurs, including such diverse families as Annonaceae, Apocynaceae, Bombacaceae, Euphorbiaceae, and Sapotaceae. Factors contributing to this lightweight wood syndrome may include the almost pure sand, nutrient-poor substrate in which they grow; the regular annual flooding cycle of acidic, non-turbid water; and the limited temporal opportunity for growth, when the trunks and the photosynthetic tissues of the plants are not covered by water.

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