

STUDIES IN ARACEAE I: SECTION *LEPTANTHURIUM* SCHOTT  
THE *ANTHURIUM GRACILE-FRIEDRICHSTHALII* COMPLEX OF  
CENTRAL AND SOUTH AMERICA

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*Anthurium* Schott is a tropical American genus of more than 500 species, most of which are epiphytes. Species of *Anthurium* have perhaps more intraspecific variation than any other genus of the Araceae. As a result several difficult species complexes have troubled workers of the family for many years. Nowhere is this problem more evident than in the two-species complex of *Anthurium gracile* and *A. friedrichsthali*. For this group the following names have been most frequently used: *A. gracile* (Rudge) Lindl., *A. gracile* (Rudge) Engler, *A. scolopendrinum* (Ham.) Kunth, *A. linearifolium* Engler, *A. rudgeanum* Schott, and *A. friedrichsthali* Schott. The lines of distinction between these two species are usually not accurately drawn.

The taxonomic history of *A. gracile* is confused. In 1833 Lindley transferred *Pothos gracilis* Rudge to *Anthurium*. In making the transfer he described a plant which he considered to represent the species. The identification of the plant he described, however, has no taxonomic significance since the type of *A. gracile* (Rudge) Lindl. is the type of *Pothos gracilis*, Martin s.n.

Schott (1855) established three binomials: *A. acuminatum*, *A. friedrichsthali*, and *A. rudgeanum*. Schott was of the opinion that the cultivated plant described by Lindley in 1833 was not the same species as Rudge's plant, and so referred to Lindley's plant as *Anthurium gracile* Lindley and gave Rudge's plant the new name *Anthurium rudgeanum* Schott. This is nomenclaturally incorrect in terms of the present code. One species should have been *A. gracile* (Rudge) Lindley and the species illustrated by Lindley should have been given a new name.

In 1898 Engler concurred with Schott that the cultivated plant described by Lindley was a different species from *Pothos gracilis* Rudge. Engler's treatment of the names differs from that of Schott and is also nomenclaturally incorrect. Engler made the unnecessary new combination *Anthurium gracile* (Rudge) Engler, giving *A. rudgeanum* Schott as a synonym. He considered *Anthurium gracile* Lindl. as a synonym of *A. scolopendrinum* (Ham.) Kunth. He reduced *Anthurium friedrichsthali* Schott to a variety of *A. gracile* (Rudge) Engler. He repeated these errors in 1905 when he made the most recent comprehensive treatment of *Anthurium*.

In my opinion, the plant described by Lindley in 1833 is the same species as *Pothos gracilis* Rudge. This is in contrast to the views of both Schott and Engler who had a rather narrow species concept.

The Flora of Costa Rica (Standley, 1937) used *A. friedrichsthali* and *A. scolopendrinum*, names which correctly represent the two species in the complex except that *Pothos gracilis* Rudge and *P. scolopendrium* Ham. are the same species. The Flora of Guatemala (Standley & Steyermark, 1958) dealt only with *A. scolopendrinum* and apparently described a single species, although both species of the complex occur in Guatemala. In the Flora of Panama Standley (1944) treated both *A. scolopendrinum* and *A. gracile*

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(Rudge) Lindl. but included *A. rudgeanum*, *A. friedrichsthalii*, and *A. linearifolium* as synonyms of *A. gracile*. Standley used *A. gracile* (Rudge) Lindl. for the species which is *A. friedrichsthalii* Schott and he used *A. scolopendrinum* (Ham.) Kunth for the species which is *A. gracile* (Rudge) Lindl. Jonker-Verhoef and Jonker (1953) in the Flora of Surinam also treated both *A. gracile* (Rudge) Lindl. and *A. scolopendrinum* and included *A. rudgeanum* as a synonym of *A. gracile*. Both of their descriptions are of *A. gracile* (Rudge) Lindl. They did not describe *A. friedrichsthalii* under any name.

Herbarium identifications made in recent years by various aroid workers show that no clear concept of these species exists. Most recently, specimens representing the complex have been annotated *A. gracile* (Rudge) Lindley.

Field work during the last eight years in Central America and South America has resulted in the accumulation of specimens and information which helps to define the specific limits of this species-complex more adequately.

All the names in the complex should be reduced to two species. One represents a plant with thick, almost linear leaves which are conspicuously punctate beneath. The oldest name for this plant is *A. friedrichsthalii* Schott. The other plant has thinner, more or less oblanceolate leaves which are epunctate. The oldest name for this plant is *A. gracile* (Rudge) Lindl.

*Anthurium scolopendrinum* (Ham.) Kunth must be considered synonymous with *A. gracile* (Rudge) Lindl. since no adequate character separates them. They have been separated in the past by leaf size and shape. As defined, both species have been found growing from the same roots. The species is quite variable both throughout its range and in local populations studied on Barro Colorado Island in Panama.

Although Standley in the Flora of Panama (1944) considered *A. friedrichsthalii* synonymous with *A. gracile* and other recent aroid workers have been in agreement with this, it is now clear that they are distinct species.

*Anthurium friedrichsthalii* Schott has leaves which are comparable in shape with narrow-leaved forms of *A. gracile*, but are distinguishable even then by a number of other features. The following key and descriptions enumerate the differences between *Anthurium gracile* and *A. friedrichsthalii*. Because herbarium material of these species is frequently misidentified, a limited exsiccatae is also included for the regions where both occur.

#### KEY

Leaves usually thin and oblanceolate, epunctate;  
 roots whitish; cataphylls remaining  $\pm$  entire;  
 flowers in a few longitudinal rows on the spadix  
 (usually 1 or 2 but never more than 3 rows  
 visible from any angle); tepals more than  
 2 mm wide at anthesis; fruits globose, bright  
 red (Figures 1-3). ..... *Anthurium gracile* (Rudge) Lindl.

Leaves coriaceous, usually broadly linear (of  
 nearly equal width throughout), conspicuously  
 punctate on the lower surface; roots apparently  
 never whitish; cataphylls soon weathering to  
 persistent fibers; flowers in several longitudinal

We feel that the history of the group might be explained in either of the following ways: *Spathiphyllum* arose in the neotropics and underwent speciation in response to the numerous available pollinators present in the male euglossine bees. At some stage during the evolution of the genus one or more members of the section *Massowia* were the subject of long distance dispersal and reached the old world tropics. Speciation did not occur rapidly because of the lack of pollinators, but three species did evolve. Not only did three species of the section *Massowia* of *Spathiphyllum* evolve in the old world tropics, but the genus *Holochlamys* evolved from the original immigrant(s) as well. Fused tepals would have already been present in the group, having evolved in the neotropical group of species. Further speciation has been impeded by the lack of pollinators which has also caused a lack of widespread populations of the group in the old world tropics. An alternative explanation would be to have *Holochlamys* and *Spathiphyllum* originating in the old world and migrating to the new world where they underwent rapid speciation in response to the available euglossine pollinators. This rapid adaptation to the euglossine pollinators would explain the numerous species of *Spathiphyllum* in the neotropics, but still would leave unanswered the question of the fused tepals being the primitive condition of the genus. We feel that a new world origin of the Spathiphyllaeae obviates this question of fused tepals. We would also suggest that our explanation accounts for the presence of the most advanced genus in the tribe in the old world. The lack of a fossil record, however, makes it difficult to choose between these two hypotheses. We feel that additional study might indicate that the section *Massowia* is not the most primitive or oldest group in the genus, nor even a natural subgroup of the genus.

Work in progress on floral fragrances and anatomy will be reported later.

TABLE 5: PRIMITIVE AND ADVANCED CHARACTERS IN Spathiphyllaeae\*

PRIMITIVE	ADVANCED
perianth free	perianth fused
perianth 4-6-sided (if fused)	perianth 4-sided
ovary 2-4-locular	ovary unilocular
axile placentation	basal placentation
spathe persistent	spathe marcescent

\*Adapted from Bunting (1960) and Nicolson (1968).

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rows on spadix (as many as 5 rows visible from any angle); tepals less than 2 mm wide at anthesis; fruits pale yellow-orange, not globose, of irregular shapes but broader than long and truncate at the apex

(Figures 5, 6). ..... *Anthurium friedrichsthalii* Schott

In addition to the characters provided in the key the plants also differ in their habitat at least on Barro Colorado Island. Those of *A. friedrichsthalii* are usually pendent, frequently clinging to tree branches by only a few roots (Figure 4). Moreover, they are found usually at lower heights in the forest and often in shady places. *Anthurium gracile*, however, is usually erect and occurs higher in the canopy and also along the shore on trees and tree stumps in full sunlight (Figures 1, 2). The inflorescence of *A. gracile* is erect or spreading with the spadix short and usually curved or cernuous and the spathe strongly reflexed (Figures 1, 3). The inflorescence of *A. friedrichsthalii* is always pendent with the spadix straight and longer than in *A. gracile*, and the spathe spreading or pendent (Figure 4).

***Anthurium gracile*** (Rudge) Lindl., Edward's Bot. Reg. 19:t. 1635. 1833.

*Pothos gracillis* Rudge, Pl. Guian. Rar. 23, t. 32. 1805.

TYPE: French Guiana, *Martin s.n.* (Herb. Rudge, BM).

*Pothos scolopendrinus* Ham., Prod. Plant Ind. Occ. 16. 1825.

TYPE: French Guiana, *Desvaux s.n.* (P).

*Anthurium scolopendrinum* (Ham.) Kunth, Enum. 3: 68. 1841.

*Anthurium poiteanum* Kunth, Enum. 3: 68. 1841 [Fide Engler (1905)].

*Anthurium acuminatum* Schott, Oesterr. Bot. Wochenbl. 5: 66. 1855 [Fide Engler (1905)].

*Anthurium rudgeanum* Schott, Oesterr. Bot. Wochenbl. 5: 66. 1855. Based on *Pothos gracilis* Rudge.

*Anthurium inconditum* Schott, Oesterr. Bot. Z. 8: 181. 1858 [Fide Engler (1905)].

*Anthurium macilentum* Schott, Bonplandia 7: 165. 1859 [Fide Engler (1905)].

*Anthurium gracile* (Rudge) Lindl. var. *poiteanum* (Kunth) Engl. in Martius, Fl. Bras. 3(2): 82. 1878.

*Anthurium gracile* (Rudge) Engl., Bot. Jahrb. Syst. 25: 370. 1898 [redundant transfer].

*Anthurium scolopendrinum* (Ham.) Kunth var. *poiteanum* (Kunth) Engl. in Das Pflanzenr. 4(23B): 90. 1905.

*Anthurium longipes* Matuda, Soc. Bot. Mexico Bol. 14: 23. 1952, not N.E. Br., Gard. Chron. 18: 297. 1882.

TYPE: BELIZE: *Gentle 2624A* (MICH).

Epiphyte, usually erect; caudex 1.5-30 cm long, 7-10 mm wide; internodes moderately close; roots fleshy, often whitish, 4-6 mm thick; cataphylls 2-9.5 cm long, reddish or brown, the uppermost persisting and remaining intact, ultimately deciduous. Leaves moderately thin, held  $\pm$  erect; petioles distinctly broadened and sheathed to 4.5 cm at the base, rounded but with a flat rib to 2 mm wide on the upper surface, 1-20 cm long, to 3 mm wide, slightly to moderately geniculate and nodose at the apex, the geniculum not extending onto the blade; blades broadest above the middle, gradually



Fig. 1: *Anthurium gracile*, habit ( $\times\frac{1}{4}$ )

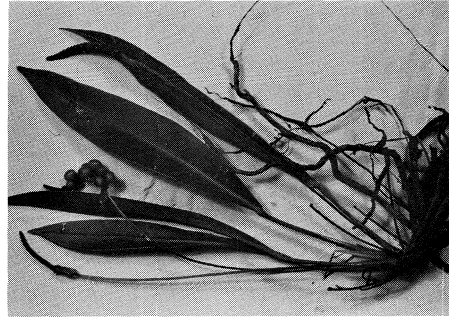


Fig. 2: *Anthurium gracile*, habit ( $\times\frac{1}{4}$ )



Fig. 3: *Anthurium gracile*, inflorescences ( $\times\frac{1}{4}$ )



Fig. 4: *Anthurium friedrichsthalii*, habit ( $\times\frac{1}{5}$ )

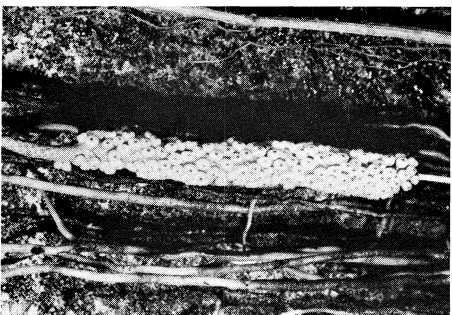


Fig. 5: *Anthurium friedrichsthalii*, fruiting inflorescence ( $\times\frac{1}{3}$ )

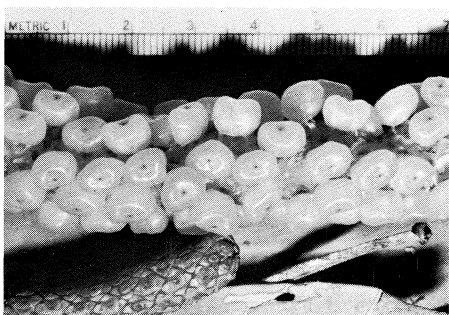


Fig. 6: *Anthurium friedrichsthalii*, close-up of flowering and fruiting inflorescences

acuminate at the apex, gradually tapered to a long-cuneate base, (8)11-32 cm long, (1)3-8.5 cm wide, essentially concolorous, glabrous, epunctate, midrib prominent above, lateral veins and collecting vein indistinct (moderately distinct on drying). Peduncles very slender,  $\pm$  erect, 21-40 cm long in flower, to 60 cm long in fruit; spathe maroon, 13-25 mm long (to 5 cm in South American material), mostly to 6 mm wide and often joining on the opposite side of the peduncle,  $\pm$  pendent; spadix sessile, mostly less than 3 cm long and 4 mm wide in flower, often  $\pm$  curved, to 10 cm long and 1.5 cm wide in fruit; tepals 2-2.7 mm wide in flower; fruiting tepals to 4.2 mm wide. Berries  $\pm$  globose, bright red, ca. 7 mm long; seeds usually 2(-4), white, embedded in a very sticky, gelatinous matrix.

The species apparently lacks any distinct seasonal behavior. Flowers and fruits may be seen at all times of the year. The species has a large root system which may sometimes become infested with black, stinging ants. It is distinguished by its thin, oblanceolate, epunctate leaves and persistent, intact cataphylls. In addition to having been confused with *A. friedrichsthali*, the species has also been confused with *A. bakeri* which has thin, linear-lanceolate, punctate leaves.

The species ranges from Guatemala and Belize to the Guianas, southern Brazil and Peru. It is also known in the West Indies from Trinidad and Hispaniola. In Panama it is known only from tropical moist forest.

GUATEMALA: ESCUINTLA: Finca Monterrey, south slope of Volcán de Fuego, *Steyermark* 64530 (F); PETÉN: Río San Martín between Cerro Ceibal and Ceibal, alt. 50 m, *Steyermark* 46166 (F). BELIZE: Stann Creek: Cocoa Branch of Sittee River, 2 km north of Victoria Peak in Cocksomb Mountains, alt. 300-500 ft, *Gentry* 7954 (MO); TOLEDO: 0.5 mi. south of Columbia Forest Station, *Vanderveen* 616, 618, 621 (MO); HONDURAS: YORO: Aguan River Valley, vicinity of Coyoles, *Yuncker et al.* 8187 (MO); ATLANTIDA: Vicinity of La Ceiba, *Yuncker et al.* 8666 (F, US); Lancetilla Valley, alt. 20-600 m, *Standley* 53378 (F, US), 54243 (F), 54613 (F). COSTA RICA: ALAJUELA: Vicinity of Los Chiles, Río Frio, alt. 30-40 m, *Holm & Iltis* 563 (F); LIMON: Finca Hamburg, on Río Reventazón below Cairo, alt. 25 m, *Standley & Valerio* 48905 (US); Finca Monte Cristo, on Río Reventazón below Cairo, alt. 25 m, *Standley* 48940 (US); Río Pacuare, alt. 50-100 m, *Burger & Liesner* 6921 (F); La Lola, along Río Madre de Dios, *Carlson* 3310 (F); Guapiles, camino a las Colonias, alt. 300 m, *J. Leon* 649 (F); La Columbiana Farm of United Fruit Co., alt. 70 m, *Standley* 36941 (US), 36993 (US); PUNTARENAS: Basin of El General, alt. 675-900 m, *Skutch* 4703 (US); CARTAGO: Atirro, *J. Donn.-Sm.* s.n. PANAMA: BOCAS DEL TORO: Little Bocas, vicinity of Chiriquí Lagoon, *von Wedel* 1268 (F), 2532 (MO); Water Valley, *von Wedel* 647 (F, MO), 1373 (F); Changuinola, *Croat & Porter* 16300 (F, MO); along railroad near Mile 10, *Croat & Porter* 16343 (MO); CANAL ZONE: Between Colón and Empire, *J. Crawford* 557 (US); Along Caño Quebrado, *Pittier* 6657 (US); *D. B. Gaillard* s.n. 9/29/190?; Río Tapia, *Standley* 26218 (US); Barro Colorado Island: *Croat* 5392 (MO), 6743 (MO), 7957a, (MO), 9522 (MO), *Ebinger* 186 (US), *Kenoyer* 187 (US), *Starry* 316 (MO); DARIEN: hill near Río Chucunaque, ca. 4 mi. below Yavisa, *Duke* 4872 (MO); Río Pirre near crossing of trail from El Real to Tucutu, 20 mi. west of El Real, *Duke* 5206 (MO); PANAMA: Villa Rosario near Interamerican Highway, *Saldaña* 9 (MO, PMA); Río Tapia, *Standley* 26218 (US). COLOMBIA: AMAZONAS: Tra-

pecio Amazonico, Río Loretoyacu, alt. 100 m, *Schultes & Black 8453* (US); Along Quebrada Arara, 2 hours by boat north of Iquitos, *Croat 7548* (MO); AMAZONAS-VAUPES: Río Apaporis between Río Pacoa and Río Kanari, *Schultes & Cabrera 13071* (US); Río Apaporis Soratama (above mouth of Río Kanari), *Schultes & Cabrera 15150* (US); CHOCÓ: Logging road 2-4 mi. northwest of Teresita, ca. 100 m. elev., *Duke 11058* (US); EL VALLE: Hacienda Valparaiso (Zarzál), near Bugulagrande forests, alt. 1020 m, *Arbelaez & Cuatrecasas 6408* (US); Valparaiso, Monte (Cauca Valley), alt. 100 m, *Dryander 2250* (US); META: Sabanas de San Juan de Arama along Río Güejar near Aterrizaje "Los Micos", alt. 500 m, *Idrobo & Schultes 1203* (US), *1233* (US), *1268* (US); Caño Tigre between Caño Grande and Caño Aquas Claras, 4.5 km southwest of Villavicentio, *Fosberg 20150* (US); 20 km southeast of Villavicentio, alt. 500 m, *Killip 34336* (US); "El Buque", *H. Garcia B. 5315* (US); NORTE DE SANTANDER: vicinity of Barranca Bermeja, Magdalena Valley between Sogamosa and Río Colorado, alt. 100-500 m, *Hauget 1375* (US); VAUPES: Riberas del Río Inirida, San Joaquin, alt. 230 m, *Fernandes 2012* (US); CAUCA: La Esmerelda near Jamundi, Cauca Valley, alt. 1100 m, *Pittier 955* (US); without locality: *Jose Celestino Mutis 56* (US).

***Anthurium friedrichsthalii*** Schott, Oesterr. Bot. Wochenbl. 5:65. 1855.

TYPE: Guatemala: Insula Cativo, *Friedrichsthal s.n.* (W). Type destroyed but drawing of type seen.

*Anthurium linearifolium* Engler, Bot. Jahrb. Syst. 25: 370. 1898.

TYPE: Panama: Canal Zone: Río Chagres, *Lehmann 4538* (B, K).

*Anthurium gracile* (Rudge) Engl. var. *friedrichsthalii* (Schott) Engl., Bot. Jahrb. Syst. 25:370. 1898.

Plant epiphytic, usually pendent, often loosely attached; caudex usually less than 15 cm long, 1-1.5 cm diam.; nodes very close, moderately rooted at nodes, the roots brownish, 3-4 mm wide; leaf scars prominently raised; cataphylls soon reduced to brown fibers, these persistent at the upper leaf bases. Leaves crowded; petioles 1.5-14 cm long, mostly less than 10 cm long, ca. 2-3 (3.5) mm wide, vaginate 12-30 mm long and enlarged at the base to 1 cm diam.; moderately to very strongly geniculate below the blade, the geniculum expanded, extending to the base of the blade; blades linear, long-acuminate at the apex, subacute at the base, 12-56 cm long, 0.8-4 cm wide (mostly less than 3 cm wide), strongly bicolored (when fresh), the lower surface light green with numerous brown punctations, midrib prominently raised above, lateral veins obscure on both surfaces (moderately prominent below when dried); collecting vein 3-4 mm from the margin. Inflorescence pendent, shorter or longer than the leaves; peduncles to ca. 2.5 mm thick, (9) 19-30 cm long (to 40 cm in fruit); spathe linear, 1-5 cm long, 3-5 mm wide, not reflexed; spadix sessile (rarely distinctly stipitate), narrowly cylindrical, 3-15 cm long, 4-5 mm wide (to 25 cm long and 2 cm wide in fruit); tepals ca. 1.7 mm high, 1-2 mm wide in flower; fruiting tepals to 4 mm long and 5 mm wide at the base, tapered upward, the apex narrow and truncate. Berries pale yellow-orange, of irregular shapes, broader than long, ca. 5 mm long, 5-8 mm wide, truncate at the apex, with a central depression, eventually falling free and suspended by the funicles of the seeds; seeds (1) 3-4 (5),  $\pm$  ovate, to 2.7 mm long, greenish or yellowish



of El Real, *Duke 4832* (MO); vicinity of El Real, Río Tuira, *Stern et al. 776* (MO, US); trail to Cerro Pirre from El Real, *Duke & Bristan 254* (MO); *Kennedy 2823* (MO); forests around Pinogana, *Pittier 6525* (NY, US); foothills of Cerro Coasi, headwaters of Río Coasi, *Duke 15566* (US); without exact locality, *Sexton 104* (MO); PANAMÁ: El Llano-Carti road, *Kennedy 2956* (MO); Peluca Hydrographic Station, *Kennedy 2964* (MO); *Lehmann 4538* (K). COLOMBIA: Chocó: Alto de Buey, alt. 1200-1800 m, *Gentry & Forero 7354* (MO); Hydro Camp #8, Helipad in premontane forest, peak over Río Curundu, alt. 1800 ft., *Duke 15324, 15325* (US); Río Trunando, Gallery between Boom and Río Saledo, *Duke 11116* (US); ANTIÓQUIA: near village of Arteaga, alt. 100 m, *Barkley 18C545* (US); between Arteaga & Chigorodó, El Tigre, rain forest, *Cuatrecasas & Willard 26116* (US); Río Caimán Nuevo, Uraba, *Archer 63* (US); EL VALLE: Buenaventura Bay, mangrove swamp, *Killip 34980* (US); Buenaventura Bay, *Killip 5224* (US); Río Calima, region of Chocó between La Trojita and Guadualito, alt. 0-5 m, *Cuatrecasas 16864* (US); NARIÑO: Gorgonilla Island, alt. 130-200 m, *Killip & Garcia 33085* (US).

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(darker on one end), embedded in a fleshy, clear matrix and bearing a slender mucilaginous, sticky appendage.

In Panama the species flowers mostly in the dry season (January-April), rarely later in the rainy season. Fruits develop slowly, requiring possibly several months, maturing mostly from June to October.

The species is recognized by the thick, linear, bicolored, punctate leaves. Juvenile plants have short, elliptic leaves. On Barro Colorado Island the plant is usually pendent from tree branches and is common in the forest from near the ground to more than 30 m high. The species ranges from Guatemala to Colombia. In Panama it is common in tropical ranges forest and is also known from premontane wet forest and from tropical wet forest.

NICARAGUA: near San Juan del Norte, *Smith 41* (F). COSTA RICA: ALAHUELA: from La Palma to San Ramón, *Brenes 5421* (F); SAN JOSE: between La Lengua and La Vibora de Puriscal, alt. 1040 m, *Jiménez M. 687* (F); CARTAGO: Tapantí, alt. 1300 m, *M. Valerio 1610* (F); HEREDIA: near bridge over Río Sarapiquí at La Virgen, *Lent 1510* (NY); PUNTARENAS: Rincon de Osa, Osa Peninsula, northwest of airfield, *Burger & Liesner 7244* (F); cloud forests above Wilson's Finca, 6 km south of San Vito de Java, alt. ca. 5000 ft., *Raven 21844* (F); province unknown: La Hondura de San Jose, *M. Valerio 724* (F). PANAMA: BOCAS DEL TORO: Río Cricamola between Finca St. Louis and Konkintoe, alt. ca. 10-50 m, *Woodson & Seibert 1883* (MO); CANAL ZONE: Barro Colorado Island: *Aviles 62* (F), *M. Brown 102* (F), *Croat 4032a* (MO), *4624* (F, MO), *5483* (MO), *6614* (MO), *6845* (MO), *6080* (MO), *8019* (MO), *8080* (MO), *8893* (MO), *12003* (MO), *Ebinger 63* (MO, US), *Kenoyer 186* (US), *Shattuck 200* (F, MO), *594* (F, MO, US), *Standley 31339* (US), *Zetek 6015* (MO); Balboa, in Powell's Garden, *Standley 2855* (US); near Gatun, *Hayes s.n.* (F); Gatun Station, *Hayes 1244* (US); hills north of Frijoles, *Standley 27457* (US); Canal Zone Road S1 between Gatun and Piña, *Liesner 1339* (MO); Río Chagres, *Lehmann s.n.* (F) (isotype of *A. linearifolium* Engl.); Mojinga Swamp, *Bailey 589* (F); Salamanca Hydrographic Station on Río Pequení, alt. 70-80 m, *Dodge, Steyermark & Allen 16523a* (MO); Colón to Empire, *Crawford 557* (NY); between Mount Hope and Santa Rita Trail, *Cowell 57* (NY); CHIRIQUI: vicinity of San Bartolo Limite, 12 km west of Puerto Armuelles, *Liesner 191* (MO); COCLÉ: Cerro Pilón, below summit, *Dwyer, Durkee, Croat & Castillon 4522* (MO); Bismark above Penonemé, *R. S. Williams s.n.* (NY, US); COLÓN: along tributary into Río Boquerón from road to Portobelo, *Kennedy 2768* (MO);  $\frac{1}{4}$  mi. southeast of Río Duque on Boyd-Roosevelt Highway, *Croat 11042* (MO); along Río Fato, alt. 10-100 m, *Pittier 3916* (US); 4 mi. southwest of Portobelo, *Croat 14120* (MO); 10 mi. southwest of Portobelo, *Kennedy 1067* (MO); Rosario near Batuncillo, *C. E. Smith et al. 3338* (F); near Peluca, on road to Nombre de Dios, 25.6 mi. from Transisthmian Highway, *Kennedy 2650* (MO); Santa Rita Ridge, ca 5.5-6 mi. from Transisthmian Highway, *Lewis et al. 5403* (MO); DARIEN: Río Balsa, between Manené and Tusijuanda, *Duke 13552* (US); along Río Tuira below El Real and Piriaque Island, *Stern et al. 974* (US); between Manené and mouth of Río Cuasi, *Kirkbride & Bristan 1420* (MO); Boca de Pauarandó on Sambu River, alt. 20 m, *Pittier 5682* (US); Estero Grande of Río Marea, *Duke 10962* (MO); vicinity of El Río Pirre, *Croat & Porter 15512* (MO); 2-3 mi. southeast

of El Real, *Duke 4832* (MO); vicinity of El Real, Río Tuira, *Stern et al. 776* (MO, US); trail to Cerro Pirre from El Real, *Duke & Bristan 254* (MO); *Kennedy 2823* (MO); forests around Pinogana, *Pittier 6525* (NY, US); foothills of Cerro Coasi, headwaters of Río Coasi, *Duke 15566* (US); without exact locality, *Sexton 104* (MO); PANAMÁ: El Llano-Carti road, *Kennedy 2956* (MO); Peluca Hydrographic Station, *Kennedy 2964* (MO); *Lehmann 4538* (K). COLOMBIA: Chocó: Alto de Buey, alt. 1200-1800 m, *Gentry & Forero 7354* (MO); Hydro Camp #8, Helipad in premontane forest, peak over Río Curundu, alt. 1800 ft., *Duke 15324, 15325* (US); Río Trunando, Gallery between Boom and Río Saledo, *Duke 11116* (US); ANTIÓQUIA: near village of Arteaga, alt. 100 m, *Barkley 18C545* (US); between Arteaga & Chigorodó, El Tigre, rain forest, *Cuatrecasas & Willard 26116* (US); Río Caimán Nuevo, Uraba, *Archer 63* (US); EL VALLE: Buenaventura Bay, mangrove swamp, *Killip 34980* (US); Buenaventura Bay, *Killip 5224* (US); Río Calima, region of Chocó between La Trojita and Guadualito, alt. 0-5 m, *Cuatrecasas 16864* (US); NARIÑO: Gorgonilla Island, alt. 130-200 m, *Killip & Garcia 33085* (US).

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