

New species and a new combination of *Anthurium* (Araceae) from Central America

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ABSTRACT

Five species of *Anthurium* are described as new. These are *Anthurium breedlovei* Croat, Vannini & Fred Mull. (sect. *Pachyneurium*) from Mexico, *A. diabloense* Vannini, Croat, & Cast.Mont (sect. *Andiphilum*) from Guatemala and Belize, *A. fredmulleri* Vannini, Croat & Cast.Mont from northern Central America (sect. *Andiphilum*), *A. ixtenamense* Croat, Cast.Mont & Vannini from Guatemala (sect. *Andiphilum*) and *A. ustupoense* Croat, Fred Mull. & Vannini from Panama (sect. *Cardiolonchium*). One new combination is made, elevating *Anthurium clidemioides* Standl. subsp. *pacificum* to the species level, *A. pacificum* (Croat & Grayum) Vannini & Croat. *Anthurium andreslovinense* Matuda is re-evaluated and re-described with a new, more complete description.

Keywords: Araceae, *Anthurium*, sect. *Andiphilum*, sect. *Cardiolonchium*, sect. *Pachyneurium*, new species.

INTRODUCTION

With 382 species (389 taxa) known from Central America, *Anthurium* is one of the larger genera among the region's flora. This constitutes nearly half of the total 784 species of Araceae in Central America. The last treatment of the genus *Anthurium* for Central America (Croat, 1983; 1986) included 122 species in Part I (Mexico and Middle America) and 148 in Part II (Panama) with 6 new species published in Part I and 82 new species in Part II, for a total of 270 species documented for the region by the mid-1980s.

Several new species have been published since that time including *Anthurium bagsaterianum* Haager (Haager, 1991); *A. acutifolium* var. *berrerae* Croat (Croat, 1991); *A. clidemioides* ssp. *pacificum* Grayum and *A. obtusum* ssp. *puntarenense* Grayum (Grayum, 1997); *A. faustomirandae* Pérez-Farr. & Croat (Pérez-Farr. & Croat, 2001); *A. darcyi* Croat (Croat, 2005); *A. guatemalense* Croat, Cast.Mont & Vannini, (Croat et. al., 2008); a new species in sect. *Cardiolonchium* from Panama,

A. kunayalense Croat & Vannini (Croat & Vannini, 2010); 16 species of sect. *Calomystrium*, mostly from Panama (Croat et. al., 2013), *A. coicoyanense* Croat & Ávila Blomb., a member of sect. *Andiphilum* from Mexico (Croat & Avila Blomberg, 2015); *A. carrasquillanum* Croat & O. Ortiz in sect. *Decurrentia* (Ortiz & Croat, 2015); *A. monteaquilense* Croat, O. Ortiz & Baldini and *A. batistae* Croat, O. Ortiz & Baldini in sect. *Xialophyllum* (Ortiz et al., 2015); several species of *Anthurium* sect. *Polyneurium*, *A. christeliae* Croat & O. Ortiz, *A. intactum* Croat & O. Ortiz and *A. palosecense* Croat & O. Ortiz (Croat & Ortiz, 2016); two species from the Chucantí Nature Reserve, *A. annularum* O. Ortiz, Baldini & Croat in sect. *Xialophyllum* and *A. chucantiense* O. Ortiz, Baldini & Croat in sect. *Polyneurium* (Ortiz et al., 2016); two species of sect. *Andiphilum* from Guatemala, *A. archibae* Croat, *A. altaverapazense* Croat & Hormell (Croat & Hormell, 2017); four new species in sect. *Calomystrium* from Mexico and Panama, *A. totontepecense* Croat from Mexico and *A. hartmanii* Croat & O. Ortiz, *A. mikenei* Croat and *A. virididifusiforme* Croat & O. Ortiz, all from Panama (Croat et al., 2017); 31 new species from Central America and Panama (Ortiz et al., 2020) as well as three new species of sect. *Andiphilum* from Mexico, *A. ixtlanense* Diaz Jim., Pérez-Farr. & Croat and *A. luzense* Diaz Jim., Pérez-Farr. & Croat (Diaz Jim. et al., 2020), and *A. roseonervium* Croat & Hodel from northern Oaxaca State (Croat & Hodel, 2020a; 2020b). Thus, a total of 51 species and three subspecies or varieties were published in Central America since the last revisions by Croat and up to the present time. In addition to the above mentioned, two additional new species of *Anthurium* were recently discovered in Mexico in sect. *Andiphilum*: *Anthurium tacotalpense* Pérez Farr., Díaz-Jim. Croat, Hentrich, Padilla Veg. and Aguilar-Rod., 2022; and another is in the process of being published by several regional botanists including Mexican botanists, Pedro Díaz Jiménez and Miguel Pérez-Farrera, and Costa Rican botanist, Marco Cedeño Fonseca. Curiously few species previously described from South America and not accounted for in earlier treatments have been found in Central America.

In summary, the Central American taxa of *Anthurium*, now numbering 389 are distributed in 15 different sections in the following quantities: *Andiphilum* (45); *Belolonchium* (8); *Calomystrium* (60); *Cardiolonchium* (31); *Dactylophyllum* (4); *Decurrentia* (11); *Digitinervium* (1); *Leptanthurium* (1); *Cordato-punctatum* (7); *Pachyneurium* (45); *Polyneurium* (13); *Polyphyllum* (4); *Porphyrochitonium* (128); *Semaeophyllum* (7); *Tetraspermium* (5) and *Xialophyllum* (22).

Recent fieldwork by botanists and naturalists working in Mesoamerica has revealed several new *Anthurium* species. As our understanding of regional phytogeography improves and plant collections are made in previously unexplored or lightly botanized, biodiverse regions of Mexico and Central America, many more novelties are to be expected. Finally, five new species are being published in this paper.

Methods and Materials

Species described here were studied from both living material in the field and herbarium specimens at the Missouri Botanical Garden (MO) and at the Universidad San Carlos (AGUAT) in Guatemala City as well as in the living collections of Jay Vannini. Species were compared with all similar species from Central America as well as adjacent areas of Colombia as well as all

appropriate type specimens which are mostly available for study at the Missouri Botanical Garden or by using online databases. The Lucid Anthurium Key which was used to help isolate the new species is a multi-entry computerized key wherein all appropriate conservative character states have been recorded and the key works by a process of elimination. As conservative character states are entered into the computer, any species lacking that state are eliminated, resulting in a list of up to ten or more species. These species are then carefully compared with the material being studied to see if there are matches. To assure that a species is a novel one, other attempts are used in the key using other characters. The Lucid Anthurium Key was first developed at Kew Gardens, but for the past 15 years the key has been further modified and greatly augmented with more species at the Missouri Botanical Garden. More information can be obtained from Lucid, see <https://www.lucidcentral.org/key-search/>

Colors referenced by HEX numbers can be defined as a series of numbers. For more information see <https://www.codeconquest.com/hex-color-codes/>

NEW SPECIES DESCRIBED HERE

Anthurium breedlovei Croat, Vannini & Fred Mull., **sp. nov.** — Type: MEXICO. Chiapas: Municipio de Berriozábal, on flats near Berriozábal, thorn woodland (secondary growth), ca. 16°47'22"N, 93°14'58"W, 830 m, 23 Aug. 1981, *D. E. Breedlove 52375* (holotype, MO-3028705; isotype, CAS, not seen). **Figures 1–9.**

Diagnosis: *Anthurium breedlovei* is most characteristic of *Anthurium* sect. *Pachyneurium* in having short internodes, a dense cluster of roots and rosulate leaves but is quite different from any other member of the sect. in Mexico. In the Lucid Anthurium Key, the species tracks to *Anthurium nizandense* Matuda which sometimes shares a similar leaf blade shape, but that species differs by its more long-petiolate leaves, blades that dry darker brown and less coriaceous with the primary lateral veins extending mostly to the margins as well as by having inconspicuous tertiary veins. *Anthurium breedlovei* might be confused with young plants of *A. jimenezii* Matuda, but even in their juvenile condition, they do not have petioles shaped like those of *A. breedlovei*, but rather they are subrounded or trapezoidal.

Terrestrial or epiphytic; stems short, less than 6 cm long; internodes short, ca. 1 cm diam.; cataphylls 4.5–5.6 cm long, 1-ribbed, persisting intact, gray-brown, matte. *Leaves* with petioles (2.5)3.0–3.5 cm long, sharply and deeply sulcate adaxially on drying, narrowly rounded abaxially, sometimes sharply quadrangular, drying light brown, matte; blades lanceolate, 27–40.5 cm long, 4.2–9.5 cm wide, 2.6–3.8 times longer than wide, acute with a short apiculum at apex, acute to weakly attenuate at base, drying grayish yellow-brown and weakly glossy above, slightly paler, yellow-brown and semiglossy below; midrib narrowly rounded, drying irregularly and prominently ridged above, narrowly rounded, finely and regularly ridged, darker below; primary lateral veins 6 to 8(11) per side, departing midrib at a 40–50° angle, narrowly rounded and only weakly apparent above, narrowly rounded and moderately prominent, concolorous below; tertiary veins prominulous upon drying on both surfaces; collective veins arising from middle to upper primary lateral veins, 7–10 mm from margins; upper surface smooth and



Figure 1. *Anthurium breedlovei* Croat, Vannini & Fred Mull. Habit.



Figure 2. *Anthurium breedlovei* Croat, Vannini & Fred Mull. Habit, showing abaxial leaf blades.



Figure 3. *Anthurium breedlovei* Croat, Vannini & Fred Mull. Leaf blade,



Figure 4. *Anthurium breedlovei* Croat, Vannini & Fred Mull. Leaf blade, abaxial surface.



Figure 5. *Anthurium breedlovei* Vannini & Fred Mull. Stems and petioles.



Figure 6. *Anthurium breedlovei* Croat, Vannini & Fred Mull. Juvenile plant (cultivated by J. Vannini).



Figure 7. *Anthurium breedlovei* Croat, Vannini & Fred Mull. (left) Compared with *A. guatemalense* (right), juvenile plants (cultivated by Jay Vannini, photo J. Vannini).



Figure 8. *Anthurium breedlovei* Croat, Vannini & Fred Mull. Herbarium specimen showing entire plant with leaf blade, abaxial surface, with apex folded over, revealing adaxial surface.



Figure 9. *Anthurium breedlovei* Croat, Vannini & Fred Mull. Herbarium specimen showing entire plant with leaf blade, abaxial surface and inflorescence.

glossy at higher magnifications, sometimes sparsely pustular; lower surface matte and granular at higher magnifications. *Inflorescence* erect; peduncle 23–35 cm long, drying 2.5 mm diam, bluntly ribbed; spathe oblong-lanceolate, green, 4.3–5 cm long, 0.5–1.5 cm wide, reflexed; spadix green becoming red post-anthesis, cylindroid-tapered, sessile, 3.3–4.7 cm long, 5.3–7 mm diam. at base, 3.5–5 mm diam. at 1 cm from apex; flowers 7–8 visible per spiral, 1.5–1.8 mm long and wide; tepals; stamens held in contiguous cluster around the style at the level of the tepals; anthers 5–6 mm long, 7–8 mm wide; thecae narrowly ovate, somewhat divaricate. *Infructescence* not seen.

Distribution and ecology — *Anthurium breedlovei* is endemic to Mexico and is known only from the type locality in eastern Chiapas State at 830 m in a *Tropical deciduous forest* life zone (Holdridge, 1967).

Etymology — This species is named in honor of the late, Dr. Dennis Breedlove from the California Academy of Science who discovered the type specimen. Breedlove spent several years collecting in Chiapas while working on an ethnobotanical study under the direction of Peter Raven at Stanford University.

Comments — Another similar *Pachyneurium* in the region is *Anthurium guatemalense* Croat, Cast. Mont & Vannini which differs in having longer, more-or-less oblong, darker brown drying and proportionately much narrower blades that are more than 8 times longer than broad. Seemingly similar in appearance are some specimens of *Anthurium seleri* Engl. and *A. ixtenamense* in sect. *Andiphilum* with which this species shares many features, especially the sharply sulcate petiole and long, narrow leaf blades.

Paratype: CULTIVATED. California. Origin: Mexico. Chiapas: Vic. of Berriozábal, ca. 16°49'N, 93°17'W, 1000 m, vouchered, July 2021, *T. B. Croat & J. Vannini 107941* (CHIP, MO).

Anthurium diabloense Vannini, Croat & Cast.Mont, **sp. nov.** Type: GUATEMALA. Izabal: onshore, immediately adjacent to Cayos del Diablo, Aldea Las Pavas, Santo Tomás de Castilla Municipality, 15°26'56"N, 88°38'49"W, 8 m, *J. J. Castillo Mont & J. Vannini 3108* (holotype, AGUAT; isotypes, K, MO). **Figures 10–17.**

Diagnosis: *Anthurium diabloense* is in sect. *Andiphilum* and is distinguished by its mostly lithophytic habit, short internodes, terete or slightly flattened petioles distally, and its conspicuously triangular-sagittate, coriaceous, highly glossy, gray-green or pewter-colored fresh leaf blades that are held upright with elongated posterior lobes and with flat, slightly concave, or slightly convex lateral margins as well as the bright orange berries with large seeds. In addition, it has an unusual and characteristic arcuate to subcordate venation pattern where the first pair of collective veins form a narrowly ovate line from the very base to the apex of the blade.

Lithophyte on exposed karst, occasionally terrestrial loosely rooted into leaf litter; foliage to 50 cm tall; stem short; internodes short; cataphylls chartaceous-subcoriaceous, 5.0–9.0 cm



Figure 10. *Anthurium diabloense* Vannini, Croat & Cast. Mont. Plant in habitat.



Figure 11. *Anthurium diabloense* Vannini, Croat & Cast. Mont. Cultivated plant showing side view of leaf.



Figure 12. *Anthurium diabloense* Vannini, Croat & Cast. Mont. Petioles and cat-



Figure 13. *Anthurium diabloense* Vannini, Croat & Cast. Mont. Leaf blade, adaxial surface.



Figure 14. *Anthurium diabloense* Vannini, Croat & Cast. Mont. Fruits.



Figure 15. *Anthurium diabloense* Vannini, Croat & Cast. Mont. Seeds.



Figure 16. *Anthurium diabloense* Vannini, Croat & Cast. Mont. Flattened leaf with inflorescence.



Figure 17. *Anthurium diabloense* Vannini, Croat & Cast. Mont. Herbarium specimen showing leaf blade, adaxial surface with petiole and inflorescence.

long, narrow acuminate, with two acutely margined ribs at base, pale greenish pink when fresh and drying light brown, persisting intact at apex, and splitting at base. *Leaves* with petioles terete for most of their length, slightly flattened in distal $\frac{1}{4}$ to $\frac{1}{3}$, geniculum shallowly sulcate 1–2 cm long, scarcely thicker than or paler than petiole; blades conspicuously triangular-sagittate, to 35 cm long, 24 cm wide, 0.8–1.5 times longer than wide; posterior lobes directed upward and outward from the midrib (rarely almost touching) and the sinus spatulate to narrowly spatulate, the lobes more spreading when flattened and the sinus parabolic to open V-shaped or arcuate; basal veins 2 or 3 pairs, etched in upper surface, weakly raised below, 1st pair free to the base, 2nd & 3rd pairs fused to 1 cm, entirely naked along the sinus; upper surface usually gray-green or pewter-colored, drying light yellowish brown; anterior lobe 9.5–16.0 cm long, the margins flat, at least in the lower half, somewhat concave or broadly convex toward apex and narrowly acuminate and downturned at apex; posterior lobes 7–19 cm long, 4–8 cm wide, 1.5–2.0 times longer than wide; midrib slightly raised above and below and concolorous above, narrowly rounded and slightly paler below; primary lateral veins 2 per side, sunken above and slightly raised below, departing midrib at a 65° angle; collective veins arising from the 1st pair of arcuate to subcordate basal veins, spreading broadly then prominently curved toward the apex and obliquely merging with the margins near the tip of the blade; 2nd pair of collective veins reflexed-spreading toward apex and merging with the margin above the middle of the blade. Fully mature plants hold up to 20 leaves in cultivation, although usually far fewer in nature. *Inflorescence* erect, held well above the foliage at anthesis, decumbent when in fruit; peduncle to 23 cm long, 2 mm diam., terete; spathe lanceolate, pale green, reflexed, moderately tapered, 4–8 cm long, 1.3 cm wide, narrowly long-acuminate (acumen 1.3 cm long); spadix sessile, 3–11 cm long, 1.4–7.0 mm diam. at base, tan or reddish brown at anthesis, dark green to gray-green post-anthesis if pollinated, brown if not; flowers 2(3) visible per spiral, 3.4–3.6 mm long, 3.2 mm wide; pistils weakly protruding, 1 mm diam., square, weakly raised, purplish violet; stamens held at the surface of the tepals, crowded around and covering stigma, 0.6 mm long, 0.4 mm wide. *Infructescence* pendent, spadix to 11 cm long, berries subglobose, ridged or occasionally faceted when green, ripening from dark green to orange (HEX color code #fa691d) with a sunken brown apex when fully ripe, to 12 mm × 8.5 mm, seeds 1 or 2 per berry, white to cream-colored, to 7 × 7 mm.

Distribution and ecology — *Anthurium diabloense* is endemic to eastern Guatemala in the Departments of Izabal, Alta Verapaz, El Petén, and extreme southwestern Belize in the Toledo District from sea level to ca. 300 m in *Subtropical wet forest* life zones.

Etymology — The species is named for Cayos del Diablo, a pair of forested karst outcrops located adjacent to the coast in the southwestern Bahía de Amatique and just opposite the type locality on the mainland.

Comments — This species is highly localized in its distribution at all localities we are familiar with, although it can be conspicuous and locally abundant where it does occur. It is a shade-obligate, canopy-dependent species and despite successfully colonizing very old road cuts near the type locality, does not appear to survive in heavily disturbed forest fragments. Both in nature and in cultivation the species will flower and fruit year-round.

This slender rain forest understory inhabitant is visually like the Chiapan upland endemic, *Anthurium berriozabalense* Matuda, and a Tabascan lowland endemic, *A. tacotalpense*, especially owing to their coriaceous blades that are upright with elongated posterior lobes as well as bright orange berries with large seeds. Despite long held reservations by the two senior authors as to its proper taxonomic placement, it has previously been combined with that species despite key morphological and ecological differences (Croat & Vannini, 2006; this paper). *Anthurium diabloense* differs clearly from *A. berriozabalense* by its terete or slightly flattened petioles (versus D-shaped to sharply sulcate), more elongate cataphylls, its highly glossy gray-green or pewter-colored fresh leaves (versus semiglossy medium green fresh leaves) with flat, slightly concave or slightly convex margins (versus convex margins when mature) and its characteristic arcuate or subcordate vein pattern (versus numerous lateral veins departing the midrib at a ca. 100° angle that impart a “fishbone” aspect) where the 1st pair of collective veins form a narrowly ovate line from the very base to the apex and form the principal pair of collective veins. Mixed collections of the newly described *Anthurium tacotalpense* Pérez Farrera et al., *A. diabloense*, *A. berriozabalense* Matuda, and at least one central Chiapan upland sect. *Andiphilum* sp. nov. (Croat & Vannini, in prep.) stored in herbaria (including MO) and identified as *A. berriozabalense* Matuda or *Anthurium seleri* Engl., readily explain the confusion surrounding these very distinct and locally endemic *Anthurium* species.

Anthurium berriozabalense, as now defined, is a lithophytic or terrestrial species endemic to middle elevation cloud forest ecosystems of western Chiapas State, Mexico on the Gulf drainage between ca. 1,000 and 1,500 masl.

Anthurium diabloense is most closely related to *A. tacotalpense* Pérez-Farr. et al. from “bosque tropical perennifolio” of the Gulf drainage of Tabasco and northern Chiapas, Mexico between 50 and 130 masl. This species differs from *A. diabloense* in its basal and lateral vein arrangements, having a flattened or D-shaped petiole, leaf lamina broadest at the middle, bright green spadix at anthesis and smaller berries.

Paratype: CULTIVATED. California, cultivated plant grown from type locality (Guatemala. Izabal: onshore, immediately adjacent to Cayos del Diablo, Aldea Las Pavas, Santo Tomás de Castilla Municipality, 15°26'56"N, 88°38'49"W, 8 m, cultivated by Jay Vannini in California), vouchered, 11 March 2021, T. B. Croat & J. Vannini 107917 (BIGU, MO, US).

***Anthurium fredmulleri* Vannini & Croat, sp. nov.** — Type: Cultivated in California. T. B. Croat & J. Vannini 107897 (holotype, MO-6940748; isotypes, AGUAT, K, TEFH, US). **Figures 18–28.**

Diagnosis: *Anthurium fredmulleri* is in sect. *Andiphilum* and is characterized by its large mature size, terrestrial habit, short internodes, short somewhat deciduous cataphylls, subterete petioles, narrowly triangular-sagittate, narrowly long-acuminate, matte, subvelvety to velvety blades which are 1.1–1.7 times longer than wide above with a parabolic to hippocrepiform



Figure 18. *Anthurium fredmulleri* Vannini, Croat & Cast. Mont. Adult leaf blade, adaxial surface.



Figure 19. *Anthurium fredmulleri* Vannini, Croat & Cast. Mont. Adult leaf blade, adaxial surface.



Figure 20. *Anthurium fredmulleri* Vannini, Croat & Cast. Mont. Adult leaf blade, abaxial surface with geniculum.



Figure 21. *Anthurium fredmulleri* Vannini, Croat & Cast. Mont. Stem apex and weathered fibrous cataphylls.



Figure 22. *Anthurium fredmulleri* Vannini, Croat & Cast. Mont. Inflorescence with nearly ripe berries.



Figure 23. *Anthurium fredmulleri* Vannini, Croat & Cast. Mont. Stem with pre-anthesis inflorescence, roots, and cataphylls.



Figure 24. *Anthurium fredmulleri* Vannini, Croat & Cast. Mont. Newly opening inflorescence at anthesis, side view.



Figure 25. *Anthurium fredmulleri* Vannini, Croat & Cast. Mont. Newly opening inflorescence.



Figure 26. *Anthurium fredmulleri* Vannini, Croat & Cast. Mont. Newly opening inflorescence at anthesis with close-up of stamens.



Figure 27. *Anthurium fredmulleri* Vannini, Croat & Cast. Mont. Inflorescence with nearly ripe berries.



Figure 28. *Anthurium fredmulleri* Vannini, Croat & Cast. Mont. Inflorescence with loose berries.

sinus, 4 or 5 pairs of basal veins with the 1st pair free to the base, a posterior rib to 8 cm long and naked throughout most of their length as well as a spreading-reflexed green spathe and a weakly to prominently stipitate medium green spadix.

Plant terrestrial in mixed rock and clay soils in very wet areas, including streamside; stems short; internodes short, 2–3(5) cm diam.; roots moderately sparse, thick, to 5 mm diam; cataphylls to 12 cm long, soon turning medium dark, yellow-brown, somewhat briefly persisting, somewhat marcescent, then deciduous. *Leaves* with petioles (16)50–90(150) cm long, (4)8–10 mm diam., terete in distal ½, becoming flattened to obscurely sulcate at base, medium green, matte, densely pale-speckled throughout, held more or less erect; geniculum (2)3–4 cm long, (5)7–9 mm diam., slightly paler and slightly thicker than shaft of petiole; blades narrowly triangular-sagittate, (25)50–90 cm long, (15)29–60 cm wide, 1.1–1.7 (averaging 1.4) times longer than wide, as long as or 1.8 times longer than petioles, sub-pendent from petioles, narrowly long-acuminate at apex, deeply lobed at base; margins sometimes broadly undulate, dark green and matte-velvety above, paler and semiglossy below, drying greenish and matte above, green and semiglossy below; anterior lobe 20–65 cm long (much larger), 1.5–2.5 times longer than posterior lobes, broadly rounded to nearly straight along the margins, occasionally undulate; posterior lobes 9–25 cm long, 6–12 cm wide, directed toward the base and slightly in-turned and with inner margins sometimes turned up against each other in life, 9–13 cm long, 6–9 cm wide; sinus parabolic to hippocrepiform when flattened, 5–20 cm deep, 4–10 cm wide; major veins on upper surface usually paler green with a discolored space along margins, especially the midrib and upper basal veins; basal veins 4–6 pairs, 1st pair free to the base, 2nd pair fused from a few mm to 3–4 cm, 3rd pair fused 4–8 cm; 4th pair fused to 12 cm; posterior ribs nearly straight, naked throughout most of their length; midrib narrowly rounded and paler above, less narrowly rounded and slightly paler below; upper surface conspicuously velvety, drying densely and uniformly granular, matte; lower surface moderately glossy with inconspicuous minor veins, drying moderately paler, semiglossy and smooth, punctations and short pale lineations absent on both surfaces. *Inflorescences* sub-erect; peduncle 7–14 cm long, 6 mm diam.; spathe spreading-reflexed, to spreading, 10 cm long, 4 cm wide, green, tinged with purple on inner surface (appearing light brown), pale green on outer surface, long-acuminate at apex, obliquely attached at ca. a 45° angle, the sides sometimes turned downward, persisting into fruit; spadix slightly tapered, medium green to yellowish green, matte to semiglossy, 9–10 cm long, (5)7–10 mm diam., weakly to prominently stipitate to ca. 1 cm (stipe medium green and glossy); stamens scarcely protruding above the tepals; anthers faintly yellowish, the filament weakly exposed; thecae weakly divaricate; pollen loose, pale yellow. *Infructescence* erect, sub-cylindroid, ca. twice as long as broad, the spadix prominently stipitate; berries dark green with a ridged, sunken apex, ripening bright orange (HEX color code #ff781f)*, subglobose, slightly longer than broad, 1.6 cm long, 1.3–1.6 mm diam., emerging and suspended on 4 slender filaments; seeds to ca. 1 cm long. *[A HEX color is expressed as a six-digit combination of numbers and letters defined by its mix of red, green and blue (RGB)].

Distribution and ecology — *Anthurium fredmulleri* is known from cultivation in Guatemala and California but wild populations occur at near 1,000 m in a *Lower montane wet forest* or *Montane moist forest* life zones. Plants in nature inhabit shady, very humid areas in the understory, in-

cluding stream banks where some plants had their root systems submerged for several months of the year during the rainy season. The exact details of the locality of the single known wild population will remain unpublished owing to the rarity and beauty of this species and its obvious interest to ornamental horticulture. This decision was made to prevent the intense commercial collecting pressure that has followed recent descriptions of several horticulturally desirable Araceae around the world with vulnerable populations (see *Philodendron patriciae* Croat and *Alocasia azlanii* K.M.Wong & P.C.Boyce for two examples).

Etymology — The species is named in honor of naturalist and explorer, Fred Muller, who discovered and photographed the species in nature. Fred, a native of the Department of Alsace in France, operates a natural history-oriented guiding business in Guatemala and has a special interest in Araceae, as well as herpetology. Because his business involves tours to remote regions of the neotropics in search of rare flora and fauna, he has opportunities to find many interesting plant species.

Comments — *Anthurium fredmulleri* is perhaps closest to *A. leuconeurum* Lem., a much smaller species with more numerous and contrast-colored leaf veins and slender, elongated inflorescences held well above the foliage that occurs in middle elevations forests of Chiapas State, Mexico, and adjacent Guatemala in the Department of Huehuetenango, and does share several characteristics, especially in its lithophytic habit, general aspect and thick, partially exposed roots. It also resembles *Anthurium archiblae* Croat from western Guatemala that also has subvelvety leaves but that species differs in being much smaller in size at maturity, having a shorter more robust peduncle, almost sessile inflorescence, and a short stubby spadix, cupped, suborbicular spathe and adaxial leaf blade surfaces that are subglossy to subvelvety in aspect. *Anthurium fredmulleri* was photographed in nature, flowering and with berries at varying stages of development in October. Young plants in cultivation will flower year-round.

Anthurium ixtenamense Croat, Cast.Mont & Vannini **sp. nov.** — Type: Guatemala: Huehuetenango: San Sebastián Coatán, Aldea Ixtenam, ca. 1700 m, cultivated by Jay Vannini, California, 1 Jan. 2004, *J. J. Castillo Mont & J. A. Castillo Mont 3049* (holotype, AGUAT; isotypes, K, MEXU, MO, US). **Figures 29–41.**

Diagnosis: *Anthurium ixtenamense* is an unusual member of sect. *Andiphilum* (owing to its more or less oblong leaves) and is characterized by its persisting intact cataphylls, narrow lanceolate coriaceous leaves with truncate to acuminate posterior lobes, deeply and narrowly V-sulcate petioles which may be sharply acute to 7-ribbed abaxially, 8–10 primary lateral veins per side which are etched and concolorous above, flat below, with two pairs of basal veins, a single pair of collective veins arising from the lowermost pairs of basal veins as well as a long-peduncle inflorescence with green spathe and spadix and orange berries.

Terrestrial; stem short; internodes short, to 2.5 cm diam.; cataphylls 1/2 to almost fully as long as petioles, medium green, turning brown and persisting more or less intact. Leaves with petioles 8–21 cm long, 5–10 mm thick, 3.5–8.0 mm diam., medium green, weakly glossy, deep-



Figure 29. *Anthurium ixtenamense* Croat, Vannini & Cast. Mont. Habit.



Figure 30. *Anthurium ixtenamense* Croat, Vannini & Cast. Mont. Habit showing abaxial leaf surfaces.



Figure 31. *Anthurium ixtenamense* Croat, Vannini & Cast. Mont. Juvenile leaves, abaxial surface left, adaxial surface right.

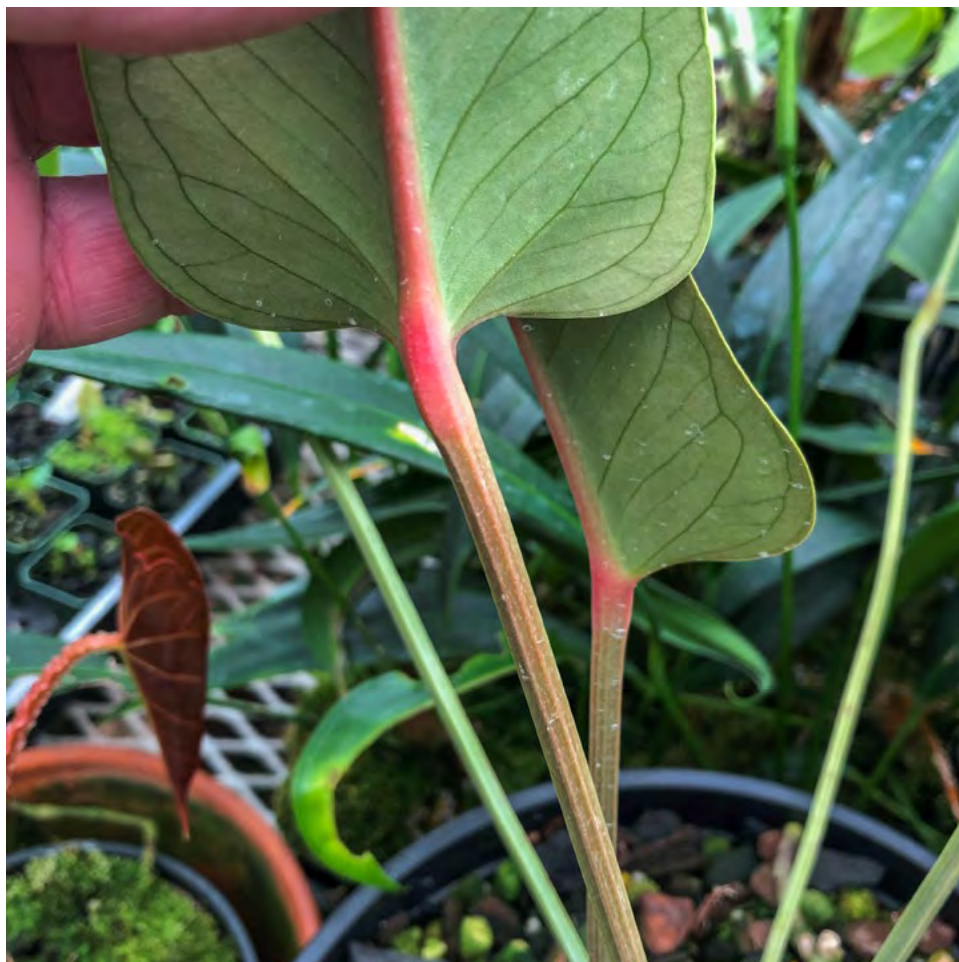


Figure 32. *Anthurium ixtenamense* Croat, Vannini & Cast. Mont. Juvenile leaf showing reddish geniculum.



Figure 33. *Anthurium ixtenamense* Croat, Vannini & Cast. Mont. Abaxial leaf surface.



Figure 34. *Anthurium ixtenamense* Croat, Vannini & Cast. Mont. Petioles.



Figure 35. *Anthurium ixtenamense* Croat, Vannini & Cast. Mont. Showing petiole cross-sectional shape.



Figure 36. *Anthurium ixtenamense* Croat, Vannini & Cast. Mont. Showing ribbing on petioles.



Figure 37. *Anthurium ixtenamense* Croat, Vannini & Cast. Mont. Inflorescence showing purplish violet spadix and green spathe.



Figure 38. *Anthurium ixtenamense* Croat, Vannini & Cast. Mont. Spadix at anthesis with small bees.



Figure 39. *Anthurium ixtenamense* Croat, Vannini & Cast. Mont. Two infructescences and one inflorescence.



Figure 40. *Anthurium ixtenamense* Croat, Vannini & Cast. Mont. Inflorescence.



Figure 41. *Anthurium ixtenamense* Croat, Vannini & Cast. Mont. Herbarium type specimen (J. J. Castillo Mont 3049).

ly and narrowly V-sulcate adaxially, sharply acute to 7-ribbed abaxially, sheathed 2.5 cm at base; geniculum 2.5 cm long (to 1.5 cm long and tinged pinkish red on younger plants), sharply and broadly sulcate adaxially, narrowly rounded abaxially, pale green; blades more or less ovate-oblong, 38–62.5 cm long, 7 cm wide, 8.9 times longer than wide, broadest near the base at in the lower 1/3 of the blade, about 13 cm above base with a weak constriction in lower 1/4 of blade, gradually tapered to apex, acute at apex, more or less truncate to weakly subcordate at base, thinly coriaceous, dark green and semiglossy above, moderately paler and weakly glossy below; midrib narrowly rounded and weakly paler above, acute and paler below, tinged pinkish red on younger plants; primary lateral veins 8–10 per side, departing midrib at a 35–40° angle, etched and concolorous above, flat distinct and darker below; basal veins 2 pairs; collective veins, 1 pair arising from the lowermost pairs of basal veins, etched and equal to primary lateral veins above, distinct and moderately loop-connected below; tertiary veins seemingly lacking. Inflorescence with peduncle 44–48 cm long, subterete, 2.5–3.0 mm diam., the side below the abaxial surface of the spathe with a bluntly acute rib; spathe green, 3.8–9.2 cm long, 1.5–3.1 cm wide at base, ca. 2 cm wide near apex, acuminate-apiculate at apex (apical 1 cm tightly rolled into a cone, the apiculum 6 mm long), tightly coiled under with apex directed back toward the base; spadix green to purplish violet, 6.3–10.7 cm long, 6–10 mm diam. midway, 8 mm diam. in apical 1/3; flowers 5(6) visible per spiral, 2.6–2.7 mm long, 2.8–3.0 mm wide, square to sub-4-lobed, margins parallel and straight to sigmoid, the side perpendicular to spirals sinuate, drying brownish, matte; tepals smooth, inner margin broadly rounded, outer margins 3-sided to shield-shaped and 4-sided; lateral tepals 1.6–2 mm wide; stamens held at level of tepals; anthers 0.5 mm long and wide; thecae weakly divaricate; pollen pale yellow, moist and sticky. *Infructescence* 10–15 cm long, sometimes curved; berries orange, obovate to 1.3 cm long, 1 cm diam., somewhat flattened apically with a brownish rectangular area surrounding the stigma; seeds 1 or 2 per berry, large, more than 1 cm long.

Anthurium ixtenamense flowers sporadically year-round, with ripe berries observed in cultivation in April through July.

Distribution and ecology — *Anthurium ixtenamense* is endemic to Guatemala, known until recently only from the type locality in pine-oak habitat in the Department of Huehuetenango just outside Aldea Ixtenam at 1647 m in a *Montane wet forest* life zone. In December 2021, both junior authors discovered a new population growing as lithophytes on limestone in the vicinity of Jacaltenango, Huehuetenango at a similar elevation to that of the type locality.

Etymology — *Anthurium ixtenamense* is named for the type locality near Aldea Ixtenam, San Sebastián Coatán Municipality in the Guatemalan Department of Huehuetenango. Aldea Ixtenam is surrounded by steep limestone cliffs and its place name translates to “the crag’s base” in the Chuj Mayan language. Note: The place name and species are pronounced “ISH ten ahm” or “EESH ten ahm”.

Comments — *Anthurium ixtenamense* is visually similar and closely related to *Anthurium seleri* Engl., another sect. *Andiphilum* occurring in western Guatemala and eastern Chiapas. It also

bears a strong resemblance to *Anthurium guatemalense* Croat, Cast.Mont & Vannini, another Guatemalan endemic species. That species differs by being a generally larger plant and typical member of sect. *Pachyneurium* with the leaf blades narrowly oblanceolate and 43–110 cm long, 5–20 cm wide with a spadix 5.5–11.5 cm, 6–10 mm diam. whereas *A. ixtenamense* is a member of sect. *Andiphilum* and lacks a rosulate habit with more or less oblong leaves only 38 cm long and 7 cm wide with the spadix 6.3 cm long and 6–7 mm diam. More importantly while members of sect. *Pachyneurium* have involute ptyxis with the leaf blades rolled inward from both margins while in bud, members of sect. *Andiphilum* have supervolute ptyxis with one margin of the leaf in bud rolled inward and the other rolled around it in the same direction. Its conspicuously ribbed petioles and lightly ribbed peduncles appear to be unique in sect. *Andiphilum* and are a key diagnostic character that differentiates it from individuals of *Anthurium seleri* with subcordate leaf lobes.

Anthurium ustupoense Croat, Fred Mull. & Vannini **sp. nov.** — Type: PANAMA: Comarca Guna Yala: Mainland opposite Isla Ustupo, 09°08'21" N, 77°55'23"W, 5 m, cultivated in California by Jay Vannini, vouchered 4 Sep. 2020, T. B. Croat & J. Vannini 107901 (holotype, MO-6939302; isotypes, COL, K, PMA, US). **Figures 42–45.**

Diagnosis: *Anthurium ustupoense* is a member of sect. *Cardiolonchium* and is characterized by its terrestrial habit, short internodes, sharply U-shaped, broadly and sharply sulcate petioles, subtriangular-hastate, narrowly acuminate bicolorous blades with flaring posterior lobes and with anterior lobes broadly convex and broadly confluent onto posterior lobes as well as by the short-pedunculate inflorescence with a linear-lanceolate narrowly long-acuminate spathe and the short-stipitate green, semiglossy to glossy, sub-cylindroid to cylindroid-tapered green to yellowish brown spadix.

Terrestrial; internodes short, 1.5 cm diam.; cataphylls 5 cm long, 3 cm wide at base, then markedly constricted above the base to 9 mm, drying gray-brown, matte with a subapical apiculum to 5 mm long. *Leaves* with petioles 7.0–18.3 cm long, sharply U-shaped, broadly and sharply sulcate; blade subtriangular-hastate, 17.4–22.0 cm long, 9.7–21.0 cm wide, 1.6–2.5 times longer than wide, 1.1–2.5 times longer than petioles, subcoriaceous, semiglossy, dark green above, moderately paler below, drying semiglossy above, weakly glossy below; anterior lobe broadly concave in its lower half, broadly convex toward middle, narrowly acuminate at apex, nearly truncate at base with the spreading lateral lobes; lateral lobes 4.5–11.0 cm long, 2–4 cm wide, spreading at a nearly 90° angle, narrowly rounded at apex; sinus absent or broadly arcuate and 7–20 mm deep; basal veins 3 pairs, 1st and sometimes 2nd pairs free to base; 3rd pair marginal to sinus; posterior ribs 0.7–3.0 cm long, naked throughout; midrib narrowly raised to bluntly acute and concolorous above, narrowly rounded to bluntly acute and nearly concolorous, matte and weakly side-ribbed below; primary lateral veins 3–4(5) per side, departing midrib at a 20° angle, narrowly rounded and concolorous on both surfaces; collective veins arising from the 1st or 2nd pairs of basal veins; tertiary veins moderately raised; upper surface faintly and sparsely short pale-lineate; lower surface faintly pale-speckled, lacking punctations. *Inflorescence* erect with faint medicinal scent at anthesis; peduncle 10.0–12.5 cm long, dark green; spathe



Figure 42. *Anthurium ustupoense* Croat & Vannini. Habit of potted plant.



Figure 43. *Anthurium ustupoense* Croat & Vannini. Petiole showing flattened adaxial surface.



Figure 44. *Anthurium ustupoense* Croat & Vannini. Petiole showing ribbed sides and abaxial rib.



Figure 45. *Anthurium ustupoense* Croat & Vannini. Showing inflorescences with spathe constricted above newly opening inflorescence.

5–7 cm long, 8–10 mm wide, (drying 4.3 cm long, 6 mm wide), linear-lanceolate, spreading-reflexed, green to yellow-green, sometimes weakly tinged brownish purple, semiglossy outside, paler and medium green, matte inside, nearly twice as long as spadix in early stages with the spathe somewhat inrolled about the end of the spadix; spadix medium green, brownish yellow to bright yellow, 4.0–5.5 cm long 4–6 mm diam., sessile with stipe to 2 mm long, short tapered-cylindroid to oblong-tapered, bluntly and narrowly rounded at apex; flowers (2)3–4 visible per spiral, the margin parallel to the spiral moderately straight to jaggedly sigmoid, those perpendicular to the spiral prominently and jaggedly sigmoid, 2.1–2.3 mm long, 1.4–1.6 mm wide on drying; tepals smooth and moderately glossy; lateral tepals 0.8–1 mm wide, subovate to 4-sided and shield-shaped; stamens held at level of tepals, anthers 0.1 mm long, 0.5 mm wide; thecae, broadly divaricate, pollen pale yellow, loose. *Infructescence* unknown.

Distribution and ecology — *Anthurium ustupoense* is endemic to Panama, known only from the type locality on the mainland adjacent to Isla Ustupo in the Comarca de Guna Yala near sea level in a *Tropical moist forest* life zone.

Etymology — *Anthurium ustupoense* is named for the type locality adjacent to Isla Ustupo in the Comarca de Guna Yala in Panama.

Comments — *Anthurium ustupoense* is similar to the polymorphic *A. ochranthum* K. Koch, because both share the same terrestrial habit, short internodes, and semi-intact and persistent cataphylls. *Anthurium ustupoense* differs from *A. ochranthum* in having U-shaped petioles, markedly subtriangular-hastate blades, few pairs of basal veins (up to 3 pairs), and a short-stipitate green, sub-cylindroid to cylindroid-tapered green to yellowish brown spadix with usually 3–4 visible per spiral. Flowering not observed in nature. Flowers year-round in cultivation.

New taxonomic reconsiderations

Anthurium pacificum (Croat & Grayum) Vannini & Croat, **stat. nov.**

Basionym: *Anthurium clidemioides* Standl. ssp. *pacificum* Croat & Grayum, *Phytologia* 82(1): 31. 1997. — Type: COSTA RICA: Puntarenas: Cantón de Golfito, Jiménez, Alto de Carbonera, camino a Cerro Osa, 08°25'30"N, 83°19'00"W, 200–350 m, 18 Sep. 1990, *A. Chacon 1062* (holotype, MO-5096171; isotypes, CR-164143, INB).

Appressed climbing epiphytic; internodes elongate, 4–7 cm long, 2–3 mm diam., drying greenish gray, matte, finely and irregularly ridged; roots intermodal, slender, smooth except for portions densely covered with root hairs; cataphylls absent. *Leaves* spreading; petioles 3.3–7.3 cm long, sheathed 0.3–0.6 their length or less, the base encircling the stem, matte, subterete, sharply and narrowly sulcate; geniculum less than 5 mm long, sulcate with a medial rib; blades narrowly ovate-subcordate, to ovate, thinly coriaceous, gradually short-acuminate to almost acute, rounded-truncate to subcordate at base, 10–19 cm long, 6.0–10.5 cm wide, (1.3)1.6–3.0 times longer than wide, 2.3–4.8 times longer than petioles, broadest 2.0–5.5 cm above point of petiole attachment; the anterior lobe 9.5–17.5 cm long; the posterior lobes when present

rounded, 1–2 cm long; dark green and subvelvety, smooth to weakly bullate, matte above, slightly paler and matte below; major veins sunken above; sinus when present arcuate, 3–6(15) mm deep, 1.0–1.5 cm wide; basal veins 3 or 4 pairs, major veins sunken above, drying flattened with 1–3 low ribs; midrib paler and acutely raised below, drying 3-ribbed, moderately paler, densely granular; surfaces densely areolate. *Inflorescence* spreading; peduncle 1.0–1.3 cm long, drying 1.5 mm diam., conspicuously warty and short-pale-lineate; spathe green, 8 cm long, 1 cm wide, reflexed-spreading; spadix 5–8 cm long, 6–7 mm diam., dark green tinged purplish, becoming purplish violet at anthesis; flowers 4–5 visible per spiral, 4.0–4.6 mm long and wide; tepals drying dark, sparsely pale-glandular; lateral tepals 2.4–2.6 mm wide; broadly rounded on inner margin, 2-sided on outer margin; pistils green, soon protruding purplish; berries 1.2–1.6 cm long, drying 6–9 mm diam., tapered to a mammiliform tip. *Infructescence* not seen.

Distribution and ecology — *Anthurium pacificum* is known from the Atlantic and Pacific lowlands of Costa Rica and on the Atlantic lowlands of adjacent Panama in Bocas del Toro Province in a *Tropical wet forest* life zone from sea level to 800 m elevation.

Comments — *Anthurium pacificum* is a member of sect. *Polyphyllum*, one of the smaller sections of *Anthurium* with only six species, four of which are restricted to Mexico and Central America, which will be enumerated in a forthcoming revision of the section. It is characterized by its lack of cataphylls, internodal roots on slender, wiry stems, short petiolate leaves, subterete, sharply and narrowly sulcate petioles which are sheathed to about the middle, moderately smooth, narrowly ovate-subcordate to ovate, mostly gradually short-acuminate, subvelvety, greenish drying blades which are rounded-truncate to subcordate at base with 3 or 4 pairs of basal veins, short-pedunculate inflorescences with a green lanceolate spathe and a short tapered spadix with early-emergent pistils. In addition to making a new combination, the species is completely redescribed as well owing to the availability of more information.

This taxon has long been considered a subspecies of *Anthurium clidemioides*, but both entities have markedly distinct morphological characteristics, therefore, a new combination is made to consider *A. clidemioides* subsp. *pacificum* as a distinct taxon at the species level. *Anthurium clidemioides* differs from *A. pacificum* by having proportionately broader more conspicuously bullate ovate-cordate leaf blades with a typically narrowly V-shaped sinus and the blades length to width ratio ranging from 1.1 to 1.6 times longer than broad and with the total blade length 4.6–7.5 times longer than the depth of the sinus. It also differs by having a green spadix. In contrast, *Anthurium pacificum* has a purple spadix and typically larger (10.0–18.7 cm long) more narrowly ovate leaf blades which are rounded to subtruncate at the base or if they are lobed have a broadly arcuate sinus and the length/width ratio is 1.6–3.0 times longer than wide and the blades are 15–30 times longer than the depth of the sinus.

Anthurium andreslovinense Matuda, Acta Botánica Anales Inst. Biol. Univ. Nac. México 36: 108, f. 2. 1966. — Type: MEXICO. Oaxaca: San Andrés Lovene, Miahuatlán, [16°02'22"N, 96°12'17"W, 1200 m], on rocks, *T. MacDongall* 384, 9 Nov. 1959 (holotype, MEXU-224916). **Figure 46.**



Figure 46. *Anthurium andrelovinense* Matuda. Herbarium specimen (M. Dougall 384). On left leaf blade, adaxial surface, on right leaf blade, abaxial surface.

Epiphytic habit, erect; caudex unknown. *Leaves* moderately long-petiolate; petioles 40–45 cm long, subterete, drying 2.5–3.0 mm diam., drying yellowish brown, weakly glossy, smooth, finely ribbed on magnification; blades narrowly triangular-sagittate, 29 cm long, 10.8 cm wide, 2.6 times longer than wide, 0.6–0.7 times longer than petioles, broadest across the tips of posterior lobes, subcoriaceous, drying scarcely bicolorous, brownish gray and matte above, slightly paler and grayish green and weakly glossy below, narrowly pointed at apex, prominently lobed at base; anterior lobe 20.5 cm long, 6.8 cm wide, broadest just above petiolar plexus, concave to straight along margins; posterior lobes 2.8–3.4 times longer than broad, 9.3–10.5 cm long, 3.0–3.4 cm wide midway; sinus spatulate-triangular, 8.4 cm deep, 2.5–3.0 cm wide; basal veins 4 pairs, the first pair of which are free to the base and spreading at ca. 90°; 2nd pair 1.3–2.0 cm long, 3rd and 4th pairs fused 3.0–3.5 cm, naked 1.3–3.0 cm; posterior ribs naked ¼ to ½ its length. *Inflorescence* erect; peduncle terete, 28.7 cm long, drying 2 mm diam., spathe lanceolate, 4.3 cm long, 1.3 cm wide, green, spreading-reflexed; spadix tapered-cylindroid, green, stipitate 5 mm (stipe 3 mm diam.), 7.8 cm long, drying 0.7 mm diam.; flowers 3.2–3.8 mm long, 2.6–3.0 mm wide; lateral tepals 2.1–2.3 wide; inner margins rounded, outer margin 2-sided; stamens clustered around the stigma; anthers 0.5 mm long, 0.6 mm wide; thecae ovoid, weakly divaricate. *Infructescence* not seen.

Distribution and ecology — *Anthurium andreslovinense* is endemic to Mexico, known only from the type locality in southern Oaxaca at ca. 1200 m elevation in subtropical moist regions.

Comments — *Anthurium andreslovinense* is recognized by its epiphytic habit, moderately long-petiolate leaves, subterete, slender petioles which dry yellowish brown, narrowly triangular-sagittate, greenish, drying scarcely bicolorous, narrowly pointed leaves, which are brownish gray matte-drying above, slightly paler and grayish green and weakly glossy below, 4 pairs of basal veins, the first pair of which are free to the base and spreading at ca. a90° angle, posterior ribs naked ¼ to ½ its length, slender posterior lobes with spatulate-triangular sinus, anterior lobes which are straight to shallowly concave as well as an erect inflorescence, green spreading-reflexed spathe and a stipitate green spadix.

Anthurium andreslovinense was considered a synonym of *A. seleri* in the revision of *Anthurium* of Mexico and Middle America by Croat (1983), but the species is now considered to be isolated from *A. seleri* and distinct based on its blade shape, petiole profile and mature size. *Anthurium seleri* is more coriaceous and while the leaf blades are somewhat variable in shape, the posterior lobes of that species are either, proportionately much shorter and directed somewhat outward, or if the posterior lobes are longer, they are not directed toward the base as in *A. andreslovinense* but rather they are prominently directed outward. *Anthurium seleri* has sharply sulcate, D-shaped petioles and narrow leaf blade to almost 100 cm in length. In contrast, the posterior lobes of *Anthurium andreslovinense* are much longer than broad and directed toward the base and the petioles are subterete in cross-section.

Anthurium andreslovinense has also been confused with *A. cerrobaulense* Matuda, which occurs in dry forest ecosystems on the Pacific versant of eastern Oaxaca and southwestern Chiapas

but that species, like *A. seleri* Engl., has sharply sulcate, D-shaped petioles and attains a much larger overall size when mature.

In his description, Matuda commented on the similarity between *Anthurium andreslovinense* and the terrestrial-epipetric *A. berriozabense* from Chiapas but noted the much longer and narrower anterior lobes evident in this species.

As the mixed collections of Thomas MacDougall (384, 384A) suggest, *Anthurium andreslovinense* appears closely related to *A. ocoatepecense* Matuda, which Croat (1983) erroneously placed in synonymy with *A. ovandense* Matuda (a more recently published name). While outside the scope of this description, their respective ranges suggest that *Anthurium ovandense* and *A. ocoatepecense* may also prove to be distinct species.

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