THE DISTRIBUTION OF ANTHURIUM (ARACEAE) IN MEXICO, MIDDLE AMERICA AND PANAMA

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ABSTRACT. The phytogeography of Anthurium (Araceae) is discussed for Central America on a sectional basis and notes are presented about the general distribution of each section represented as it occurs elsewhere. Out of a total of 221 species in Central America, Mexico has 41 species, Guatemala 25, Nicaragua 30, Costa Rica 76 and Panama 155. Section Porphyrochitonium is the largest section with 56 species, followed by Belolonchium (46 species), Pachyneurium (32 species), Calomystrium (23 species) and Xialophyllium (12 species); all of the remaining 12 sections contain fewer than eight species, with eight sections having four or fewer species. While species in section Schizoplacium and section Belolonchium (both A. andicola Liebm. alliance, and A. verapazense Engl. alliance) are predominantly or wholly Mexican, most sections have the bulk of their species in Costa Rica and Panama, especially the latter. Anthurium habitats in Mexico tend to have relatively low species diversity, while those in Costa Rica and Panama have high species diversity.

The genus Anthurium (Araceae), with estimates of up to 1,000 species, is one of the largest and most complex genera in the American tropics. The genus inhabits a wide variety of life zones and habitats, from sea level to over 3,000 m, but is most common in moist to wet forest and especially cloud forests at elevations of up to 1,500 m. It is especially common in areas with premontane wet, tropical wet or premontane rain forest life zones. Most species are epiphytes, though many become terrestrial or epipetric in areas where the dry season is particularly severe, such as in western Mexico. The distinction also breaks down in montane regions, where the accumulation of debris on the surface of the ground forms a substrate similar to that available to plants growing on the sides of tree trunks.

A more detailed discussion of the distribution of *Anthurium* on a species by species basis is presented in the recent revision of *Anthurium* (Croat, 1983a, 1986), but this is the first attempt to describe the distributional patterns of the sections of the genus *Anthurium* as they occur in Central America. The sections of *Anthurium* have been described and illustrated elsewhere (Croat, 1983b), but will be defined again in this paper.

MATERIALS AND METHODS

The data were accumulated by studies of herbarium specimens collected throughout Central America and by field studies made in Central America since 1965. These field trips, numbering more than 15 in all, resulted in several thousand collections of *Anthurium*. Most of the collections are deposited in the Herbarium of the Missouri Botanical Garden (MO).

RESULTS AND DISCUSSION

Endemism is a common feature of Anthurium in Central America with 26 endemic species in Mexico and 85 endemic species in Panama. Middle America, especially areas northwest of Costa Rica, are relatively poor in endemic species. Guatemala has two endemic species, A. armeniense Croat and A. retiferum Standley & Stevermark. Anthurium parvispathum Hemsl., previously reported as endemic to Guatemala (Croat, 1983a), is now known in Chiapas. Honduras and Nicaragua each have one endemic species, A. lancetillense Croat and A. beltianum Standl. & L. O. Wms., respectively. An abrupt change in species diversity seems to occur in Nicaragua along the depression created by the San Juan River. The Costa Rican side of this depression is rich in species, but the Nicaraguan side is poor in species. Only in the very wet and poorly known southeast corner of Nicaragua is species diversity comparatively rich. Much of northern Nicaragua is covered by pine forests and such areas are notably poor in species.

It is not known whether changes in sea level have had any bearing on the modern day *Anthurium* flora, but the sea level was believed to have been up to 100 m higher at the close of the Tertiary (some 800,000 years ago) than it is now, and if so, much of Nicaragua might have been under water (Holmes, 1969). More than likely, the modern day distribution and the stark contrasts of species diversity on either side of the San Juan depression is owing to differences of rainfall and especially to the relative length and severity of the dry seasons.

Several other general features regarding the

complements characteristic for many Tillandsioideae (Marchant, 1967; McWilliams, 1974). Studies of bimodal chromosome complements in selected Tillandsioideae taxa are now underway.

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TABLE 1. Number of species in sections of Anthurium in Central America.

Anthurium sections	Number of species			
	Mexico and Middle America	Costa Rica	Panama	Total
Tetraspermium	4	4	4	4
Porphyrochitonium	14	13	51	56
Pachyneurium	29	22	20	32
Polyphyllium	3	2	1	3
Leptanthurium	1	1	1	1
Oxycarpium Xialophyllium	3	3	2	3
microspadix alliance	3	3	4	4
caucanum alliance	8	5	10	12
Polyneurium	3	3	7	7
Urospadix	0	1	6	6*
Digitinervium	1	1	1	1
Cardiolonchium	3	0	5	8
Calomystrium	9	7	18	23
Belolonchium (typical)	10	5	14	21
andicola alliance	19	0	0	19
verapazense alliance	6	0	1	7
Semaeophyllium	2	2	6	7
Schizoplacium	3	0	0	3
Dactylophyllium	4	4	4	4
Totals	125	76	155	221

^{*} Possibly section Oxycarpium (see discussion under sections Oxycarpium and Urospadix).

phytogeography of Anthurium are born out by this study. First, Mexico and Guatemala are seen to have a closely related Anthurium flora which bears little relationship with the floras of the lower part of Central America, especially of those of Costa Rica and Panama. Mexican species are the least well defined, though in general the area is rich in diversity at the sectional level, with two or more sections or species alliances being almost or entirely restricted to the area. These include sections Schizoplacium and Belolonchium (both andicola alliance and verapazense alliance). Species distribution shows evidence that the Mexican species evolved in isolation from those in Panama and Costa Rica. Of the 221 species known from Central America, 41 occur in Mexico, and of these 26 are endemic. Of the total in Mexico only six species (A. flexile Schott, A. microspadix Schott, A. pentaphyllum var. bombacifolium (Schott) Madison, A. salviniae Hemsl., A. scandens (Aubl.) Engl. ssp. scandens and A. trinerve Miq.) reach Costa Rica.

Second, species diversity increases dramatically as one approaches South America, with Mexico having 41 species, Belize ten species, Guatemala 25 species, El Salvador three species, Honduras ten species, Nicaragua 30 species, Costa Rica 75 species and Panama 150 species. It is estimated that Colombia may have roughly 400 species, with most of these restricted to the for-

ested Pacific slope of the Andes from sea level to 2,000 m elevation.

Third, while the species of some Anthurium sections are fairly evenly distributed throughout their range (generally richer in South America), some sections of Anthurium are richer in one area than in another (TABLE 1). For example, section Pachyneurium is richest in lower Central America and in the western Amazon basin in Ecuador and Peru. Sections Porphyrochitonium and Polyneurium are richest at low to middle elevations along the Pacific slope of Colombia and Ecuador. Section Calomystrium is rich in the latter area as well. It is comparatively much more diverse at higher elevations in the Andes, especially in Colombia, occurring on both sides of the Central Cordillera and it is prevalent in the Eastern Cordillera of Colombia as well. Section Cardiolonchium is diverse only in Andean Colombia and section Dactylophyllium (Croat, 1983b) is principally distributed in the Amazon basin.

General Notes on Distribution of Central American Anthurium by Section

SECTION TETRASPERMIUM SCHOTT. This small, but unique, section consists of small leaved scandent or subscandent plants with usually elongate internodes, elliptic to lanceolate or oblanceolate

short-petioled blades, which are dark glandular punctate on one or both surfaces. The pistils may have two or more ovules per locule. The group is also unique chromosomally, being based on 2n = 24

In general the section *Tetraspermium* consists of widespread taxa, with *A. scandens* (Aubl.) Engl. ssp. *scandens* essentially ranging throughout the range of the genus, and the ssp. *pusillum* Sheffer ranging from Honduras to Colombia and Venezuela, while *A. trinerve* Miq. ranges from Guatemala to Central Brazil. Only *A. tonduzii* Engler is more restricted, occurring only in Costa Rica and Panama. The center of diversity for the section is probably Pacific coastal Ecuador where there are several additional species.

SECTION PORPHYROCHITONIUM SCHOTT. This section is characterized by its usually short, densely rooted stems, its elongate, non-cordate leaf blades with glandular punctations on one or both surfaces, and having usually more than one ovule per locule.

The section *Porphyrochitonium* is largely restricted to Costa Rica and Panama in Central America. Only five of the 56 Central American species range north of Costa Rica and only one species, *A. bakeri* Hook. f., further north than southern Nicaragua. The latter is a wide ranging species, ranging from Guatemala to Colombia and Venezuela. The center of diversity for the section is in the Pacific coastal part of northern South America, especially in the Chocó Refugium. By contrast, there are relatively few species in section *Porphyrochitonium* from the Amazon slope of the Andes and in the Amazon basin.

In Central America, the section is richest in Panama, with 51 of the 56 Central American species occurring there. The species in the section are largely new ones, with relatively few species having been included in Engler's revision (1905). Forty of the 56 species in Panama have been found to be new to science within the past few years. Many of these (37, or 66 percent of the total) are currently considered to be endemic to Panama, but some of the Darién species will no doubt be found on the Colombian side of the Serranía del Darién.

SECTION PACHYNEURIUM SCHOTT. Commonly referred to as the bird's-nest anthuriums, this section is characterized by its generally oblanceolate or obovate coriaceous leaf blades arranged in a tight rosette. In addition, the section has short stems with short internodes and densely compacted roots. The blades generally have thick primary lateral veins which extend to the margin without uniting into a collective vein near the margin. Most importantly, the leaves have

involute vernation, a feature almost unique in the family.

In Central America most of the 32 species occur in Costa Rica and Panama, but the section Pachyneurium (Croat, 1983b) is comparatively richer in Costa Rica (with 22 species) than Panama (with 20 species). The small difference is significant because Costa Rica is smaller than Panama and because Panama has about twice as many total species of Anthurium as Costa Rica. Mexico has several endemic taxa including A. halmoorei Croat, A. machetioides Matuda, A. nizandense Matuda and A. schlechtendalii ssp. iimenezii Matuda; and a few wide ranging species, including A. cubense Engl. and A. schlechtendalii Kunth, which range throughout much of Central America. The section Pachyneurium prefers areas with pronounced dry seasons and becomes decreasingly diverse in wetter areas. For this reason the Chocó Department of Colombia, which is very wet and is perhaps the richest area for diversity of Anthurium, has no species of section Pachyneurium. The center of diversity for the section is probably the western Amazon basin and the adjacent foothills of the Andes, especially in Amazonian Ecuador and Peru.

SECTION POLYPHYLLIUM ENGL. This section is unique in having slender wiry stems with adventitious roots along the internodes (restricted to the nodes in other sections) and in having usually more than one leaf per branch (one per branch in other sections). It is also unique in lacking cataphylls and in having conspicuously sheathed petioles.

This is one of the smallest sections of the genus Anthurium and it is currently known only from Central America. One of the three taxa, A. flexile Schott ssp. muelleri Macbride occurs only in Mexico and Guatemala, while the subspecies flexile ranges from Mexico to Panama. One species, A. clidemioides Standl. occurs in Panama and Costa Rica.

Section Leptanthurium Schott. Characterized by a chromosomal polyploid series of 2n = 20, 40 and 60, and velamen covered roots, this is one of the smallest sections in Central America, with only one species, *A. gracile* (Rudge) Lindl., yet it is one of the most widespread of all sections, ranging from Guatemala and Belize to the Guianas, southern Brazil and Bolivia. There may be an additional one or two species in Ecuador.

SECTION OXYCARPIUM SCHOTT. The section Oxycarpium is poorly known, but is best circumscribed by having short stems with short internodes, more or less lanceolate epunctate leaves

with supervolute vernation and primary lateral veins that are conspicuously more prominent than the interprimary or tertiary veins.

It is one of the smallest sections in the genus as it was defined by Engler (1905) and Schott (1860). Only one species, A. pittieri Engl., occurs in Central America. The variety pittieri ranges from Costa Rica to South America. The other two varieties, var. fogdenii Croat and var. morii Croat, occur in Costa Rica and Panama, respectively. As defined by Engler, the section has only one or two additional species in South America. Still, if its circumscription is broadened to include those eglandular, lanceolate-leaved, shortstemmed species in western South America which Engler placed in his section *Urospadix*, the group could become one of the largest sections in the genus. No decision has been made to do this yet, but the Central American species in this section clearly are not closely related to typical Brazilian members of section *Urospadix* (Croat, 1983b).

Section Xialophyllium is distinguished by having elongate internodes and more or less elongate, epunctate leaf blades. It can easily be divided into two groups, provisionally called the *Anthurium microspadix* Schott alliance, and the *A. caucanum* Engl. alliance (Croat, 1983b). The former group is small in Central America with one wide ranging species, *A. microspadix* Schott, ranging from Mexico to Ecuador and with two species endemic to Costa Rica and Panama, *A. davidsoniae* Standley and *A. pallens* Schott, as well as one species, *A. myosuroides* (HBK) Endl., known from Panama and Colombia.

It is distinguished from the A. caucanum alliance by having thinner, generally more veiny blades, which are commonly matte. In contrast, the A. caucanum alliance has thicker, glossier blades.

Of the two groups the caucanum alliance of the section Xialophyllium is much larger in Central America, with the majority of the species in Costa Rica and Panama, especially the latter. Only one species, A. interruptum Sodiro is wide ranging, extending from Belize to Ecuador. The other species are apparently endemic to Costa Rica and Panama.

The A. microspadix alliance clearly has its center of diversity in Pacific coastal Ecuador and Colombia, with most of the species on the forested slopes of the Andes, often at moderately high elevations. The caucanum alliance is probably even larger than the microspadix alliance in South America. It is also concentrated heavily in northwestern South America.

SECTION POLYNEURIUM ENGL. The section

Polyneurium is characterized by having stems with moderately short internodes and relatively thin, mostly oblong-triangular or panduriform blades with many primary lateral veins.

This section is primarily South American, with only seven species known from Central America. All of the Central American species are known from Costa Rica or Panama, with three and seven species known from each area, respectively. Of these species, only A. panduriforme Schott and A. williamsii Krause are at all widespread, ranging from Costa Rica to Ecuador. Anthurium caperatum Croat & Baker is known from Costa Rica and Panama, while the remainder are apparently narrow Panamanian endemics.

The center of diversity for the section is Pacific coastal Colombia and Ecuador.

Section Urospadix Engl. Although Engler included most neotropical lanceolate-leaved species with short stems in this section, it is probably restricted to Brazil; it probably only includes those species with many close primary lateral veins, or species where there is little distinction between the primaries and the interprimaries. Some Central American species are still tentatively placed in this section for lack of a known section in which to place them. All but two of these are endemic to Panama. The species A. michelii Guillaumin and A. llanoense Croat are known from both Costa Rica and Panama.

The species in this group will probably eventually be placed in a section of their own; or perhaps into a much expanded section *Oxycarpium*. In Central America the group is small, with only six species, but their relatives in South America, which have short stems, basically lanceolate leaves and epunctate blades, are quite numerous.

Section Digitinervium Sodiro. Characterized by having thick, glandular-punctate blades with several prominently ascending basal veins, each interconnected with scalariform veins, the section *Digitinervium* is a moderately small section. Blades are also commonly broad, usually elliptic to ovate or subcordate. It is almost exclusively South American, with most species inhabiting middle elevations in the Andes. In Central America only one species, *A. lentii* Croat & Baker, is represented and it is restricted to Costa Rica and Panama.

SECTION CARDIOLONCHIUM SCHOTT. Commonly referred to as "velour *Anthuriums*," this group is characterized by their short stems and cordate blades with usually velvety upper surface, smooth, matte lower surface and also by their frequently ribbed petioles or peduncles. In addition, many

species in the section have chromosomal segments referred to as B-chromosomes.

Section Cardiolonchium has a center of diversity in the wet, Pacific coastal slope of Colombia, but has mostly narrowly ranging species elsewhere in the Andes, as far away as Peru, Venezuela and Mexico. In Central America there are eight species in the section, three of them, A. clarinervium Matuda, A. leuconeurum Lem., and A. lezamae Matuda, are endemic to Mexico and five of them, A. cerrocampanense Croat, A. crystalinum Linden & André, A. dressleri Croat, A. folsomianum Croat, and A. papillilaminum Croat, are from Panama. All are endemic, except A. crystalinum, which ranges into Colombia.

SECTION CALOMYSTRIUM SCHOTT. This group, which is characterized by its thick, usually cordate blades, and especially by its thick intact persistent cataphylls, is one of the largest sections of *Anthurium*. Thick, often colorful spathes and colorful, moderately blunt spadices with thick, often fragrant flowers, are also characteristic for section *Calomystrium*.

The section, which begins to become diverse in Panama, is richest in Colombia and is one of the few sections, aside from section *Belolon-chium*, which is well represented at higher elevations in Colombia and in the Eastern Cordillera of the Andes. Only four species range as far east as Venezuela and the Guianas, and no more than one or two inhabit the Amazon basin in Brazil. A few occur as far south as Bolivia in the Andes, and increasingly larger numbers occur in Peru and especially in Ecuador (in the latter case they are distributed on both sides of the Andes).

In Central America there are 23 species, but only a single, moderately wide ranging species, A. huixtlense Matuda, occurs in Mexico, ranging to Nicaragua; and a single endemic species each occurs in Guatemala and Nicaragua, namely, A. armeniense Croat and A. beltianum Standl. & L. O. Wms., respectively. Of the remaining 20 species, only A. formosum Schott and A. ravenii Croat & Baker range north of Costa Rica, and of these only A. ravenii ranges as far as Honduras. Even Costa Rica is relatively poor in species with only eight, while Panama has 18 species. Of the Costa Rican species, two are endemic, namely A. clavatum Croat & Baker and A. monteverdense Croat & Baker, whereas in Panama, 13 are endemic.

Section Belolonchium Schott. As defined by Engler, the section *Belolonchium* essentially accommodates all short-stemmed *Anthurium* species with cordate blades, that do not fit into sections *Calomystrium*, *Polyneurium*, or *Cardiolonchium*. It is probably an unnatural assemblage and further studies will, hopefully, find oth-

er ways of dividing it into smaller, more natural assemblages.

Until its exact boundaries are better defined, the Central American species are best arranged into three groups. Separated from the "typical" members of the section is the *Anthurium andicola* Liebm. alliance (Croat, 1983a, 1983b), which consists of 19 species, all restricted to Mexico. Judging from the appearance of this group, these Mexican species may have evolved in isolation from other Central American species or from other more wide ranging species in Central America.

A second, smaller, but even more distinctive group, recognized by its cordate blades with glandular punctations, is referred to as the *Anthurium verapazense* Engl. alliance. It has four species endemic to Mexico and two additional species, *A. lucens* Standl. ex Yuncker and *A. verapazense* Engler. The latter is known only from Mexico, Belize and Guatemala, while the former ranges from Mexico to Honduras. One additional Central American species, *A. hornitense* Croat, which appears to belong in this group also, is endemic to Panama.

The remaining species of Central America in section *Belolonchium* total 20, and are moderately well distributed throughout Central America. Four species, *A. cerropelonense* Matuda, *A. ovandense* Matuda, *A. umbrosum* Liebm. and *A. yetlense* Matuda are narrow Mexican endemics.

Anthurium silvigaudens Standl. & Steyerm. ranges from Guatemala to Honduras and A. lancetillense Croat is endemic to the latter. A. ochranthum Schott and A. pluricostatum Croat & Baker occur in Costa Rica and Panama. Only two species are moderately wide ranging, with A. ochranthum Schott ranging from Nicaragua to Panama and A. brownii Masters ranging from Costa Rica to Colombia. Of the 13 Panamanian species, seven are endemic. In addition to A. brownii, A. watermaliense Hort. ex Bailey also ranges from Costa Rica and to Colombia, while four additional species range only as far as Costa Rica.

As constituted, the section *Belolonchium* is the second largest section of *Anthurium* in Central America, with 45 species. The group is, however, very much richer in South America, with many of the species apparently undescribed. It is widely distributed and rich in a variety of elevations and life zones, but it is especially rich along the slopes of the Andes. In the strictest sense, as the section was first defined by Schott (1860), the species of this section may be principally restricted to relatively high elevations in the Andes of South America.

SECTION SEMAEOPHYLLIUM SCHOTT. Consisting of three-lobed species with generally falcate lobes,

this section constitutes one of the smaller ones in Central America with only seven species, all of which are restricted to Costa Rica and Panama. Costa Rica has only two species, with A. tilaranense Standl., which also occurs in Panama, and A. subsignatum Schott, which is endemic. Two of the Panamanian species, A. cineraceum Croat and A. garagaranum Standl., are also known from Colombia. The remaining three species, A. angustilobum Croat, A. impolitum Croat and A. madisonianum Croat, are endemic to Panama.

The section Semaeophyllium is chiefly distributed in Panama and along the Pacific slope of Colombia and Ecuador, but a few species occur in the Amazon basin near the Andes; and two species occur in the western Andes of Venezuela, near the Colombian border.

SECTION SCHIZOPLACIUM SCHOTT. Recognized by palmately incised leaf blades with five or more lobes, the section Schizoplacium Schott is a small, but widespread, section with only six taxa described (Croat, 1983b). There are three taxa in Central America, all restricted to Mexico. They are A. podophyllum (Cham. & Schlect.) Kunth, A. pedatoradiatum Schott and A. pedatoradiatum ssp. heleborifolium (Schott) Croat. There is one species in the Lesser Antilles, A. palmatum (L.) G. Don; one from northern and western Venezuela, A. longissimum Pittier; and one from eastern Venezuela and Suriname, A. expansum Gleason. One new species has recently been discovered from Peru.

SECTION DACTYLOPHYLLIUM SCHOTT. This section is characterized by having leaves which are pedately divided clear to the base, with three or more segments. The segments are usually entire, but may be sinuate or lobed.

There are 15 species in the section *Dactylophyllium*, most of them from the Amazon basin or from the eastern slope of the Andes. Only four species are truly widespread and range from Central to South America. These are *A. clavigerum* P. & E., one of the most widespread species of *Anthurium*, ranging from Honduras to the Guianas, Brazil and Bolivia; *A. kunthii* Poepp., ranging from Nicaragua to Peru; *A. trisectum* Sodiro, ranging from Costa Rica to Ecuador; and *A. pentaphyllum* (Aubl.) G. Don, perhaps the most widespread species of all, ranging from Mexico to southern Brazil. However, in Central America, only the variety *bombacifolium* (Schott) Madison occurs, ranging from Mexico to Panama

The only other widespread species in the section are A. eminens Schott and A. triphyllum Brongn., both of which range from Venezuela to Ecuador and Bolivia.

CONCLUSION

The Central American Anthurium flora is unevenly distributed, with the greatest concentration of species in Costa Rica and Panama, and with a lesser center of diversity in Mexico. Mexican species, though relatively large in number, are more scattered, with a single area rarely having more than a few species. In contrast, single habitats in Panama or Costa Rica, especially in cloud forests at middle elevations, generally have many species. The remainder of Middle America is somewhat between the Mexican region and the Panamanian-Costa Rican area. With only 37 species, the region is less species rich than Mexico, but single habitats, especially along the Caribbean coast in Guatemala, Honduras, or Nicaragua, can be richer in species than those in Mexico. On the other hand, these same habitats are less rich than those in Costa Rica or Panama.

Distribution along sectional lines also shows this same delimitation with Mexico having three unique groups almost or entirely restricted there (section Schizoplacium, section Belolonchium, A. andicola alliance and A. verapazense alliance) and Costa Rica and Panama having most or all Central American species of sections Porphyrochitonium, Polyneurium, Urospadix, Digitinervium and Semaeophyllium.

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