

CHROMOSOME NUMBER AND COMPATIBILITY IN THE GENUS
ANTHURIUM (ARACEAE) WITH A TAXONOMIC REVISION
OF THE SECT. TETRASPERMIUM

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INTRODUCTION

Anthurium Schott with over 500 species is the largest genus in the family Araceae and comprises about one-third of the number of species in the family. This taxon is of somewhat easy identification having the spathe and spadix common to the family, an apically geniculated petiole which is never flat and leaflike, four perianth segmented, perfect flowers, and a flat and persistent spathe (Hutchinson, 1959). This genus extends from the central part of South America to Mexico and the West Indies.

The most recent taxonomic treatment attempting to classify all Anthurium species to sections was that of Engler (1905). Engler divided the genus into 18 sections with the primary categorization being based upon the number of ovules per locule, one or less, or two or more. Further categorizations of the sections were based on the leaf shape and texture, and inflorescence shape, but the majority of the sections was finally separated on the basis of berry shape. Although these primary separations indicate knowledge of inflorescence shape, berry shape, and number of ovules per locule of all included Anthurium species, these characters were often lacking in the actual descriptions of individual taxa. Evidently some species were placed into sections primarily on the basis of leaf shape and texture alone.

Most recent taxonomic studies have only covered specific countries such as Peru (MacBride, 1936), Panama (Standley, 1944), Mexico (Matuda, 1954), Brazil (Reitz, 1957), and Guatemala (Standley & Steyermark, 1958), without attempting to place the species into

sections. A revision of Engler's basic work is needed to reassess the species relationships and to incorporate the approximately 100 newly described species as to section, but such a task would be enormous. The task can be divided into somewhat more manageable terms by examining individual sections recognized by Engler.

The modes of reproduction of aroids in general and Anthurium in particular lacks adequate investigation. In aroids, however, the modes of reproduction of the various genera appear to range from cross-fertilization to obligate apomixis (Fryxell, 1957). Some investigators consider aroids to be primarily reproducing by vegetative means whether the plants are sexually fertile or not (Mookerjea, 1955; Sharma, 1956; and Sharma & Bhattacharya, 1966). These authors did not clearly indicate whether they were referring to plants under cultivation or natural conditions. Nevertheless, numerous hybrids have been reported in Anthurium (Engler, 1905). The mode of reproduction in Anthurium has generally been assumed to be cross-pollination. The flowers are usually protogynous making self-pollination impossible (Campbell, 1900). In Sect. Tetraspermium, casual determinations appear to indicate that A. scandens (Aubl.) Engl. (A. violaceum var. leucocarpum Engl.) was pollinated by small ants carrying pollen from older inflorescences to younger ones (Campbell, 1900, 1905; Gaiser, 1927). This was the extent of the knowledge of the mode of reproduction in Anthurium.

Based on numerous chromosome counts within Araceae in recent years (Sharma & Das, 1954; Mookerjea, 1955; Pfitzer, 1957; Sharma &

Bhattacharyya, 1961; Sharma & Bhattacharya, 1966; Marchant, 1970, 1971a, 1971b, 1973) seven is believed to be the basic number of the family (Mookerjea, 1955; Larsen, 1969; Marchant, 1973). Counts within Anthurium are still incomplete and conflicting. Three general reviews of chromosome numbers for Anthurium have noted 60-70 chromosome counts of different species which are about 10-15% of the known species (Itô, 1942; Pfitzer, 1957; Fedorov, 1969). The basic number of this genus is believed to be 15 (Marchant, 1973). Differences in observed chromosome numbers would appear often to be due to the presence of B chromosomes, as with A. crystallinum Lind., however sometimes the differences cannot easily be explained (Marchant, 1970). For Anthurium, chromosome numbers of $2n = 34, 35, 56,$ and 63 have been reported from only one laboratory (Mookerjea, 1955; Sharma, 1956).

The present investigation was initiated to identify and name Anthurium species assembled at the University of Hawaii; to clarify their relationships through chromosome number determinations, sexual compatibility studies and hybrid analysis; and to prepare a taxonomic revision of the Sect. Tetraspermium.

MATERIALS AND METHODS

Living Anthurium species are a part of the University of Hawaii collection, and Table I lists the 65 Anthurium taxa used in this study. Most of these specimens were collected by Dr. Kamemoto and Dr. Sagawa in 1968, but some specimens were obtained from private and commercial sources. The identification of the Panamanian specimens was based principally on the taxonomic treatment by Standley (1944). Engler's work (1905) and the taxonomic works for specific countries were consulted for identification of non-Panamanian specimens and Panamanian specimens which could not be identified through Standley's work. Unfortunately, many of Engler's descriptions (1905) are brief, and information about the berry and inflorescence is lacking, making identification very difficult. Standley's taxonomic treatment of Panamanian species remains also inadequate due to the large number of species and inadequate herbarium material (Standley, 1944). Identification of Panamanian species therefore, was troublesome and undoubtedly subject to error. Herbarium voucher specimens were prepared and deposited in the University of Hawaii Herbarium.

Chromosome preparations were made from root tips which were young and actively growing. Samples were taken between 9:00 a.m. and 12:00 noon and placed in a 15-20 ppm *o*-isopropyl-N-phenylcarbamate (IPC) pretreatment solution for 3-5 hours at 18°C (Sawamura, 1965; Mann & Storey, 1966; Storey & Mann, 1967). Fixation was in a Carnoy (6:3:1) mixture of 95% ethyl alcohol, chloroform, and glacial acetic acid respectively for 20 minutes at 18°C. The root tips were then hydrolyzed

in 1N hydrochloric acid for eight minutes at 50°C. They were immediately washed and placed in 45% acetic acid for 10 minutes. After removing the root caps, the root pieces were squashed and stained with 1% aceto-orcein. Chromosome numbers were determined from suitable squash preparations. Photomicrographs were taken with a Zeiss photomicroscope at a magnification of 550X on Kodak High Contrast Copy film.

The mode of reproduction was determined indirectly by using the methods of Powers and Rollins (1945) which were later summarized by Burnham (1962). The following modifications were made to fit this material. Pollination was accomplished by grasping the pollen laden spadix between the fingers and then transferring the pollen to the receptive stigmas which are easily recognized by a sticky exudate (Kamemoto & Nakasone, 1963). Emasculation where needed was accomplished by removing the tip of the spadix with a scalpel and then removing everything down to the receptacle except for two or three pistils. All inflorescences were covered with plastic bags which were punched with small holes the size of a pencil tip.

Sexual compatibility studies were conducted using the 56 species which were flowering. Ideally all possible cross-combinations including reciprocals and selfings would be desirable. However 3136 pollinations would be necessary for only a single pollination of every combination. If each pollination were to be duplicated, then 6272 pollinations would be necessary. It would be impractical to accomplish that many pollinations within four years, especially due to

insufficient spadices. In order to bring the number of pollinations necessary into more manageable terms, the 56 species were divided morphologically into 6 different groups. Cross-pollinations were then attempted among these groups, but no attempt was made to insure that each species of a group was crossed with every other group. Many crosses, however, were made among these groups to insure that a representative sample of each group was crossed with members of the other groups. Within each group, all possible cross-pollinations were attempted depending on the availability of receptive spadices and pollen. Data were taken on the date and time of pollination, date of abscission of fruit harvest, number of seeds per locule, fruit set (estimated), and seed germination percent determined on twenty-five seeds placed on a filter paper in a petri dish. Eight seedlings per combinations were grown and evaluated both morphologically and chromosomally.

Pollen preparations were made from freshly collected pollen samples stained in 1% aceto-orcein. Fifty pollen grain per preparation were measured with an ocular micrometer, and 500 per preparation were classified as large well formed pollen grains or small poorly formed pollen grains. These preparations were made on each of ten different plants: five were A. scandens (A174, A201, A211, A328, and A329), one was a spontaneous tetraploid seedling of A211, three were A. trinerve (A100, A238, and A275), and one was a colchicine induced tetraploid seedling of A100. Photomicrographs were taken at a magnification of 200X on Kodak High Contrast Copy film.

Leaves were collected of A201, A211, A238, and A275. Sections were cut from positions near the midrib on each of the leaves. The

leaves were killed and fixed in Nawaschin's formula (Craff) III (Sass, 1958). The leaf pieces were embedded in paraffin wax and microtomed at 12 and 14 microns. The sections were stained with Johansen's Quadruple Stain (Johansen, 1940). Photomicrographs were taken at a magnification of 75X on Kodak High Contrast Copy film.

TABLE I.
LIST OF ANTHURIUM TAXA EXAMINED AND THEIR SOURCE

Taxa	Source
<u>A. acutangulum</u> Engl., Bot. Jahrb. Syst. 25: 371. 1898.	Panama
<u>A. aemulum</u> Schott, Bonplandia 7: 165. 1859.	Panama
<u>A. allenii</u> Standl., Field Mus. Nat. Hist., Bot. Ser. 22: 66. 1940.	Panama
<u>A. andreanum</u> Linden, Ill. Hort. 24: 43, t. 271. 1877.	In Cultivation
<u>A. aureum</u> Engl., Bot. Jahrb. Syst. 25: 414. 1898.	Panama
<u>A. baileyi</u> Standl., Field Mus. Nat. Hist., Bot. Ser. 22: 66. 1940.	Panama?
<u>A. bakeri</u> Hook. f., Bot. Mag. t. 6261. 1879.	In Cultivation, Panama
<u>A. chiriquense</u> Standl., Field Mus. Nat. Hist., Bot. Ser. 22: 67. 1940.	Panama
<u>A. clarinervium</u> Matuda, Anales Inst. Biol. Univ. Mac. México 22: 375. 1952.	In Cultivation
<u>A. concinatum</u> Schott, Prodr. Aroid. 522. 1860.	Costa Rica
<u>A. crystallinum</u> Linden & André, Linden Cat. n. 90, t. 128. 1873.	Panama?
<u>A. denudatum</u> Engl., Bot. Jahrb. Syst. 6: 280. 1885.	In Cultivation, Panama
<u>A. digitatum</u> G. Don, in Sweet, Hort. Brit. 3rd. ed. 633. 1839.	In Cultivation, Trinidad
<u>A. ellipticum</u> C. Koch & Bouché, Index Sem. Hort. Berol. 6. 1853.	In Cultivation
<u>A. flavo-viride?</u> Engl., Bot. Jahrb. Syst. 25: 447. 1898.	Panama
<u>A. forgetii</u> N. E. Brown, Gard. Chron., Ser. 3, 39: 161. 1906.	Trinidad

TABLE I. (Continued)

LIST OF ANTHURIUM TAXA EXAMINED AND THEIR SOURCE

Taxa	Source
<u>A. gladiifolium</u> Schott, J. Bot. 1: 5. 1863.	Brazel
<u>A. gracile</u> (Rudge) Lindl. Bot. Reg. 19: 1635. 1833.	Panama
<u>A. grande</u> hort., Gard. Chron. 2: 934. 1865.	In Cultivation
<u>A. grandiifolium</u> Kunth, Enum. Pl. 3. 77. 1841.	Panama?
<u>A. gustavii</u> Regel, Gartenflora 324. 1878.	Panama
<u>A. hacumense</u> Engl., Bot. Jahrb. Syst. 25: 363. 1898.	Panama
<u>A. hoffmannii</u> Schott, Oesterr. Bot. Z. 8: 181. 1858.	Panama
<u>A. holtonianum</u> Schott, Oesterr. Bot. Z. 8. 350. 1858.	Panama
<u>A. hookeri</u> Kunth, Enum. Pl. 3: 74. 1841.	Trinidad
<u>A. joseanum</u> Engl., Pflanzenreich 21: 68. 1905.	Panama
<u>A. lindenianum</u> C. Koch & Augustin, Berliner Allg. Gartenzeitung 1: 234. 1857.	In Cultivation
<u>A. littorale</u> Engl., Bot. Jahrb. Syst. 25: 405. 1898.	Panama
<u>A. magnificum</u> Linden, Linden Cat. 2. 1865.	Panama?
<u>A. mexicanum</u> Engl., in DC. Monog. Phan 2: 105. 1879.	Mexico
<u>A. micromystrium</u> Sodiro, Anales Univ. Centr. Ecuador 15: 292, 293. 1902	Panama
<u>A. montanum</u> Hemsl., Diag. Pl. Nov. 36, 1879.	Mexico
<u>A. nymphaeifolium</u> C. Koch & Bouché, Index Sem. Hort. Berol. 1854.	Venezuela
<u>A. pedato-radiatum</u> Schott, Bonplandia 337. 1859.	Panama?
<u>A. pentaphyllum</u> G. Don, in Sweet, Hort. Brit. 3rd. ed. 633. 1834.	In Cultivation

TABLE I. (Continued)

LIST OF ANTHURIUM TAXA EXAMINED AND THEIR SOURCE

Taxa	Source
<u>A. pichincae</u> Engl., Bot. Jahrb. Syst. 25: 426. 1898.	Panama
<u>A. pittier</u> Engl., Bot. Jahrb. Syst. 25: 373. 1898.	Panama
<u>A. procerum?</u> Sodiro, Anales Univ. Centr. Ecuador 15: 203. 1902.	Panama
<u>A. ramonense</u> K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 11: 611. 1932.	Panama
<u>A. ranchoanum</u> Engl., Bot. Jahrb. Syst. 25: 421. 1898.	Panama
<u>A. regale</u> Linden, Belgique Hort. 16: 200. 1866.	In Cultivation
<u>A. rhodostachyum</u> Sodior, Anales Univ. Centr. Ecuador 16: 9. 1903.	Panama
<u>A. roraimense</u> N. E. Brown, Trans. Linn. Soc. London, Bot., Ser. 2, 286. 1887.	Panama?
<u>A. scandens</u> Engl., Mart. Fl. Bras. 3: 78. 1878	Costa Rica, Mexico, Panama, Trinidad
<u>A. scherzerianum</u> Schott, Oesterr. Bot. Wochenbl. 53. 1857.	In Cultivation
<u>A. scolopendrinum</u> Kunth, Enum. Pl. 3: 68. 1841.	Surinam, Trinidad
<u>A. seleri</u> Engl., Bot. Jahrb. Syst. 25: 459. 1898.	Mexico
<u>A. splendidum</u> Hort. Bull ex Ill. Hort. 30: t. 510. 1883.	In Cultivation
<u>A. subhastatum</u> Schott, Oesterr. Bot. Z. 350. 1858.	Panama
<u>A. subsignatum</u> Schott, Bonplandia 9: 368. 1862.	Panama
<u>A. supianum</u> Engl., Bot. Jahrb. Syst. 25: 438. 1898.	Trinidad

TABLE I. (Continued)

LIST OF ANTHURIUM TAXA EXAMINED AND THEIR SOURCE

Taxa	Source
<u>A. terryae</u> Standl. & L. Wms., Ceiba 3: 106. 1952.	Panama
<u>A. trianae</u> Engl., Pflanzenreich 21: 147. 1905.	Panama
<u>A. triangulum</u> Engl., Bot. Jahrb. Syst. 25: 383. 1898.	Panama
<u>A. trinerve</u> Miq., Linnaea 17: 66-67. 1843.	In Cultivation, Panama
<u>A. turrialbense</u> Engl., Bot. Jahrb. Syst. 25: 406. 1898.	Panama
<u>A. veitchii</u> Mast., Gard. Chron. 772, 773, 775, & fig. 143. 1876.	In Cultivation
<u>A. velutinum?</u> Engl., Bot. Jahrb. Syst. 25: 433. 1898.	Panama
<u>A. venosum?</u> Griseb., Cat. Pl. Cubens. 219. 1866.	Panama
<u>A. wallisii?</u> Mast., Gard. Chron. 429, fig. 86. 1875.	Panama
<u>A. walujewii</u> Regel, Trudy Imp. S. -Peterburgsk. Bot. Sada 4: 290. 1879.	Panama
<u>A. warocqueanum</u> J. Moore, Florist & Pomol. 31: 101. 1878.	In Cultivation
<u>A. watermaliense</u> hort., in M. C. Neal, In Gardens of Hawaii 135. 1965.	In Cultivation
<u>A. wendlingerii</u> Barroso, Bol. Soc. Benez. Ci. Nat. 26: 151. 1965.	Venezuela
<u>A. wulschlaegelii</u> Engl., Bot. Jahrb. Syst. 25: 434. 1898.	Panama

RESULTS AND DISCUSSION

CHROMOSOME NUMBERS

Chromosome numbers were determined for 63 species, of which 38 are new counts. These counts and previous counts are presented in Table II. The taxa in the table are presented according to the sections recognized by Engler (1905). Generally where previous counts were available for comparison, the present work confirms these counts. In a few instances conflicting counts were obtained.

Conflicting chromosome counts in Anthurium can generally be attributed to at least four factors: 1) misidentified specimens, 2) polyploidy, 3) supernumerary chromosomes, and 4) faulty cytological technique. The recent practice of preparing adequate voucher specimens greatly reduces the significance of the first factor, since the chromosome number can be directly traced to the specimen irrespective of the attached name. Polyploidy generally presents few problems in Anthurium. The relationship between polyploid numbers is easy to assess since most polyploids are duploids. Supernumerary chromosomes however present a problem, since finding the usual or common number of a species may be difficult because the smallest A chromosomes may not be easily differentiated from larger B chromosomes. Supernumerary chromosomes are, therefore, especially troublesome when only one or a few plants are available for study, but chromosome numbers for taxa are frequently inferred from such data. Faulty cytological technique can also easily lead to erroneous chromosome counts. Usually Anthurium plants have two satellited chromosomes. In late prophase and

TABLE II.
CHROMOSOME NUMBERS OF ANTHURIUM SPECIES

Taxa	Present Counts		Previous Counts		Authority
	2n	n	2n		
<u>Sect. I. Tetraspermium</u>					
<u>A. scandens</u>		ca.24	ca.48		Gaiser 1927
			24		Delay 1947
		24			Pfitzer 1957
ssp. <u>pusillum</u>	24				
ssp. <u>scandens</u>	48,84	16			Campbell 1905
			45-47		Marchant 1973
<u>A. trinerve</u>	24				
<u>Sect. II. Gymnopodium</u>					
<u>A. gymnopus</u>			ca.30		Gaiser 1927
<u>Sect. III. Porphyrochitonium</u>					
<u>A. scherzerianum</u>	30	ca.15	ca.30		Gaiser 1927
		16	32		Haase-Bessell 1928 ¹
			30		Kurakubo 1940 ²
		16	32		Malvesin-F 1945 ³
		15			Pfitzer 1957
			32		Tsuchiya & Takeda 1962

TABLE II. (Continued)

CHROMOSOME NUMBERS OF ANTHURIUM SPECIES

Taxa	Present Counts		Previous Counts		Authority
	2n	n	n	2n	
Sect. IV. <u>Pachyneurium</u>					
<u>A. acaule</u>		15		30	Gaiser 1927
<u>A. boucheanum</u>				56	Mookerjea 1955
<u>A. brownii</u>				ca.30	Gaiser 1927
<u>A. cordatum</u>				ca.30	Gaiser 1927
<u>A. crassinervium</u>		ca.30		ca.60	Gaiser 1927
<u>A. ellipticum</u>	30				
<u>A. glaziovii</u>				34	Mookerjea 1955
				30+	Sharma & Bhatta-
				0-2 f	charyya 1961
<u>A. grandifolium</u>	30			ca.30	Gaiser 1927
<u>A. hacumense</u>	30			ca.30	Gaiser 1927
<u>A. hookeri</u>	30,60	ca.15		ca.30	Gaiser 1927
				30	Kurakubo 1940 ²
		15			Pfitzer 1957
<u>A. joseanum</u>	30				
<u>A. maximum</u>		ca.15		ca.30	Gaiser 1927
<u>A. recusatum</u>		ca.15		ca.30	Gaiser 1927

TABLE II. (Continued)
 CHROMOSOME NUMBERS OF ANTHURIUM SPECIES

Taxa	Present Counts		Previous Counts		Authority
	2n	n	2n		
<u>A. seleri</u>	30				
<u>A. tetragonum</u>		15	30		Gaiser 1927
Sect. V <u>Polyphyllium</u>					
<u>A. mexicanum</u>	60				
Sect. VI. <u>Leptanthurium</u>					
<u>A. acutangulum</u>	30	ca.15	ca.30		Gaiser 1927
<u>A. gracile</u>	30	15	ca.30		Gaiser 1927
			40		Marchant 1973
<u>A. scolopendrinum</u>	20,40		40		Marchant 1973
Sect. VII. <u>Oxycarpium</u>					
<u>A. pittieri</u>	30				
Sect. VIII. <u>Xialophyllum</u>					
<u>A. pulchellum</u>			63		Mookerjea 1955
<u>A. subhastatum</u>	30				
<u>A. triangulum</u>	30				
<u>A. tuerckheimii</u>			ca.30		Gaiser 1927
Sect. IX. <u>Polyneurium</u>					
<u>A. wallisii?</u>	30+2B		ca.60		Gaiser 1927

TABLE II. (Continued)
 CHROMOSOME NUMBERS OF ANTHURIUM SPECIES

Taxa	Present Counts		Previous Counts		Authority
	2n	n	2n		
Sect. X. <u>Urospadix</u>					
<u>A. acutum</u>			30		Marchant 1973
<u>A. allenii</u>	30				
<u>A. aureum</u>	30,31				
<u>A. bellum</u>			56		Mookerjea 1955
<u>A. chiriquense</u>	30				
<u>A. comtum</u>		15	ca.30		Gaiser 1927
<u>A. gladiifolium</u>	30				
<u>A. harrisii</u>			30+5f		Marchant 1973
var. <u>beyrichianum</u>		ca.15			Gaiser 1927
<u>A. imperial</u>			30+2f		Marchant 1973
<u>A. littorale</u>	28	15	ca.30		Gaiser 1927
<u>A. lucidum</u>			ca.124		Marchant 1973
<u>A. olfersianum</u>		ca.15	ca.30		Gaiser 1927
<u>A. microphyllum</u>			30+1f		Marchant 1973
<u>A. sellowianum</u>		15			Pfitzer 1957
<u>A. trianae</u>	28, 29+1B				
<u>A. turrialbense</u>	30				

TABLE II. (Continued)
 CHROMOSOME NUMBERS OF ANTHURIUM SPECIES

Taxa	Present Counts		Previous Counts		Authority
	2n	n	n	2n	
<u>Sect. XI. Episeiostenium</u>					
<u>A. bakeri</u>	30	15	ca.30 28+1f		Gaiser 1927 Sharma & Bhatta- charya 1966
<u>A. consobrinum</u>		15			Pfitzer 1957
<u>A. dominicense</u>		ca.15	ca.30		Gaiser 1927
		15			Nerling 1969
<u>A. guildingii</u>		ca.15	ca.30		Gaiser 1927
<u>A. wendlingerii</u>	30				
<u>Sect. XII. Digitinervium</u>					
<u>A. rhodostachyum</u>	28,29,30,31				
<u>Sect. XIII. Cardiolonchium</u>					
<u>A. clarinervium</u>	30				
<u>A. crystallinum</u>	30+1B	ca.15	ca.30 34		Gaiser 1927 Mookerjea 1955
		15+	30+		Pfitzer 1957
		0-2B	0-2B		
			30+2f		Marchant 1973

TABLE II. (Continued)
 CHROMOSOME NUMBERS OF ANTHURIUM SPECIES

Taxa	Present Counts	Previous Counts		Authority
	2n	n	2n	
<u>A. forgetii</u>	30	15+	30+	Pfitzer 1957
		0-2B	0-2B	
<u>A. grande</u>	30			Mookerjea 1955
<u>A. leuconeurum</u>			35	
<u>A. magnificum</u>	60**	ca.15	ca.30	Gaiser 1927
		16	32	Haase-Bessell 1928
		15+	30+	Pfitzer 1957
		0-2B	0-2B	
<u>A. regale</u>	30+1B			
<u>A. splendidum</u>	30+2B			
<u>A. velutinum?</u>	30			
<u>A. venosum?</u>	30			
<u>A. walujewii</u>	30+2B			
<u>A. warocqueanum</u>	30+3B		ca.30	Gaiser 1927
		15		Pfitzer 1957
<u>A. wulschlaegelii</u>	30			
Sect. XIV. <u>Chamaerrepium</u>				
<u>A. radicans</u>			ca.50	Gaiser 1927
		15		Pfitzer 1957

TABLE II. (Continued)
 CHROMOSOME NUMBERS OF ANTHURIUM SPECIES

Taxa	Present Counts	Previous Counts		Authority
	2n	n	2n	
Sect. XV. <u>Calomystrium</u>				
<u>A. hoffmannii</u>	30			
<u>A. lindenianum</u>	30			
<u>A. montanum</u>	30			
<u>A. nymphaeifolium</u>	30		ca.30	Gaiser 1927
<u>A. pichincha</u>	30			
<u>A. ranchoanum</u>	30			
<u>A. roraimense</u>	30			
<u>A. veitchii</u>	30	15	ca.30	Gaiser 1927
		15		Pfitzer 1957
Sect. XVI. <u>Belolonchium</u>				
<u>A. andreanum</u>	30	ca.15	ca.30	Gaiser 1927
		16	32	Haase-Bessell 1928 ²
			30	Kurakubo 1940
			30	Simmonds 1954
		15		Pfitzer 1957
			30	Sharma & Bhatta- chryya 1961
			32	Tsuchiya & Takada 1962

TABLE II. (Continued)
 CHROMOSOME NUMBERS OF ANTHURIUM SPECIES

Taxa	Present Counts		Previous Counts		Authority
	2n	n	n	2n	
<u>A. concinatum</u>	30				
<u>A. denudatum</u>	30	ca.15		ca.30	Gaiser 1927
<u>A. flavo-viride?</u>	30				
<u>A. gustavii</u>	30				
<u>A. micromystrium</u>	30				
<u>A. patulum</u>				28+1f	Sharma & Bhattacharya 1966
<u>A. procerum?</u>	30				
<u>A. supianum</u>	ca.90				
Sect. XVII. <u>Semaeophyllum</u>					
<u>A. holtoniaum</u>	30				
<u>A. signatum</u>				34	Mookerjea 1955
<u>A. subsignatum</u>	30			ca.30	Gaiser 1927
				30+1f	Marchant 1973
Sect. XVIII. <u>Schizoplacium</u>					
<u>A. aemulum</u>	30,60				
<u>A. digitatum</u>	30			ca.60	Gaiser 1927
			30		Pfitzer 1957

TABLE II. (Continued)
 CHROMOSOME NUMBERS OF ANTHURIUM SPECIES

Taxa	Present Counts		Previous Counts		Authority
	2n	n	2n	n	
<u>A. pedato-radiatum</u>		ca.15	ca.30		Gaiser 1927
<u>A. pentaphyllum</u>	60	15			Pfitzer 1957
<u>A. undatum</u>			ca.30		Gaiser 1927
			60 &		Marchant 1973
			60+1B		
<u>A. variabile</u>		15	ca.30		Gaiser 1927
			60+4F		Sharma & Bhatta- charya 1966
Sections Undetermined					
<u>A. baleyi</u>	60				
<u>A. ramonense</u>	30				
<u>A. watermaliense</u>	30				
<u>Anthurium</u> sp.	30				
<u>Anthurium</u> sp.			ca.124		Marchant 1973

**Indicates that the count is within two chromosomes.

1. In Fedorov 1969.
2. In Itô 1942.
3. In Delay 1951.

prometaphase difficulty in counting can result since the satellites are often very loosely associated with the chromosome. Depending on the size and number of satellites loosely held or "broken off", these satellites may be interpreted as A or B chromosomes (compare Figures 1, 2, 3, and 4). At a later stage of mitosis the extra pieces are usually no longer visible (compare Figures 5 and 6 with Figure 7).

Section Tetraspermium Schott is the only section with $2N = 24$. Polyploids have also been counted. The count of $2n = 24$ for A. trinerve Miq. is new. Most of the counts for this section are in agreement with $2n = 24$, or the tetraploid number of $2n = 48$. Campbell's (1905) count of $n = 16$ for A. scandens was taken from sectioning and was presented as an approximation. Marchant's (1973) count of 45-47 chromosomes for A. scandens Engl. perhaps reflected his difficulty in getting good chromosomal spread for this species. Mexican populations are heptaploids with $2n = 84$.

As shown in Table II, previous chromosome counts are available for both Sections Gymnopodium Engl. and Chamaerepium Schott. However members of neither of these sections were available, and these counts could not therefore be confirmed. Gaiser's (1927) count of ca.50 for A. radicans C. Koch seems interestingly suggestive of a relationship of this species with A. scandens of Sect. Tetraspermium where $4N = 48$ is commonly encountered. If Pfitzer's count of $2n = 30$ is considered as the correct count, then Gaiser's specimen was perhaps a tetraploid with $4N = 60$ instead of ca.50.

The distributions of chromosome numbers within the Sections Porphyrochitonium Schott and Belolonchium Engl. appear similar. Both

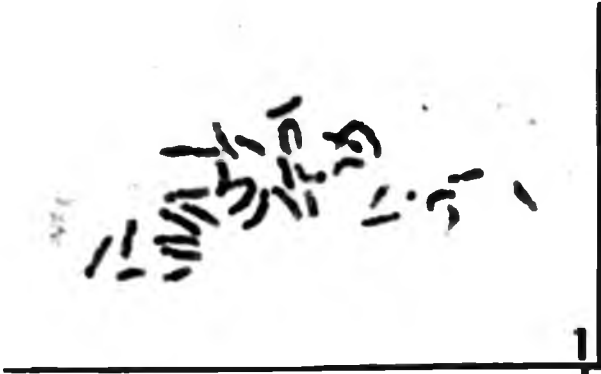
sections are apparently based on $2n = 30$, with a single hexaploid A. supianum Engl. being observed in Sect. Belolonchium. Five species A. concinnatum, Schott, A. flavo-viride? Engl. (Figure 10), A. gustavii Regel., A. micromystrium Sodiro, and A. procerum? Sodiro (Figure 11) have been newly counted with $2n = 30$. Photomicrographs are also provided for A. scherzerianum Schott (Figure 8) and A. denudatum Engl. (Figure 9). The photomicrographs (Figures 8, 9 and 10) show that within a karyotype the length of the chromosomes are usually diverse, with some chromosomes much longer than others, and the centromeric position varies ranging from near telocentric to metacentric. Counts in A. andreanum Linden and A. scherzerianum appear confused where both 30 and 32 have been recorded. Anthurium species have at least two satellited chromosomes, and the satellites often are only loosely held until midmetaphase. Possibly earlier counts of $2n = 32$ were made from late prophase figures, and the two extra chromosomes were the satellites.

The Sections Pachyneurium Schott, Semaeophyllum Schott, and Schizoplacium Schott apparently are composed of mostly diploids of $2n = 30$ and a few tetraploids. Several species, A. aemulum Schott (Figure 16), A. digitatum (Jacq.) G. Don (Figure 17), A. hookeri Kunth (Figure 14), A. pentaphyllum G. Don (Figure 19), A. undatum Schott, and A. variabile Kunth, have both diploid and tetraploid representatives within the same species, and A. undatum and A. variabile apparently have B chromosomes or fragments. Three species, A. glazorii Hook. f., A. signatum C. Koch & Mathieu, and A. subsignatum Schott (Figure 15)

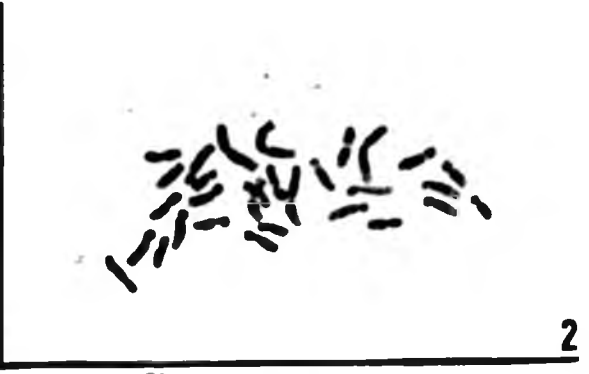
Plate I. Somatic chromosomes of Anthurium species (1100C).

Figure:

1. A. lindenianum, $2n = 30 + 1$ satellite which appears as an extra piece.
2. A. lindenianum, $2n = 30$ with no visible extra pieces.
3. A. clarinervium, $2n = 30 + 1$ piece in late prophase.
4. A. clarinervium, $2n = 30$ with no visible extra pieces in metaphase.
5. A. warocqueanum, $2n = 30$ with 4 pieces.
6. A. warocqueanum, $2n = 30$ with 5 pieces.
7. A. warocqueanum, $2n = 30 + 3B$.
8. A. scherzerianum, $2n = 30$.
9. A. denudatum, $2n = 30$.
10. A. flavo-viride?, $2n = 30$.
11. A. procerum?, $2n = 30$.



1



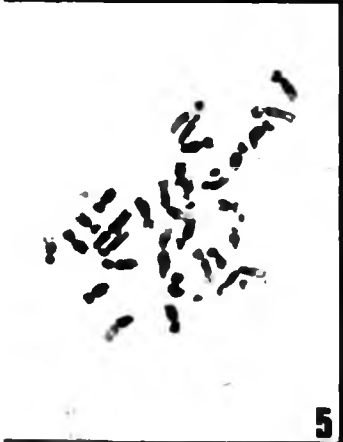
2



3



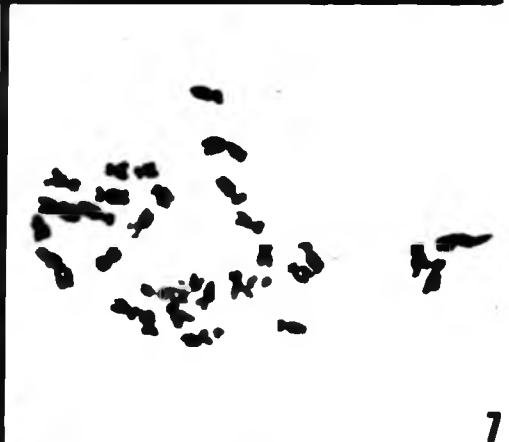
4



5



6



7



8



9



10



11

has been reported to be diploids with B chromosomes present in varying numbers, but B chromosomes in these species were not observed by the author. Anthurium ellipticum (Figure 12), A. hacumense (Figure 13), and A. holtonianum (Figure 18) also have $2n = 30$. A. pulchellum Engl. reported as $2n = 63$ by Mookerjea (1955) is probably a tetraploid with B chromosomes. The count of 56 for A. boucheanum C. Koch (Mookerjea, 1955) cannot easily be explained, and possibly could be a miscount or an atypical form of the species.

Section Polyphyllium Engl. has only a single species, A. mexicanum Engl. with $2n = 60$ a tetraploid number. This is the only species where a related diploid was not found.

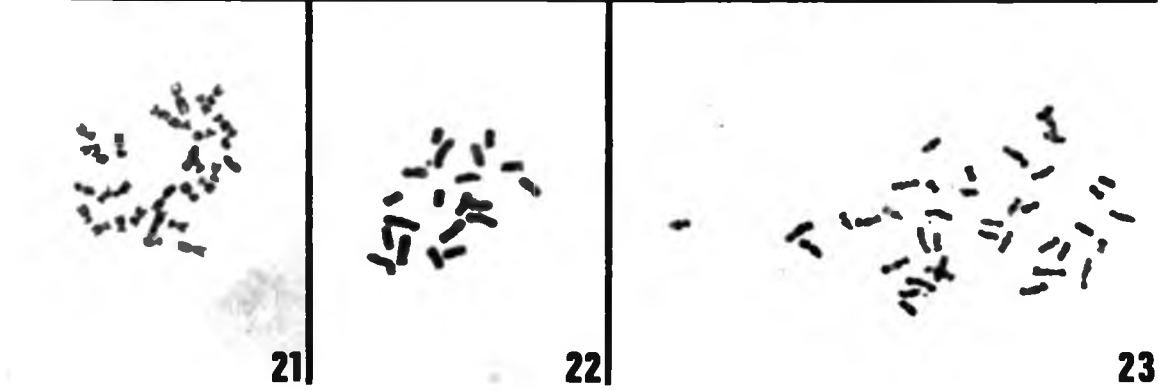
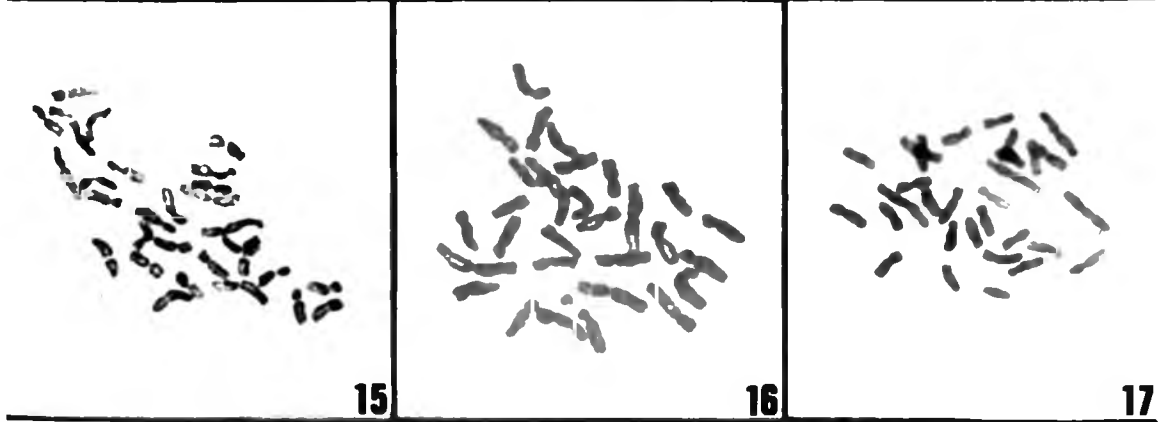
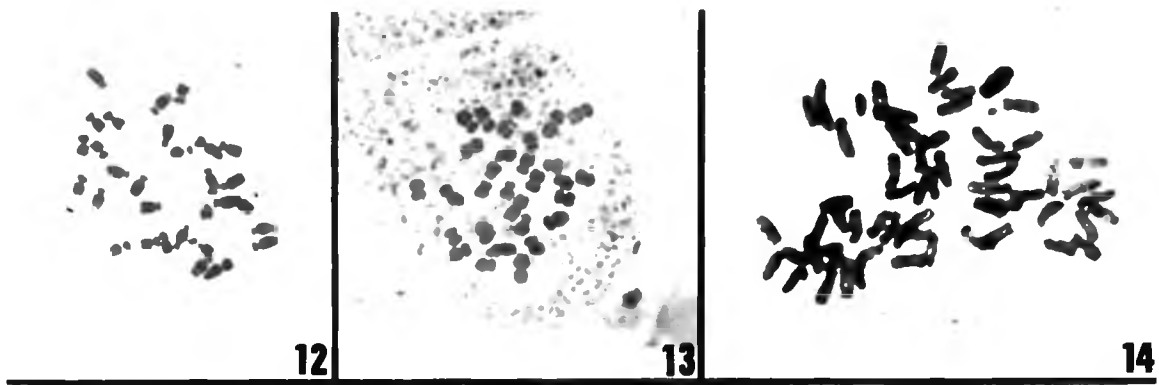
Sect. Leptanthurium Schott is a small section of only six species with apparent taxonomic confusion between A. gracile and A. scolopendrinum. Using Standley's (1944) concept of the species A. gracile (Rudge) Lindl. and A. scolopendrinum Kunth, both are quite distinct. This treatment of these two species was used for separation of the author's specimens.

The chromosome numbers of three species of Sect. Leptanthurium were determined. Unlike the two species A. acutangulum and A. gracile (Figure 31) with $2n = 30$, A. scolopendrinum Kunth is $2n = 20$ (Figure 22) and 40 (Figure 23). Based on the previous count of 40 by Marchant (1973) and the present counts, tetraploids appear to be at least as common as the diploids if not more prevalent. The diploid $2n = 20$ is the lowest chromosome number observed in the genus. Marchant's count of 40 for A. gracile evidently reflects a specimen that Standley would refer to as A. scolopendrinum.

Plate II. Somatic chromosomes of Anthurium species (1100X).

Figure:

12. A. ellipticum, $2n = 30$.
13. A. hacumense, $2n = 30$.
14. A. hookeri, $2n = 60$.
15. A. subsignatum, $2n = 30$.
16. A. aemulum, $2n = 30$.
17. A. digitatum, $2n = 30$.
18. A. holtonianum, $2n = 30$.
19. A. pentaphyllum, $2n = 60$.
20. A. pittieri, $2n = 30$.
21. A. gracile, $2n = 30$.
22. A. scolopendrinum 2N, $2n = 20$.
23. A. scolopendrinum 4N, $2n = 40$.



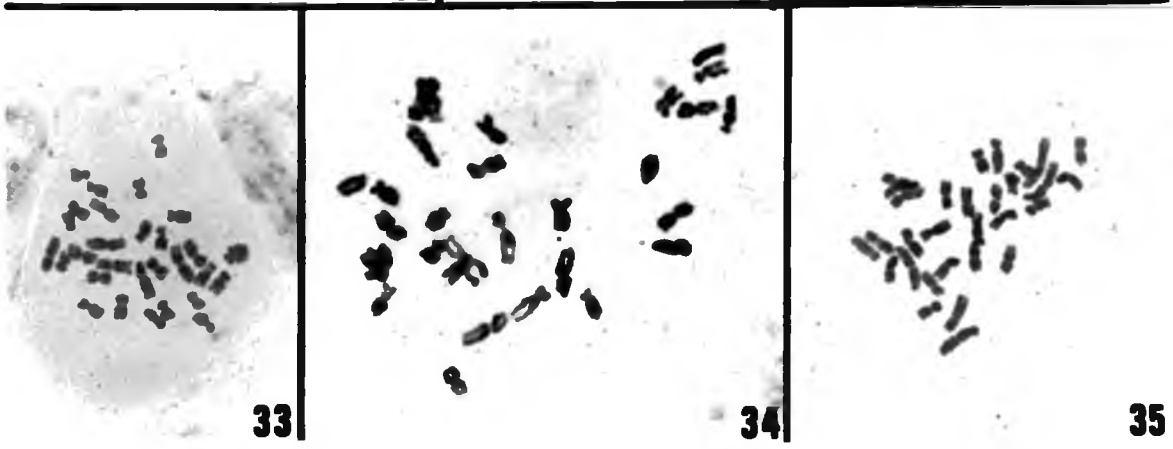
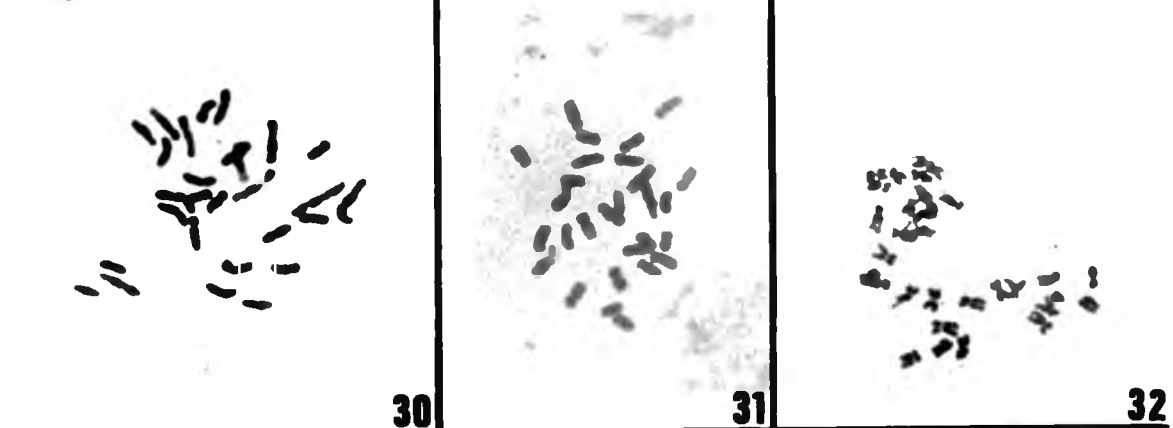
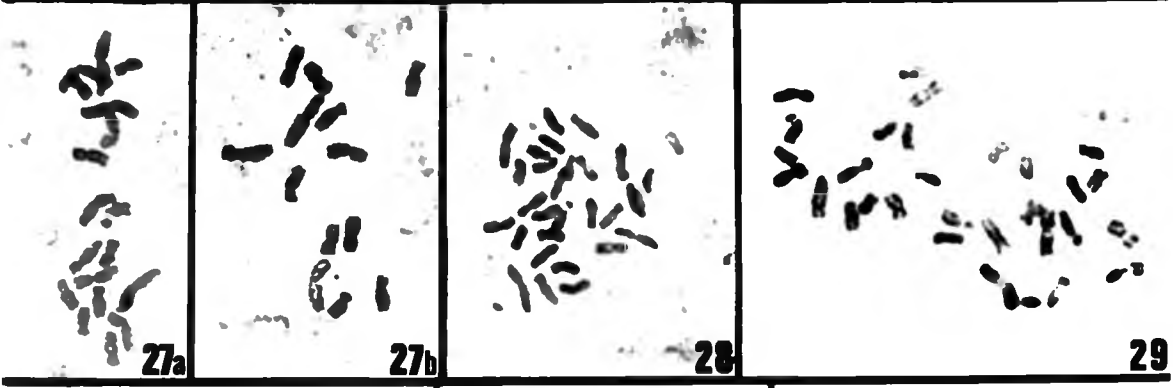
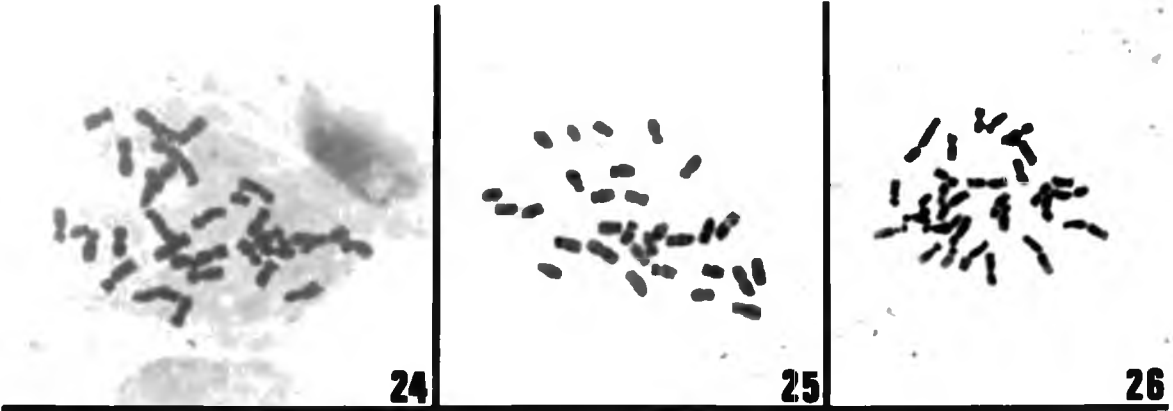
Only a single species of Sect. Polyneurium Engl. has been counted. The description of A. wallisii? Mast. is however somewhat brief. Since neither Gaiser's specimen (1927) nor the author's specimen was apparently compared with the type, two different species actually may have been counted. If both specimens are considered as representatives of the same species, then the counts would seem to indicate that both the diploid and the tetraploid forms are present. B chromosomes were also seen in the species (Figure 24).

Generally the Sect. Urospadix Engl. is characterized by $2n = 30$. Six species which have been newly counted include A. allenii Standl. $2n = 30$ (Figure 26); A. aureum Engl. $2n = 30$ (Figure 26) and $2n = 31$ (Figure 27a, b); A. chinquense Standl. $2n = 30$ (Figure 28); A. gladifolium Schott $2n = 30$ (Figure 29); A. trianae Engl. $2n = 28$ (Figure 32) and $2n = 29+1B$; and A. turrialbense Engl. $2n = 30$ (Figure 33). Polyploidy is evident by the counts of 56 (A. Bellum Schott) by Mookerjea (1955) and ca.124 (A. lucidum Kunth) by Marchant (1973), and B chromosomes are also present. In this group aneuploidy apparently also is evident in at least two species A. aureum ($2n = 30, 31$) and A. trianae ($2n = 28, 29 = 1B$), but the aneuploid number does not appear to be the common number for these species. Evidently for A. littorale Engl. the discrepant counts of $2n = 28$ (Figures 30, 31) and 30 (Gaiser, 1927) are due to different species being examined. Unfortunately Gaiser's (1927) specimen was identified by Standley through a leaf specimen alone. Although the entire plant was available for study of the author's specimen ($2n = 28$), this specimen was not compared with the type specimen of the species. However the importance of this

Plate III. Somatic chromosomes of Anthurium species (1100X).

Figure:

24. A. wallisii?, $2n = 30 + 2B$.
25. A. allenii, $2n = 30$.
26. A. aureum, $2n = 30$.
27. A. aureum, $2n = 31$.
28. A. chiriquense, $2n = 30$.
29. A. gladiifolium, $2n = 30$.
30. A. littorale, $2n = 28$.
31. A. littorale, $2n = 23$.
32. A. trianae, $2n = 28$.
33. A. turrialbense, $2n = 30$.
34. A. bakeri, $2n = 30$.
35. A. wendlingerii, $2n = 30$.



discrepancy will be placed in its proper perspective when discussed later in relationship to cross-compatibilities within this group.

The three Sections Episeiostenium Schott, Calmystrium Schott, and Oxycarpium Schott are also characterized by $2n = 30$. Eight new chromosome counts of $2n = 30$ have been determined in these groups including A. hoffmannii Schott (Figure 36), A. lindenianum C. Koch & Augustin (Figure 37), A. montanum Hemsl. (Figure 38), A. pichincha Engl. (Figure 40), A. pittieri Engl. (Figure 20), A. roraimense N. E. Brown (Figure 42), and A. wendlingerii Barroso (Figure 35). The counts of $2n = 30$ for A. nymphaeifolium C. Koch & Bouché (Figure 39) and A. veitchii Mast. (Figure 43) confirmed previous counts for these two species. Anthurium bakeri Hook. f. ($2n = 30$, Figure 34) was counted by Sharma & Bhattacharya (1966) as $2n = 28 + 1f$, but they also observed cells with 20 and 30. Their plants were in cultivation and may not reflect the situation in natural populations.

Only a single species A. rhodostachyum Sodiro of Sect. Digitinervium Sodiro was counted, but each specimen examined had a different chromosome number. If $2n = 30$ (Figure 46), the common diploid number in Anthurium, is considered as the diploid number of this species, then an aneuploid series 28 (Figure 44), 29 (Figure 45), and 31 (Figure 47) occurs. This is the only species which has exhibited an aneuploid series. A. rhodostachyum has a very heavy textured semicordate leaf and appears quite distinct taxonomically from the other Anthurium species examined.

Section Cardiolonchium Schott also generally has diploids with $2n = 30$, but B chromosomes are very common. Eight species of this

section have been newly counted. These are A. clarinervium Matuda, $2n = 30$ (Figure 4); A. grande hort., $2n = 30$; A. regale Linden, $2n = 30+1B$ (Figure 50); A. splendidum hort., $2n = 30+2B$ (Figure 51); A. velutinum? Engl., $2n = 30$; A. venosum? Griseb, $2n = 30$ (Figure 53); A. walujewii Regel, $2n = 30+2B$ (Figure 52); and A. wulschlaegelii Engl., $2n = 30$ (Figure 54). The count of $2n = 30$ for A. forgetii N. E. Brown (Figure 49) confirms the earlier count for this species. Only a single species, A. magnificum Linden, is at the tetraploid level. B chromosomes are more numerous in this section than in any of the other sections examined. The size of the B chromosomes is quite variable, being almost dot-like in A. warocqueanum J. Moore (Figure 7) or approaching the size of the smallest A chromosomes as in A. crystallinum Linden & André (Figure 48), A. regale (Figure 50), A. splendidum (Figure 51), and A. walujewii (Figure 52). The two counts of 34 (A. crystallinum) and 35 A. leuconeurum Lemaire by Mookerjea could reflect her observance of four or five B chromosomes in her specimens.

Three species and an unidentified species of undetermined sectional affiliation have been newly counted. Anthurium baileyi Standl. is a tetraploid with $2n = 60$ (Figure 55). The other two included species are A. ramonense K. Krause (Figure 56) and A. watermaliense hort. which are $2n = 30$. The unidentified species examined by the author had $2n = 30$ (Figure 57). An unidentified species and A. lucidum Kunth were both reported by Marchant (1973) to have $2n = ca. 124$, which is the highest chromosome number observed.

Table III shows the frequency distribution of chromosome numbers. In the previous counts, the investigator's decisions were upheld for

Plate IV. Somatic chromosomes of Anthurium species (1100X).

Figure:

36. A. hoffmannii, $2n = 30$.
37. A. lindenianum, $2n = 30$.
38. A. montanum, $2n = 30$.
39. A. nymphaeifolium, $2n = 30$.
40. A. pichincha, $2n = 30$.
41. A. ranchoanum, $2n = 30$.
42. A. roraimense, $2n = 30$.
43. A. veitchii, $2n = 30$.
44. A. rhodostachyum, $2n = 28$.
45. A. rhodostachyum, $2n = 29$.
46. A. rhodostachyum, $2n = 30$.
47. A. rhodostachyum, $2n = 31$.

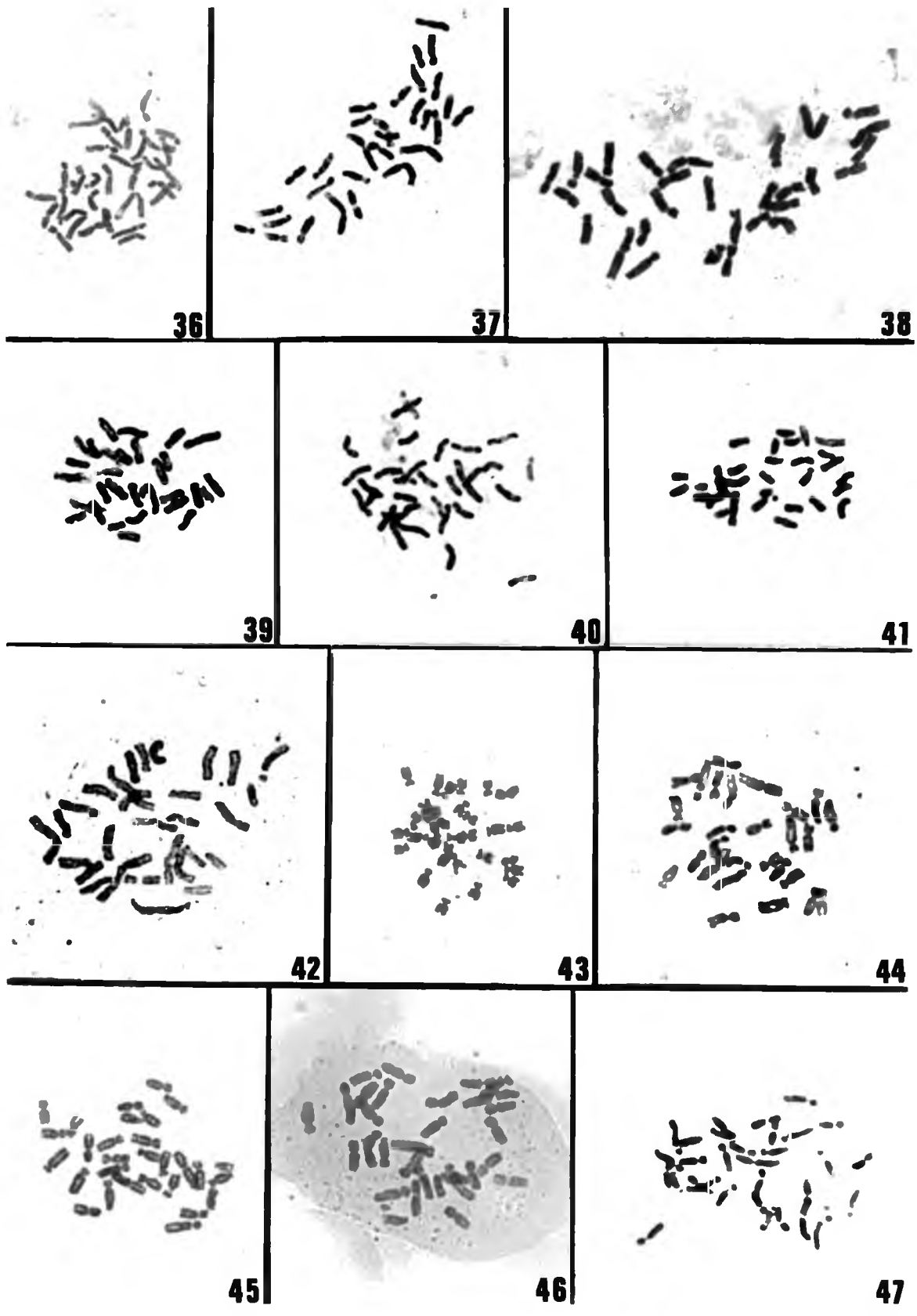


Plate V. Somatic chromosomes of Anthurium species (1100X).

Figure:

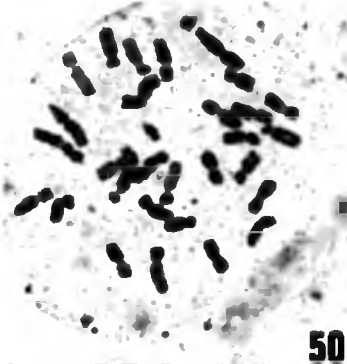
48. A. crystallinum, $2n = 30+1B$
49. A. forgetii, $2n = 30$.
50. A. regale, $2n = 30+1B$.
51. A. splendidum, $2n = 30+2B$
52. A. walujewii, $2n = 30+2B$.
53. A. venosum?, $2n = 30$.
54. A. wulschlaegelii, $2n = 30$.
55. A. baileyi, $2n = 60$.
56. A. ramonense, $2n = 30$.
57. Anthurium sp., $2n = 30$.



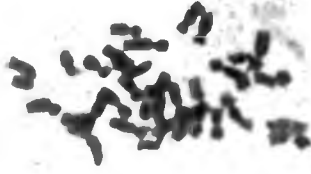
48



49



50



51



52



53



54



55



56



57

chromosome numbers. B chromosomes are not included in the table since generally these can be considered as variants of the usual chromosome numbers for these taxa. Both the previous and present counts indicate a similar distribution with 30 as the most common number. The composite distribution of the chromosome numbers reflects the consideration of both the previous counts and present counts for each taxa, and only chromosome numbers thought to be representative of each taxa are included.

The three chromosome numbers 34, 35 and 63 present a problem. All of these counts were made by a single investigator (Mookerjea, 1955), and none of them have been confirmed by other workers. These counts may reflect aneuploidy or the presence of B chromosomes in plants under cultivation. These counts will not therefore be considered in establishing a basic number for the genus.

The chromosome numbers indicated below 30 are 20, 24 and 28, suggesting basic numbers of 5, 6 and 7. Even though 15 was considered as the basic number of Anthurium by Gaiser (1927) and Marchant (1973), 15 is obviously a secondary basic number (x_2). Although no diploids were observed with chromosome numbers of $2n = 10, 12$ and 14 , the shift in the basic number is considered to occur at this level. If the shift would have occurred with basic numbers of $10, 12$ and 14 (with $2n = 20, 24$ and 28), then one would also expect numbers of 11 and 13 ($2n = 22$ and 26). Diploids with $2n = 22$ and 26 were not observed, therefore the shift among basic numbers must have occurred at the original level indicated. Thus a shift at $5, 6$ and 7 with chromosome doubling would

TABLE III.
 FREQUENCY OF CHROMOSOME NUMBERS IN ANTHURIUM TAXA

	Chromosome Numbers														
	20	24	28	30	32	34	35	40	48	56	60	63	84	90	124
Previous Counts	0	1	2	50	4	3	1	2	1	3	5	1	0	0	2
Present Counts	1	2	2	54	0	0	0	1	1	0	6	0	1	1	0
Composite*	1	2	2	87	0	1	1	1	1	3	10	1	1	1	2

*Only chromosome numbers thought to be representative of each taxa are included.

give plants with $n = 10, 12$ and 14 ($2n = 20, 24$ and 28). These are the observed gametic numbers.

The other chromosome numbers presented in Table III form polyploid series of the four previously considered numbers as: 20-40 (2), 24-48-84 (4), 28-56? (6) and 30-60-90-ca. 124 (100). The number given in parenthesis indicates the number of species in the complex (but a few species have been counted twice where both the diploid and tetraploid are present in the same species). Curiously almost all the counted Anthurium species are a part of the polyploid complex of $2n = 30$. The relationship between the basic numbers of 5, 6, 7 and 15 (x_2) can be better assessed through correlation with crossability studies.

The richest development of Araceae occurs in the Old World flora with most endemic species and genera occurring in this region (Rendle, 1967). Anthurium occurs only in North and South America (Engler, 1905). If the Old World is considered as the origin of Araceae, then the genus Anthurium must have had its origin from one of the other related genera of the New World. If the closely related genera to Anthurium of the New World (as indicated by Bentham & Hooker, 1883; and Hutchinson, 1959), are examined for chromosome numbers, most of these counts reflect a basic number of six. Other indication of six as the basic number for the genus will be examined after morphological data and crossabilities of Anthurium species are reviewed.

SEXUAL COMPATIBILITY STUDIES

The present study involved 1600 cross- and self-pollinations of 56 species. These pollinations included 292 different cross-

combinations (including reciprocals) and 29 different selfs (including sibling and clonal pollinations). In total, 321 combinations were attempted. Availability of proper receptive spadices and pollen at the right time proved to be the limiting factor. The 1600 pollinations resulted in 330 fruiting spadices which yielded 220 seedling populations. One hundred thirty-nine seedling populations were evaluated both morphologically and chromosomally. Three seedling populations were found to be contaminants. Before cross-compatibilities can be presented in detail, the construction of the six groups involved must be examined.

The present sectional division of Anthurium (Engler, 1905) is often misleading for assessing species relationships, which therefore necessitates the construction of morphologically related groups for study. Although the sections recognized by Engler were to be natural groupings, evidently much of the information necessary for sectional placement was missing. Although the berry features--number of ovules per locule, color and shape--were prominent features of Engler's key, this information is often missing in the included species descriptions. Tables IV and V were compiled of some morphological characters of the species examined by the author. Engler's sectional category appropriate for each species is given for comparison. The author's groups are differentiated by the key presented below.

TABLE IV.
NUMBER OF SEEDS PER BERRY OF ANTHURIUM SPECIES

Taxa	Engler's Section	Seeds Per Berry		
		Av.	Range	Berries Counted
Group I				
<u>A. acutangulum</u>	<u>Leptanthurium</u>	1.9	1-4	357
<u>A. allenii</u>	<u>Urospadix</u>	3.5	1-7(-9)*	723
<u>A. chiriquense</u>	<u>Urospadix</u>	2.8	1-4	349
<u>A. gladiifolium</u>	<u>Urospadix</u>			
<u>A. gracile</u>	<u>Leptanthurium</u>	2.5	1-4	217
<u>A. littorale</u>	<u>Urospadix</u>	2.1	1-5	2053
<u>A. ramonense</u>	?	2.1	1-4	614
<u>A. scandens</u> ssp. <u>pusillum</u>	<u>Tetraspermium</u>	2.3	1-4	41
ssp. <u>scandens</u>	<u>Tetraspermium</u>	3.0	1-4(-6)	344
<u>A. scherzerianum</u>	<u>Porphyrochitonium</u>	1.9	1-4	751
<u>A. terryae</u>	?	2.2	1-4(-5)	111
<u>A. trianae</u>	<u>Urospadix</u>	2.9	1-5(-7)	162
<u>A. trinerve</u>	<u>Tetraspermium</u>	5.5	1-9 (-12)	313
<u>A. wendlingeri</u>	<u>Episeiostenium</u>	2.8	1-4	914
<u>Anthurium</u> sp.		3.6	1-6	9
Group II				
<u>A. aureum</u>	<u>Urospadix</u>	1.5	1-2(-4)	2069
<u>A. bakeri</u>	<u>Episeiostenium</u>	1.8	1-2(-4)	1706
<u>A. pittieri</u>	<u>Oxycarpium</u>	1.2	1-2	107
<u>A. scolopendrinum</u> 2N	<u>Leptanthurium</u>	1.7	1-2	576
4N	<u>Leptanthurium</u>	1.7	1-2	561
<u>A. turrialbense</u>	<u>Urospadix</u>	1.1	1-2	456
Group III				
<u>A. ellipticum</u>	<u>Pachyneurium</u>	1.5	1-2(-3)	1421
<u>A. hacumense</u>	<u>Pachyneurium</u>			
<u>A. hookeri</u>	<u>Pachyneurium</u>	1.3	1-2(-3)	1406
<u>A. joseanum</u>	<u>Pachyneurium</u>	1.6	1-2	867
Group IV				
<u>A. aemulum</u> 2N	<u>Schizoplacium</u>	1.1	1-2	63
4N	<u>Schizoplacium</u>	1.0	1	120
<u>A. digitatum</u>	<u>Schizoplacium</u>	1.3	1-2	219
<u>A. pentaphyllum</u>	<u>Schizoplacium</u>	1.7	1-2	156
X <u>A. macrolobium</u>	<u>Schizoplacium</u>			

*The parenthesis indicates that less than 5% of the berries counted had the indicated number of seeds.

TABLE IV. (Continued)

NUMBER OF SEEDS PER BERRY OF ANTHURIUM SPECIES

Taxa	Engler's Section	Seeds Per Berry		
		Av.	Range	Berries Counted
Group V				
<u>A. clarinervium</u>	<u>Cardiolonchium</u>	1.1	1-2	13
<u>A. crystallinum</u>	<u>Cardiolonchium</u>	1.1	1-2	1174
<u>A. denudatum</u>	<u>Belolonchium</u>			
<u>A. forgetii</u>	<u>Cardiolonchium</u>	1.3	1-2	1400
<u>A. grande</u>	<u>Cardiolonchium</u>	1.1	1-2	27
<u>A. grandifolium</u>	<u>Pachyneurium</u>	1.3	1-2(-3)	2519
<u>A. magnificum</u>	<u>Cardiolonchium</u>	1.2	1-2	620
<u>A. regale</u>	<u>Cardiolonchium</u>	1.2	1-2	1775
<u>A. splendidum</u>	<u>Cardiolonchium</u>	1.4	1-2	20
<u>A. subsignatum</u>	<u>Semaeophyllum</u>	2.0	(1-)2	1143
<u>A. velutinum?</u>	<u>Cardiolonchium</u>	1.4	1-2	919
<u>A. venosum?</u>	<u>Cardiolonchium</u>	1.3	1-2(-3)	1773
<u>A. wallisii?</u>	<u>Polyneurium</u>	1.7	1-2	443
<u>A. walujewii</u>	<u>Cardiolonchium</u>	1.6	1-2	2484
<u>A. warocqueanum</u>	<u>Cardiolonchium</u>	1.6	1-2(-3)	647
<u>A. wulschlaegelii</u>	<u>Cardiolonchium</u>	1.5	1-2	172
Group VI				
<u>A. andreanum</u>	<u>Belolonchium</u>	1.6	1-2(-3)	4190
<u>A. baileyi</u>	?	1.5	1-2	332
<u>A. concinnatum</u>	<u>Belolonchium</u>	1.6	1-2(-4)	692
<u>A. flavo-viride?</u>	<u>Belolonchium</u>	1.3	1-2	778
<u>A. hoffmannii</u>	<u>Calomystrium</u>	1.3	1-2	543
<u>A. lindenianum</u>	<u>Calomystrium</u>	1.4	1-2(-3)	2519
<u>A. micromystrium</u>	<u>Belolonchium</u>	1.5	1-2	776
<u>A. nymphaeifolium</u>	<u>Calomystrium</u>	1.9	1-2	67
<u>A. pichincha</u>	<u>Calomystrium</u>	1.5	1-2	1445
<u>A. procerum?</u>	<u>Belolonchium</u>	1.3	1-2(-3)	858
<u>A. ranchoanum</u>	<u>Calomystrium</u>	1.2	1-2	69
<u>A. rhodostachyum</u>	<u>Digitinervium</u>	1.3	1-2	384
<u>A. roraimense</u>	<u>Calomystrium</u>	1.1	1-2	47
<u>A. subhastatum</u>	<u>Xialophyllum</u>			
<u>A. supianum</u>	<u>Belolonchium</u>			
<u>A. triangulum</u>	<u>Xialophyllum</u>	1.3	1-2	476
<u>A. watermaliense</u>	?	1.2	1-2	283

TABLE V.

BERRY, LEAF AND SPADIX CHARACTERS OF ANTHURIUM SPECIES

Taxa	Berry		Leaf Shape	Spadix	
	Shape ^a	Color ^b		Shape ^c	Color
Group I					
<u>A. acutangulum</u>	DG	LP	Ovate-truncate	CA	Gr
<u>A. allenii</u>	DG	LP	Elliptic	CY	DP
<u>A. chiriquense</u>	DG	LP	Elliptic	CA	Ol
<u>A. gladiifolium</u>			Long-lanceolate	CY	DP
<u>A. gracile</u>	DG	Y	Linear	A-CY	Br
<u>A. littorale</u>	DG	YOr	Ovate-elliptic	A	Ol
<u>A. ramonense</u>	DG	YOr	Elliptic	CY	Br
<u>A. scandens</u> ssp. <u>pusillum</u>	DG	V	Ovate-lanceolate	CY	WGr
ssp. <u>scandens</u>	DG	LV	Ovate-lanceolate	CY	WGr
<u>A. scherzerianum</u>	O	ROr	Lanceolate	C-A	var.
<u>A. terryae</u>	DG	Y	Elliptic	CY	GR
<u>A. trianae</u>	DG	Y	Elliptic	CY	BrP
<u>A. trinerve</u>	AO	W	Lanceolate	CY-A	P, W
<u>A. wendlingerii</u>	OB-O	ROr	Linear	C-A	YG
<u>Anthurium</u> species	AO	La	Lanceolate	CY-A	W
Group II					
<u>A. aureum</u>	AO	P	Wide-lanceolate	CY	YG
<u>A. bakeri</u>	AOB	R	Linear-lanceolate	CY	W
<u>A. pittieri</u>	OB	Y	Lanceolate	A	Gr
<u>A. scolopendrinum</u> 2N	O	R	Oblanceolate	CY	GyP
4N	O	R	Oblanceolate	CY	GyP
<u>A. turrialbense</u>	AO	DP	Lanceolate	CY	Gr
Group III					
<u>A. ellipticum</u>	OB-O	ROr	Oblanceolate	A	DP
<u>A. hacumense</u>			Oblanceolate	CY	LP
<u>A. hookeri</u>	OB-O	W	Obovate	A	Bl
<u>A. joseanum</u>	AO	Or	Linear-lanceolate	A	P
Group IV					
<u>A. aemulum</u> 2N	AO	DP	Pedately parted	CY	Cr-LP
4N	AO	DP	Pedately parted	A	LP
<u>A. digitatum</u>	O	DP	Pedately parted	A-CY	DP
<u>A. pentaphyllum</u>			Pedately parted	A	W-Lp
X <u>A. macrolobium</u>	OB	R	Palmately lobed	A	DP

^aThe following abbreviations for berry shapes were used: AO, apiculate obovoid; AOB, apiculate oblong; DG, depressed globose; Gl, globose; O, obovoid; OB, oblong; and OB-O, oblong obovoid.

^bThe following abbreviations for color were used: Bl, blue; Br, brown; BrPr, brownish purple; DP, dark purple; Gr, green; GyP, greyish purple; La, lavender; LP, light purple; LR, light red; LV, light violet; Ol, olive; Or, orange; P, purple; R, red; ROr, red orange; W, white; WGr, whitish green; Y, yellow; YG, yellow green; and YOr, yellow orange.

TABLE V. (Continued)

BERRY, LEAF AND SPADIX CHARACTERS OF ANTHURIUM SPECIES

Taxa	Berry		Leaf Shape	Spadix	
	Shape ^a	Color ^b		Shape ^c	Color
Group V					
<u>A. clarinervium</u>	GL	YOr	Ovate-cordate	A	DP
<u>A. crystallinum</u>	AO	DP	Ovate-cordate	A	Ol
<u>A. denudatum</u>	AO	DP	Hastate-trilobate	A	P
<u>A. forgetii</u>	AO	DP	Peltate	A	Y
<u>A. grande</u>	AO	DP	Oblong-cordate	A	Ol
<u>A. grandifolium</u>	AO	DP	Ovate-cordate	A	Ol
<u>A. magnificum</u>	AO	DP	Ovate-cordate	A	Ol
<u>A. regale</u>	O	DP	Ovate-cordate	A	Ol
<u>A. splendidum</u>	O	DP	Ovate-cordate	A	Ol
<u>A. subsignatum</u>	AO	DP	Hastate	A	YG
<u>A. velutinum?</u>	O	DP	Ovate-cordate	A-CY	YG
<u>A. venosum?</u>	AO	DP	Ovate-cordate	A	YG
<u>A. wallisii?</u>	AO	DP	Oblong-sagittate	A	Ol
<u>A. walujewii</u>	AO	DP	Ovate-cordate	A	Ol
<u>A. warocqueanum</u>	OB-O	ROr	Oblong-cordate	A	Ol
<u>A. wulfschlaegelii</u>	AO	DP	Ovate-cordate	A	Br
Group VI					
<u>A. andreanum</u>	AO	YOr	Ovate-cordate	CY	var.
<u>A. baileyi</u>	OB	YOr	Ovate-cordate	CA	P
<u>A. concinnum</u>	AO	YOr	Ovate-cordate	CY	W
<u>A. flavo-viride?</u>	O	YG	Ovate-cordate	CY	G
<u>A. hoffmannii</u>	AO	ROr	Ovate-cordate	A	G
<u>A. lindenianum</u>	AO	R	Ovate-cordate	CY	W
<u>A. micromystrum</u>	O	PGr ^d	Ovate-cordate	CY	DP
<u>A. nymphaeifolium</u>	OB-O	ROr	Ovate-cordate	CY	W
<u>A. pichincae</u>	OB	ROr	Ovate-cordate	CY	Y
<u>A. procerum?</u>	OB	R	Ovate-cordate	CY	Y
<u>A. ranchoanum</u>	O	R	Oblong-cordate	A-CY	Br
<u>A. rhodostachyum</u>	GL	P	Ovate-cordate	A	P
<u>A. roraimense</u>	AO	YOr	Ovate-cordate	A-CY	W
<u>A. subhastum</u>	OB	LR	Sagittate	CY	Y
<u>A. supianum</u>			Cordate-sagittate	CY-A	G
<u>A. triangulum</u>	AOB	R	Sagittate	CY	G
<u>A. watermaliense</u>	GL	Or	Sagittate	CY	DP

^cThe following abbreviations for spadix shapes were used: A, attenuate; C, coiled; CA, caudate; and CY, cylindrical.

^dApex purple, lower greenish yellow.

KEY TO THE SIX CONSTRUCTED GROUPS OF ANTHURIUM

Berries three or more seeded, shape usually depressed-globose.--Group I

Berries two or fewer seeded, shape various.

Leaves lanceolate or oblanceolate.

Plants small; leaves 60 cm or less.-----Group II

Plants large, coarse; leaves 70 cm or greater.-----Group III

Leaves cordate, hastate-trilobed, palmately lobed, or
pedately parted.

Leaves palmately lobed or pedately-parted.-----Group IV

Leaves cordate or hastate-trilobed.

Leaves usually velvety; berry shape apiculate

obovoid, apex dark purple base

lighter (if not purple, then leaf velvety);

spadix attenuate.-----Group V

Leaves leathery; berry shape various, color

red or orange, infrequently purple; spadix

cylindrical or slightly attenuate-----Group VI

Although this key essentially follows Engler's, different species groupings are inferred with the exception of Groups III and IV which follow his Sections Pachyneurium Schott and Schizoplacium Schott respectively. Each of the other groups differs from Engler's presentation and will be examined individually.

The greatest departure from Engler's sectional categories occurs in Groups I and II. Engler has three sections which would fit into Group I, Sections Gymnopodium Engl., Porphyrochitonium Schott, and

Tetraspermium Schott. With increased data on number of seeds per berry, some species of Sections Episeiostenium Schott emend. Engl., Leptanthurium Schott, and Urospadix Engl. are obviously misplaced and therefore should also be included in Group I. From the number of misplaced species indicated in this study, the sectional integrity of Sections Episeiostenium, Leptanthurium, and Urospadix becomes very doubtful. Group I forms a very natural grouping, quite distinct from the other five groups.

Group II contains Sect. Oxycarpium Schott emend. Engl. and the residual elements of Sections Episeiostenium, Leptanthurium, and Urospadix. Primarily Group II is a gathering of the small lanceolate leaved species with two or fewer seeds per berry into a single unit for study.

Group V primarily follows the Sect. Cardiolonchium Schott emend. Engl., but also includes A. denudatum, A. subsignatum, and A. wallisii?. Unfortunately information regarding the number of seeds per berry for A. denudatum was not available. Placement in this group of A. denudatum, A. subsignatum, and A. wallisii? was based upon berry shape and color, and spadix shape and color. The leaf texture of these three species is not velvety as it is in many of the other species in this group.

Group VI is basically a union of Sections Belolonchium Schott and Calomystrium Schott emend. Engl. which were divided by Engler on the basis of spathe shape and color. Although this division may be a convenient technique of splitting a large number of species (122) into more manageable size, the biological significance of such a split is

doubtful. Included in Group VI also are three species A. rhodostachyum, A. subhastatum, and A. triangulum which are quite different from the other species used in this study. Group VI is however, their closest affiliation, and these species are included primarily for convenience. If these groupings are acceptable as a more or less natural set of groups, then cross-compatibilities can be examined among and within these groups.

One last feature which must be considered is the mode of reproduction. Little emphasis has been given to this, since most Anthurium species were found to be cross-pollinating, but with a few notable exceptions. A. bakeri, A. scandens, A. scolopendrinum and A. trinerve are apparently self-pollinating. Unfortunately the spadices of these species are small and difficult to handle, especially for emasculation. Emasculations were performed on A. trinerve and resulted in no fruit set, but with baggings without emasculations fruit set was very high. Seedlings from open pollination and attempted cross-pollinations (without emasculations) appeared exactly like the maternal parents. No hybrids were obtained. With this information, the constructed groups can now be analyzed for sexual compatibilities.

Intergroup Cross-compatibilities

Intergroup cross-compatibilities support the group delineation as indicated, but a few surprising intergroup combinations were obtained (Table VI). All possible intergroup combinations were attempted except for Group III X Group IV (the reciprocal was attempted). Most of the intergroup hybridization attempts were failures except for Group V

TABLE VI.
 NUMBER OF ATTEMPTED POLLINATIONS AND FRUITS HARVESTED
 AMONG CONSTRUCTED ANTHURIUM GROUPS

♀ \ ♂	I	II	III	IV	V	VI
I		71,0 ^a	13,0	15,0	60,0	107,0
II	43,5 ^b		3,0	6,2 ^c	9,1 ^d	37,1 ^e
III	5,0	1,0		-	5,0	8,0
IV	13,0	6,0	3,0		13,0	29,4 ^f
V	22,2 ^g	6,1 ⁿ	7,1 ⁱ	11,1 ^j		65,17 ^k
VI	62,0	58,6 ^l	26,0	21,1 ^m	132,3 ⁿ	

- a. The first number indicates the number of attempted pollinations, and the second number indicates the number of fruits harvested.
- b. Four, 0% germination.
A. aureum X A. acutangulum, 2% germination, died as seedlings.
- c. One, 0% germination.
A. aureum X A. pentaphyllum, 18% germination, died as seedlings.
- d. A. aureum X A. denudatum, 89% germination, died as seedlings.
- e. A. turrialbense X A. ranchoanum, 79% germination, died as seedlings.
- f. Three, 0% germination.
A. digitatum X A. triangulum, 8% germination, died as seedlings.
- g. Two, 0% germination.
- h. One, 0% germination.
- i. One, 0% germination.
- j. One, 0% germination.
- k. Nine, 0% germination.
A. crystallinum X A. procerum?, 3% germination, died as seedlings.
A. grandifolium X A. subhastatum, 4% germination, good hybrid, produced viable seed.
A. subsignatum X A. pichincha, 10% germination, died as seedlings.
A. grandifolium X A. pichincha, 24% germination, good hybrid.
A. walujewii X A. concinnatum, 31% germination, good hybrid.
A. subsignatum X A. lindenianum, 36% germination, good hybrid.
Two, A. grandifolium X A. nymphaeifolium, 66 and 71% germination, good hybrid.
- l. Six, 0% germination.
- m. A. triangulum X A. digitatum, 81% germination, good hybrid.
- n. A. lindenianum X A. walujewii, 3% germination, died as seedlings.
A. andreanum X A. clarinervium, 10% germination, died as seedlings.
A. andreanum X A. walujewii, 100% germination, died as seedlings.

X Group VI and its reciprocal, which will be discussed individually below. Although seeds were obtained in several intergroup crosses, most failed to germinate; or if germination occurred, the seedlings died before maturity. One plant A. aureum ($2n = 31$), an aneuploid, was responsible for many of the seedlings which germinated but failed to grow; perhaps a few unreduced gametes were responsible for this fruit development. The relationship between A. turrialbense (Group II) and A. ranchoanum (Group VI) may be a bridge between these two groups. Although the original seedlings died, others are alive but growing very slowly. These seedlings have not yet been properly analyzed for hybridity. A single hybrid was obtained between Groups IV and VI. Anthurium triangulum X A. digitatum produced a vigorous sterile hybrid, but the reciprocal resulted in weak seedlings which died early. These two species are undoubtedly distinct but related. Engler reported a similar cross A. leuconeurum Lemaire (Group V?) X A. pedato-radiatum Schott, but this cross was not attempted by the author. Confirmation of the reported hybrid of (A. andreanum X A. nympheae-folium) X A. scherzerianum (in Engler, 1905) was not obtained, although 28 similar pollinations were attempted.

The most common exception to the genetic integrity of the six morphological groups was between Groups V and VI. Mature plants were not obtained from the crosses between Group VI X V, but the reciprocal crosses of V X VI resulted in five flowering hybrid progenies. Three species A. grandifolium, A. subsignatum, and A. walujewii can bridge these two groups. Engler (1905) had also indicated that A. subsignatum (Group V) could be crossed to what the author calls Group VI.

Engler included crosses between A. andreanum and two velvety leaf types (A. magnificum and A. warocqueanum), but these hybrids could not be obtained by the author. Verification of the reported hybrid (Engler 1905) between A. crystallinum and A. veitchii was impossible, since the author's specimen of A. veitchii is still juvenile. From the data presented, Groups I through IV are genetically distinct, but V and VI are related at least through a few intermediates.

Intragroup Sexual Compatibilities

Within these constructed groups, interspecific hybridizations were common. Unfortunately all possible combinations were not performed, but enough data were obtained to present a general view of cross-compatibility within these groups. Each of the groups will be considered individually below.

The very distinct Group I is formed of several genetically isolated species and a group of crossable species. The results of the attempted pollinations among the species of this group are presented in Table VII. A summary and reorganization of these data are presented in Table VIII for easier interpretation. The chromosomally distinct A. scandens and A. trinerve form an isolated unit which does not cross with other species within this group. Anthurium gracile, A. gladiifolium and A. scherzerianum could not be crossed with other species within this group, but only a few spadices of A. gracile and A. gladiifolium were available for study. The remaining species of the group are apparently closely related, and hybrids were obtained to form hybrid links among them. The range of seed germination percentages within a

cross varies widely and depends upon the exact two plants used (Table VII). Generally no difference was observed whether a species was used as a maternal or paternal parent (Table VIII).

Group II forms a small genetically closely related group except for A. scolopendrinum (see Table IX). A. scolopendrinum ($2n = 20, 40$) is chromosomally very different from the rest of the species ($2n = 30$). This difference may be the principle factor for the inability to set fruit on A. aureum, the only one tried. The remaining species of this group form hybrid links among themselves which indicate the genetic closeness of these species.

The three species A. ellipticum, A. hookeri and A. josoanum of Group III are genetically closely related (Table X), but hybrids with A. hacumense were not obtained. Germination percents appear more consistent among hybrids of these species than found in the previous groups. Anthurium ellipticum X A. joseanum gave 96-100% germination of the hybrids while A. hookeri X A. ellipticum and A. hookeri X A. joseanum gave 2% and 8-12% respectively. Based on these percentages, the relationship between A. ellipticum and A. joseanum is closer than either species to A. hookeri. The relationship of A. hacumense with the other species is difficult to assess, since even selfing failed to produce fruits. Perhaps a sterile specimen of this species was collected, or the specimen had not sufficiently matured.

The sexual compatibilities of the small Group IV, consisting of only three species and a hybrid, are given in Table XI. Anthurium aemulum and A. pentaphyllum are genetically closely related. Anthurium

TABLE VII.

SEXUAL COMPATIBILITIES WITHIN GROUP I

♀ \ ♂	<u>A. acutangulum</u>	<u>A. chiriquense</u>	<u>A. gladiifolium</u>	<u>A. gracile</u>	<u>A. littorale</u>
<u>A. acutangulum</u>	1,0	2,2(52) ^a			2,1(100 f)
<u>A. allenii</u>	3,3(47 f) ^b	2,2(0)			2,0
<u>A. chiriquense</u>		1,1(100 f)			2,0
<u>A. gladiifolium</u>				2,0	
<u>A. gracile</u>		1,0	1,0	3,3(44) ^c	
<u>A. littorale</u>	8,5(66 f) ^d	2,2(75 f) ^e	2,0		11,4(71 f) ^f
<u>A. ramonense</u>	2,1(98)	1,1(96 f)	1,0		2,0
<u>A. scherzerianum</u>	3,1(0)	2,0			2,0
<u>A. trianae</u>	2,2(64 f) ^g				2,1(88)
<u>A. wendlingerii</u>	1,1(0)		1,0		

Note: 1. Each entry is formed such that the first number indicates the total number of attempted pollinations; the second number indicates the number of fruits harvested; the number in parenthesis indicates the average percent of seed germination with the range given below, and f indicates that the hybrids flowered.

2. Anthurium scandens and A. trinerve were not included as maternal parents since they are apparently self-pollinating.

3. A. allenii was not included as a pollen parent since little pollen was available for distribution.

- a. Range, 4-100%.
- b. Range, 14-86%.
- c. Range, 16-60%.
- d. Range, 39-100%.
- e. Range, 50-100%.
- f. Range, 6-96%.
- g. Range, 39-89%.

TABLE VII. (Continued)
SEXUAL COMPATIBILITIES WITHIN GROUP I

♀ \ ♂	<u>A. ramonense</u>	<u>A. scandens</u>	<u>A. scherzerianum</u>	<u>A. trianae</u>	<u>A. trinerve</u>	<u>A. wendlingerii</u>
<u>A. acutangulum</u>	1,1(96)	3,0	5,1(0)	1,0		2,0
<u>A. allenii</u>			1,0			1,0
<u>A. chiriquense</u>			1,0	1,0	1,0	
<u>A. gladiifolium</u>						
<u>A. gracile</u>						4,0
<u>A. littorale</u>	5,2(90 f)	2,0	10,0	3,3(100 f)	2,0	4,0
<u>A. ramonense</u>	1,1(96 f)		1,0		1,0	
<u>A. scherzerianum</u>			5,2(40) ^h		3,0	1,0
<u>A. trianae</u>	1,0		3,0			1,0
<u>A. wendlingerii</u>			1,0			1,1(96)

h. Range, 6-73%.

TABLE VIII.

NUMBER OF ATTEMPTED INTERSPECIFIC POLLINATIONS AND HYBRIDS
OBTAINED FROM CROSS-POLLINATIONS WITHIN GROUP I

Species	Seed Parent		Pollen Parent		Composite		Per cent Success ^a
	# Pollinations	# Hybrids Obtained	# Pollinations	# Hybrids Obtained	# Pollinations	# Hybrids Obtained	
<u>A. acutangulum</u>	7	3	6	4	13	7	54
<u>A. allenii</u>	5	1	-	-	5	1	20
<u>A. chiriquense</u>	4	0	6	3	10	3	30
<u>A. gladiifolium</u>	2	0	5	0	7	0	0
<u>A. gracile</u>	3	0	1	0	4	0	0
<u>A. littorale</u>	9	4	6	2	15	6	40
<u>A. ramonense</u>	6	2	3	2	9	4	44
<u>A. scandens</u>	-	-	2	0	2	0	0
<u>A. scherzerianum</u>	5	0	7	0	12	0	0
<u>A. trianae</u>	5	2	3	1	8	3	38
<u>A. trinerve</u>	-	-	4	0	4	0	0
<u>A. wendlingerii</u>	3	0	6	0	9	0	0
Total	49	12	49	12	98	24	

A. Percent success equals the number of hybrids obtained divided by the number of attempted inter-specific pollinations.

TABLE IX.

SEXUAL COMPATIBILITIES WITHIN GROUP II

$\begin{array}{c} \text{♀} \\ \text{♂} \end{array}$	<u>A. aureum</u>	<u>A. bakeri</u>	<u>A. pittieri</u>	<u>A. scolopendrinum</u>	<u>A. turrialbense</u>
<u>A. aureum</u>	11,10(75 f) ^a	5,2(96 f) ^b	3,0	3,0	3,3(56 f) ^c
<u>A. pittieri</u>	2,0	1,0			2,1(25)
<u>A. turrialbense</u>	2,1(95)		2,1(100) ^d		1,1(27)

- Note: 1. Each entry is formed such that the first number indicates the total number of attempted pollinations; the second number indicates the number of fruits harvested; the number in parenthesis indicates the average percent of seed germination with the range given below, and f indicates that the hybrids flowered.
2. Anthurium bakeri and A. scolopendrinum were not included as maternal parents since they are apparently self-pollinating.

- a. Range, 0-96%.
 b. Range, 92-100%.
 c. Range, 8-100%.
 d. Only one seed.

TABLE X.

SEXUAL COMPATIBILITIES WITHIN GROUP III

$\begin{matrix} \text{♀} \\ \text{♂} \end{matrix}$	<u>A. ellipticum</u>	<u>A. hacumense</u>	<u>A. hookeri</u>	<u>A. joseanum</u>
<u>A. ellipticum</u>	1,1(100 f)	3,1(0)	2,2(2 f) ^a	2,2(98 f) ^b
<u>A. hacumense</u>	2,0	1,0	3,0	1,0
<u>A. hookeri</u>	2,2(2 f) ^c	1,1(0)	1,1(72 f)	3,1(8)
<u>A. joseanum</u>	1,1(100)		2,1(12 f)	

Note: Each entry is formed such that the first number indicates the total number of attempted pollinations; the second number indicates the number of fruits harvested; the number in parenthesis indicates the average percent of seed germination with the range given below, and f indicates that the hybrids flowered.

- a. Range, 0-4%.
- b. Range, 96-100%.
- c. Range, 0-4%.

TABLE XI.

SEXUAL COMPATIBILITIES WITHIN GROUP IV

♀ \ ♂	<u>A. aemulum</u>	<u>A. digitatum</u>	<u>A. pentaphyllum</u>	<u>XA. macrolobium</u>
<u>A. aemulum</u>	2,1(0)	4,1(0)	3,3(16) ^a	1,0
<u>A. digitatum</u>	4,0	1,1(80 f)	4,0	3,0
<u>A. pentaphyllum</u>	1,1(78 f)	5,0	1,1(88 f)	
<u>XA. macrolobium</u>		1,0		2,0

Note: 1. Each entry is formed such that the first number indicates the total number of attempted pollinations; the second number indicates the number of fruits harvested; the number in parenthesis indicates the average percent of seed germination with the range given below, and f indicates that the hybrids flowered.

2. Anthurium holtonianum was not included since this species has not flowered.

a. Range, 0-48%.

digitatum evidently is reproductively isolated from both A. aemulum and A. pentaphyllum. The hybrid X A. macrolobium is sterile, although pollen is formed.

Within Group V (Table XII), most species are crossable with each other, however three species could not be hybridized. Anthurium grande, A. denudatum and A. splendidum were not hybridized, therefore cross-compatibilities did not lead to positive genetic evidence for inclusion of these species in this group. Anthurium grande formed seeds with several of the other species of this group, but the seed failed to germinate. Anthurium denudatum and A. splendidum were involved in few attempted pollinations so their relationships have not really been clarified. Further study is necessary before the interspecific relationships of these two species can be assessed.

Table XIII has been prepared as an aid to understanding the relationships among the crossable species. The table is divided into a section for each species as a seed or pollen parent, so that these can be compared. Whether a species is used as a maternal or paternal parent seems to make little difference in general. In some species, A. clarinervium, A. magnificum, A. venosum and A. warocqueanum, reciprocal differences are suggested. If these reciprocal differences are considered real, then perhaps A. clarinervium and A. venosum exhibit cytoplasmic incompatibility (see Stebins, 1958). Anthurium magnificum, a tetraploid, exhibits a characteristic common in polyploids, where the greatest success in crossing occurs when the maternal parent has the larger chromosome number. This characteristic of polyploids was attributed by Stebbins (1958) to incompatibility between the embryo

TABLE XII.

SEXUAL COMPATIBILITIES WITHIN GROUP V

♀ \ ♂	<u>A. clarinervium</u>	<u>A. crystallinum</u>	<u>A. denudatum</u>	<u>A. forgetii</u>	<u>A. grandifolium</u>
<u>A. clarinervium</u>				1,1(40)	
<u>A. crystallinum</u>				1,1(64 f)	
<u>A. denudatum</u>					1,0
<u>A. forgetii</u>	2,0	1,0			1,0(100 f)
<u>A. grande</u>	1,0	1,1(0)		2,1(0)	
<u>A. grandifolium</u>					
<u>A. magnificum</u>					
<u>A. regale</u>	3,0	2,1(28)	2,0	2,1(68)	1,1(55)
<u>A. splendidum</u>					
<u>A. subsignatum</u>			1,0		
<u>A. velutinum?</u>		3,1(92 f)	1,0	1,1(92 f)	
<u>A. venosum?</u>		1,1(96)			
<u>A. walujewii</u>					
<u>A. warocqueanum</u>	3,0	1,0		1,0	1,0
<u>A. wulschlaegelii</u>	1,0				

- Note: 1. Each entry is formed such that the first number indicates the total number of attempted pollinations; the second number indicates the number of fruits harvested; the number in parenthesis indicates the average percent of seed germination with the range given below, and f indicates that the hybrids flowered.
2. Little pollen was available for A. grande and A. splendidum.
3. Very few spadices of A. wallisii? were available for study, but the cross between A. wallisii? X A. grandifolium was successful, 1,1(100 f).

TABLE XII. (Continued)

SEXUAL COMPATIBILITIES WITHIN GROUP V

$\frac{\text{♀}}{\text{♂}}$	<u>A. magnificum</u>	<u>A. regale</u>	<u>A. subsignatum</u>	<u>A. velutinum?</u>	<u>A. venosum?</u>
<u>A. clarinervium</u>		2,1(0)		2,0	2,1(0)
<u>A. crystallinum</u>	1,1(0)	1,1(56 f)			1,1(0)
<u>A. denudatum</u>					
<u>A. forgetii</u>		2,1(84)		1,1(84 f)	
<u>A. grande</u>	1,0	1,0	1,0	2,1(0)	1,0
<u>A. grandifolium</u>			1,1(80)		
<u>A. magnificum</u>		1,0			
<u>A. regale</u>	2,2(0)	1,1(69)	1,1(80)	1,1(0)	1,0
<u>A. splendidum</u>		1,0		1,0	
<u>A. subsignatum</u>		1,0			
<u>A. velutinum?</u>		3,1(100)			
<u>A. venosum?</u>		1,1(92 f)		1,1(0.0 f)	
<u>A. walujewii</u>	1,1(0)		3,2(98 f) ^a		
<u>A. warocqueanum</u>	1,0	2,0	1,0	1,0	2,0
<u>A. wulschlaegelii</u>	1,0	1,0		1,1(83 f)	

a. Range, 96-100%.

TABLE XII. (Continued)

SEXUAL COMPATIBILITIES WITHIN GROUP V

♀ \ ♂	<u>A. wallisii?</u>	<u>A. walujewii</u>	<u>A. warocqueanum</u>	<u>A. wulschlaegelii</u>
<u>A. clarinervium</u>			1,0	2,1(82)
<u>A. crystallinum</u>			3,3(4 f) ^b	1,1(98)
<u>A. denudatum</u>	1,0	1,0	1,0	
<u>A. forgetii</u>			1,1(12 f)	1,1(96 f)
<u>A. grande</u>			2,2(0)	1,0
<u>A. grandifolium</u>			1,0	
<u>A. magnificum</u>			2,2(56 f) ^c	1,1(56 f)
<u>A. regale</u>		2,2(86 f) ^d	7,0	2,2(89 f)
<u>A. splendidum</u>			1,1(0)	
<u>A. subsignatum</u>		1,1(88)		1,1(92)
<u>A. velutinum?</u>	1,0		2,1(4 f)	
<u>A. venosum?</u>			1,1(4 f)	
<u>A. walujewii</u>	1,1(24)	1,1(80 f)	1,1(0)	
<u>A. warocqueanum</u>			4,2(14) ^e	2,0
<u>A. wulschlaegelii</u>		1,1(84)	1,0	1,0

b. Range, 0-8%.

c. Range, 40-72%.

d. Range, 78-93%.

e. Range, 0-28%.

TABLE XIII.

NUMBER OF ATTEMPTED INTERSPECIFIC POLLINATIONS AND HYBRIDS
OBTAINED FROM CROSS-POLLINATIONS WITHIN GROUP V

Species	Seed Parent		Pollen Parent		Composite		Per Cent Success ^a
	# Pollinations Obtained	# Hybrids Obtained	# Pollinations Obtained	# Hybrids Obtained	# Pollinations Obtained	# Hybrids Obtained	
<u>A. clarinervium</u>	6	2	5	0	11	2	18
<u>A. crystallinum</u>	6	4	6	3	12	7	58
<u>A. forgetii</u>	7	5	6	4	13	9	69
<u>A. grandifolium</u>	2	1	3	2	5	3	60
<u>A. magnificum</u>	3	2	6	0	9	2	22
<u>A. regale</u>	12	6	11	4	23	10	43
<u>A. subsignatum</u>	4	2	5	3	9	5	55
<u>A. velutinum?</u>	6	4	8	3	14	7	50
<u>A. venosum?</u>	4	4	5	0	9	4	44
<u>A. wallisii?</u>	-	-	3	1	3	1	33
<u>A. walujewii</u>	4	2	4	3	8	5	62
<u>A. warocqueanum</u>	10	0	13	5	23	5	21
<u>A. wulfschlaegelii</u>	6	2	8	6	14	8	57
Total	70	34	83	34	153	68	

a. Percent success equals the number of hybrids obtained divided by the number of attempted interspecific pollinations.

and its surrounding tissue. Anthurium warocqueanum perhaps exhibits an interaction of the B chromosomes with the cytoplasm, but the exact nature of this interaction would be very difficult to explain without more data.

Although the percentages of successes of Table XIII are not statistically different, the range is great from 18-69 suggesting possible differences if a larger sample was taken. Seemingly a break in the distribution occurs around 30-40%. The 33% figure was determined from only three observations. If this species is considered to belong to the group of 43% and above, then only three species have lower percentages. These three species had low composite percentages, but complete failure was observed on the maternal or paternal side. Perhaps a better indicator for these three species would be just the percentages for the maternal or paternal side which showed crossing behavior. When this is done the range of the percentages is greatly narrowed and differences are no longer suggested.

If a compilation is made of the percent successes of the species with the same chromosome number and an average determined, then the following percent successes for the various chromosome numbers are: $2n = 30$, 50.6%; $2n = 30+1B$, 48.5%; $2n = 30+2B$, 54.5%; $2n = 30+3B$, 21.7%; and $2n = 60^{**}$, 22.2%. The larger B-chromosomes as found in $2n = 30+1B$, and $2n = 30+2B$, have little affect on interspecific crossability. The small B-chromosomes of $2n = 30+3B$ seem to affect crossability especially in the maternal parent, although the effect is statistically nonsignificant. At present as indicated above sufficient evidence is not available to indicate the role, if any, of

these small B's in affecting crossability.

Within Group VI, sexual compatibilities lead to recognition of several distinct entities including a single species which only produced a viable hybrid with Group IV. All of the attempted crosses of Group VI are compiled in Table XIV. However as an aid to analysis, the data are summarized in Table XV. Evidently A. ranchoanum, A. rhodostachyum, A. subhastatum, and A. supianum are distinct and reproductively isolated from the other species used in this study. Anthurium triangulum, although non-crossable within this group, did cross with A. digitatum of Group IV which suggests a closeness of this species with Group IV. The cross between A. watermaliense X A. baileyi produced a hybrid, but these two species could not be crossed with any of the other species. Although the pollination of A. flavo-viride? by A. procerum? produced nonviable seeds, fruit set alone probably indicates that these two species are perhaps more closely related to each other than to the other species of the group. The remaining species A. andreanum, A. concinatum, A. hoffmanii, A. lindenianum, A. micromystrum, A. nymphaeifolium, A. pichincae produced hybrid links among themselves. The closeness of these last seven species was also observed by Engler (1905). Although Engler did not taxonomically circumscribe these species into the same section, the hybrids that he included between Sections Belolonchium and Cardiolonchium indicate his awareness of their closeness.

Intraspecific pollinations although scanty indicate no clear examples of self-incompatibility (see Table XVI). Selfing in natural populations generally does not occur since most species are

TABLE XIV.

SEXUAL COMPATIBILITIES WITHIN GROUP VI

♀ \ ♂	<u>A. baileyi</u>	<u>A. concinatum</u>	<u>A. flavo-viride?</u>	<u>A. hoffmanii</u>	<u>A. lindenianum</u>
<u>A. andreanum</u>	11,2(0)	3,2(45 f) ^a	6,0	6,6(65 f) ^b	4,3(73 f) ^c
<u>A. baileyi</u>	1,0	1,0	2,0		4,0
<u>A. concinatum</u>	1,0			1,0	
<u>A. flavo-viride?</u>	1,0	1,1(20)	1,0	1,0	1,0
<u>A. hoffmannii</u>	2,0		2,0		
<u>A. lindenianum</u>	7,0		2,0	2,2(66 f) ^d	1,1(80)
<u>A. micromystrium</u>					1,1(0.0)
<u>A. nymphaeifolium</u>		1,0			
<u>A. pichincae</u>	2,0	1,1(100 f)	1,0	1,1(64)	
<u>A. procerum?</u>	6,0	3,0	4,0	2,0	3,0
<u>A. ranchoanum</u>	1,0		1,0		3,0
<u>A. rhodostachyum</u>					1,0
<u>A. roraimense</u>					
<u>A. subhastatum</u>			2,0		1,0
<u>A. supianum</u>					1,0
<u>A. triangulum</u>	1,0		2,0		2,0
<u>A. watermaliense</u>	1,1(6)				1,0

Note: 1. Each entry is formed such that the first number indicates the total number of attempted pollinations; the second number indicates the number of fruits harvested; the number in parenthesis indicates the average percent of seed germination with the range given below, and f indicates that the hybrids flowered.

2. Anthurium andreanum cv. Uniwai (male sterile) was used as a test species. Attempt was made to cross each of the other species with this cultivar, since many clonal plants were available for study.

- a. Range, 0-90%.
 b. Range, 48-83%.
 c. Range, 56-84%.

TABLE XIV. (Continued)

SEXUAL COMPATIBILITIES WITHIN GROUP VI

♀ \ ♂	<u>A. micromystrium</u>	<u>A. nymphaeifolium</u>	<u>A. pichincae</u>	<u>A. procerum?</u>
<u>A. andreanum</u>	2,2(80 f) ^e	1,1(68 f)	5,5(86 f) ^f	8,0
<u>A. baileyi</u>		1,0	3,0	1,0
<u>A. concinnatum</u>				
<u>A. flavo-viride?</u>	1,0	1,0		3,2(0)
<u>A. hoffmannii</u>	3,1(100)	1,0	1,0	1,0
<u>A. lindenianum</u>		1,1(84 f)	3,3(59 f) ^g	6,0
<u>A. micromystrium</u>			1,1(0.0)	
<u>A. nymphaeifolium</u>			1,1	2,0
<u>A. pichincae</u>		1,0	1,1(100)	1,0
<u>A. procerum?</u>	1,0		2,0	4,4(86 f) ^h
<u>A. ranchoanum</u>				1,0
<u>A. rhodostachyum</u>				
<u>A. roraimense</u>				
<u>A. subhastatum</u>			1,0	1,0
<u>A. supianum</u>		1,0		
<u>A. triangulum</u>		1,0	1,0	
<u>A. watermaliense</u>				

- d. Range, 36-96%.
e. Range, 70-90%.
f. Range, 52-96%.
g. Range, 44-80%.
h. Range, 52-100%.

TABLE XIV. (Continued)

SEXUAL COMPATIBILITIES WITHIN GROUP VI

♀ \ ♂	<u>A. ranchoanum</u>	<u>A. rhodostachyum</u>	<u>A. roraimense</u>	<u>A. subhastatum</u>
<u>A. andreanum</u>	3,0	3,0		3,0
<u>A. baileyi</u>	1,0	1,0		1,0
<u>A. concinatum</u>	1,0	1,0		
<u>A. flavo-viride?</u>	1,0			1,0
<u>A. hoffmannii</u>	3,0		1,0	1,0
<u>A. lindenianum</u>	5,1(0)	2,0		
<u>A. micromystrium</u>				
<u>A. nymphaeifolium</u>	1,0	1,0		1,0
<u>A. pichincae</u>		1,0		
<u>A. procerum?</u>	4,0	2,0	1,0	1,0
<u>A. ranchoanum</u>	1,1(5)			1,0
<u>A. rhodostachyum</u>	1,0	1,1(100)		
<u>A. roraimense</u>	1,0			
<u>A. subhastatum</u>			1,0	
<u>A. supianum</u>	1,0			
<u>A. triangulum</u>	2,0			2,0
<u>A. watermaliense</u>	1,1(0)			

TABLE XIV. (Continued)

SEXUAL COMPATIBILITIES WITHIN GROUP VI

♀ \ ♂	<u>A. supianum</u>	<u>A. triangulum</u>	<u>A. watermaliense</u>
<u>A. anreanum</u>	5,0	4,1(0)	8,0
<u>A. baileyi</u>			1,0
<u>A. concinnatum</u>			1,0
<u>A. flavo-viride?</u>	1,0		3,0
<u>A. hoffmannii</u>			3,0
<u>A. lindenianum</u>	2,0	3,1(0)	9,0
<u>A. micromystrum</u>			1,0
<u>A. nymphaeifolium</u>	1,0		1,0
<u>A. pichincae</u>			1,1(0)
<u>A. procerum?</u>		1,0	3,0
<u>A. ranchoanum</u>		1,0	2,0
<u>A. rhodostachyum</u>			1,0
<u>A. roraimense</u>			
<u>A. subhastatum</u>		2,0	
<u>A. supianum</u>			1,0
<u>A. triangulum</u>		1,1(60)	1,0
<u>A. watermaliense</u>		2,0	3,2(27 f) ⁱ

i. Range, 10-43%.

TABLE XV

NUMBER OF ATTEMPTED INTERSPECIFIC POLLINATIONS AND HYBRIDS

OBTAINED FROM CROSS-POLLINATIONS WITHIN GROUP VI

Species	Seed Parent		Pollen Parent		Composite		Per Cent Success ^a
	# Pollinations	# Hybrids Obtained	# Pollinations	# Hybrids Obtained	# Pollinations	# Hybrids Obtained	
<u>A. andreanum</u>	15	6	-	-	15	6	40
<u>A. baileyi</u>	10	0	10	1	20	1	5
<u>A. concinnatum</u>	5	0	6	3	11	3	27
<u>A. flavo-viride?</u>	11	1	9	0	20	1	5
<u>A. hoffmannii</u>	10	1	6	3	16	4	25
<u>A. lindenianum</u>	11	3	11	2	22	5	23
<u>A. micromystrum</u>	3	2	4	2	7	4	57
<u>A. nymphaeifolium</u>	8	0	8	2	16	2	13
<u>A. pichinchae</u>	8	2	9	3	17	5	29
<u>A. procerum?</u>	13	0	9	0	22	0	0
<u>A. ranchoanum</u>	7	0	13	0	20	0	0
<u>A. rhodostachyum</u>	3	0	7	0	10	0	0
<u>A. roraimense</u>	1	0	3	0	4	0	0
<u>A. subhastatum</u>	6	0	8	0	14	0	0
<u>A. supianum</u>	4	0	4	0	8	0	0
<u>A. triangulum</u>	8	0	6	0	14	0	0
<u>A. watermaliense</u>	4	1	14	0	18	1	6
Total	127	16	127	16	254	32	

a. Percent success equals the number of hybrids obtained divided by the number of attempted interspecific pollinations.

TABLE XVI.
ATTEMPTED INTRASPECIFIC POLLINATIONS

Species	Pollinations	
	Clonal and Selfings	Other Intraspecific
Group I		
<u>A. acutangulum</u>		1,0
<u>A. chiriquense</u>	1,1(100 f) ^a	
<u>A. gracile</u>	2,2(59)	1,1(16)
<u>A. littorale</u>	1,0	10,4(71 f)
<u>A. ramonense</u>	1,1(96 f)	
<u>A. scherzerianum</u>	2,1(6)	3,1(73)
<u>A. wendlingerii</u>	1,1(96)	
Group II		
<u>A. aureum</u>	2,2(48)	9,8(82)
<u>A. turrialbense</u>	1,1(27)	
Group III		
<u>A. ellipticum</u>	1,1(100 f)	
<u>A. hacumense</u>	1,0	
<u>A. hookeri</u>	1,1(72 f)	
Group IV		
<u>A. aemulum</u>	-	2,1(0)
<u>A. digitatum</u>	-	1,1(80 f)
<u>A. pentaphyllum</u>	1,1(88 f)	-
Group V		
<u>A. regale</u>	1,1(69)	
<u>A. walujewii</u>	1,1(80 f)	
<u>A. warocqueanum</u>	4,2(28)	
<u>A. wulfschlaegelii</u>	1,0	
Group VI		
<u>A. baileyi</u>	-	1,0
<u>A. flavo-viride?</u>	-	1,0
<u>A. lindenianum</u>	-	1,1(80)
<u>A. pichincae</u>	-	1,1(100)
<u>A. procerum?</u>	-	4,4(86 f)
<u>A. ranchoanum</u>	-	1,1(5)
<u>A. rhodostachyum</u>	1,1(100)	-
<u>A. triangulum</u>	1,1(60)	-
<u>A. watermaliense</u>	2,1(43)	1,1(10)
Total	24,18(59)	39,25(66)

a. Each entry is formed such that the first number indicates the total number of attempted pollinations, the second number indicates the number of fruits harvested, the number in the parenthesis indicates the average percent of seed germination, and f indicates that the hybrids flowered.

protogynous and production of reproductively active spadices on the same plant axis do not overlap. Although this mechanical barrier exists, other reproductive barriers were not observed. From the totals, little difference is observed between the relative number with fruit set and per cent germination of selfings versus intraspecific crossings. Some of the inability to obtain viable progeny from intraspecific pollinations was undoubtedly due to the use of old pollen.

Generally the genetic integrity of the six morphologically constructed groups has been confirmed with a possible exception between Group V and Group VI. Since the groups were constructed upon the tenets that Engler indicated for his sections, Engler's basic understanding of the natural groupings within Anthurium has been upheld. The apparent exception to the integrity of the author's morphological groups between Group V and Group VI is not really critical. According to the author's key, these two groups are more closely related to each other than to any other group. Perhaps this indicates that the characters used in this final division of these two groups are not as distinctive as those used to divide the other groups. At least in Anthurium crossabilities tend to follow morphologic distinctness.

HYBRID ANALYSIS

A series of observations were made on hybrid fertility and morphology. Although few of the hybrid progenies were analyzed for fertility, all of the progenies were analyzed morphologically. Only those morphological characters of apparent taxonomic importance were included.

Chromosomal Inheritance

Chromosome counts were made on about 250 hybrids. Chromosomal inheritance of B chromosomes was irregular unlike the inheritance of A chromosomes. Whether this irregularity reflects meiotic or postmeiotic preferential distribution or preferential fertilization as described by Battaglia (1964), or later selection could not be determined from the present data. The common occurrence of B chromosome accumulation was not observed.

The inheritance of B chromosomes of several crosses is given in Table XVII. Before analysis is attempted, perhaps the method of plant selection should be emphasized. Although care was taken to obtain a range in morphologic variability, counts were not made until eight plants were selected and grown for each cross. Chromosome combinations which would lead to inviable or subviable plants were definitely selected against. The observed chromosome numbers, therefore, reflect those combinations which were viable. In the 30 X 30+1B cross and its reciprocal, the inheritance of the 15+1B gamete was definitely favored on the maternal side and perhaps slightly on the paternal side. In the 30+2B X 30 and 30+2B X 30+2B crosses, inheritance appeared regular

TABLE XVII.
 FREQUENCY OF CHROMOSOME NUMBERS OF PROGENY
 IN CROSSING WITH B CHROMOSOMES

Chromosome Numbers of Parents	Chromosome Numbers of Progeny				
	30	30+1B	30+2B	30+3B	45+3B
30 X 30+1B	2	5	0	0	0
30+1B X 30	1	17	0	0	0
30+1B X 30+1B	0	1	2	0	0
30+2B X 30	0	5	0	0	0
30+2B X 30+2B	0	3	2	0	0
30 X 30+3B	0	1	0	3	0
60 X 30+3B	0	0	0	0	3

on the maternal side, but the three 30+1B plants may reflect irregular inheritance on the paternal side of these two B chromosomes. Inheritance in the crosses involving 3 B chromosomes was non random and the gametes with 3 B chromosomes evidently had an advantage. From seven chromosome counts, only one was observed with other than 3 B chromosomes. The present data, therefore, indicate that the effective chromosomal inheritance of B chromosomes is nonrandom in Anthurium.

Hybrid Fertility

About 150 attempted pollinations were made with the primary hybrids. An accumulation of the data gathered on hybrid fertility is included in Table XVIII. Generally only those crosses with positive indications of hybrid fertility are included, since inability to obtain fruit set may be from factors other than sterility and almost impossible to interpret. Although the data are not suitable for quantitative analysis, inferences can be made. In Groups I, II and VI, interspecific hybrids were fertile although in varying degrees. Aneuploidy per se was not a barrier to fertility, but nine attempted pollinations were necessary to obtain a single fruiting spadix from a hybrid with $2n = 29$. The single triploid hybrid obtained in Group III was sterile, which is expected of most triploids. The greatest amount of positive evidence for generally fertile interspecific hybrids was in Group V. If the data are considered collectively, many of the hybrids were able to cross not only back to the parental species but also among themselves. Hybrid sterility does not appear to be a major factor in maintaining the genetic integrity (if this actually exists)

TABLE XVIII.
HYBRID FERTILITY

Cross	Chromosome Number	BCM ^a		BCP ^b		Sibling		Other	
		% Fruit Set	% Germi- nation	% Fruit Set	% Germi- nation	% Fruit Set	% Germi- nation	% Fruit Set	% Germi- nation
Group I									
<u>A. littorale</u> X <u>A. acutangulum</u>	29	0		11 ^c	86				
Group II									
<u>A. aureum</u> X <u>A. aureum</u>	30	67	84			56	86		
<u>A. aureum</u> X <u>A. bakeri</u>	31	58	97	87	97				
Group III									
<u>A. ellipticum</u> X <u>A. hookeri</u>	45	0							
Group V									
<u>A. crystallinum</u> X <u>A. forgetii</u>	?	0		12	0	14	65		
<u>A. crystallinum</u> X <u>A. regale</u>	30+1B,30+2B			20	20	80 ^d	31		
<u>A. forgetii</u> X <u>A. grandifolium</u>	?			30	63	70	98	85	83

- a. Backcross to the maternal parent.
b. Backcross to the paternal parent.
c. Eight attempts were necessary to get a single fruiting spadix.
d. Five attempts were necessary to get a single fruiting spadix.

TABLE XVIII. (Continued)

HYBRID FERTILITY

Cross	Chromosome Number	BCM ^a		BCP ^b		Sibling		Other	
		%	%	%	%	%	%	%	%
		Fruit Set	Germi- nation	Fruit Set	Germi- nation	Fruit Set	Germi- nation	Fruit Set	Germi- nation
<u>A. forgetti</u> X <u>A. velutinum?</u>	30	60	0	27	30				
<u>A. forgetti</u> X <u>A. wulschlaeglii</u>	30			33	?			0	
<u>A. regale</u> X <u>A. walujewii</u>	?	55	59						
<u>A. regale</u> X <u>A. forgetti</u>	30+1B	0		95	84	68	94	0	
<u>A. velutinum?</u> X <u>A. forgetti</u>	30			90	79	60	63		
<u>A. venosum?</u> X <u>A. velutinum?</u>	30	0				0		0	
<u>A. wulschlaeglii</u> X <u>A. velutinum?</u>	30	28	75			0			
Group VI									
<u>A. andreanum</u> X <u>A. hoffmannii</u>	30						3	92	
<u>A. andreanum</u> X <u>A. lindenianum</u>	30				9	82			
Groups V X VI									
<u>A. grandifolium</u> X <u>A. subhastatum</u>	30	4	75	0					
Groups VI X IV									
<u>A. triangulum</u> X <u>A. digitatum</u>	30	0		0					

of the parental species of this group. The fertile hybrid obtained between Groups V and VI indicates that these groups are probably sharing the same gene pool, but that the gene flow is restricted. The apparently sterile hybrid between A. triangulum and A. digitatum representing Groups IV and VI is indicative of a distant relationship between the two groups. Generally the data indicate that gene flow can occur within these morphologically constructed groups especially within Group V, and that restricted gene flow can possibly occur between Groups V and VI.

Mode of Reproduction

In the cross between A. aureum X A. bakeri (cross-pollinating X self-pollination), all of the observed seedlings were cross-pollinating. In other pollinations involving self-pollinating X self-pollinating and cross-pollinating X cross-pollinating species, all the seedlings were self-pollinating and cross-pollinating respectively. Self-pollination is apparently a recessive character in these species. However, the F_2 distribution has not been analyzed, so the number of genes involved is unclear. The method of gene action appears to be on the time of initiation of pollen release, since the period of receptivity of the stigma and the release of pollen overlap in self-pollinating species (unlike cross-pollinating species).

Berry

Generally the taxonomic character of seeds per berry, berry shape and color were consistently transmitted. Usually crossings could only be obtained between species having these same berry characters. In

all observed cases, transmission of the characters of seeds per berry and berry shape was consistent without segregation. Berry color was perhaps the least satisfactory of these three characters. In a few evaluated crosses in which the berry colors were different, the berry color of the hybrid was intermediate between the two parents. The most striking example was in the cross A. littorale (yellow berry) X A. acutangulum (purple berry), which gave a light pink berry. Although the F_2 was not grown to maturity, segregation for berry color would be expected. Seeds per berry and berry shape are good taxonomic characters. Berry color apparently may be segregating in some groups and must be evaluated for its usefulness in each group considered.

Inflorescence

Ideally both the colors and shapes of both the spathes and spadices would be evaluated, but the shapes tend to change with maturity and are not easily evaluated from juvenile plants. Spadix color is especially troublesome since the color changes with receptivity and often later with age. Spadix color therefore was recorded from the tip as the spadix became receptive. Taxonomically, Engler (1905) stressed the spathe and spadix color especially in the Sections Calomystrium and Belolonchium. The spathe color is green in most Anthurium sections, although the color of the spadix varies widely. In the two sections indicated above, white, red and purple spathes are common. Generally when white was crossed with white, the resulting progeny was white. When white was crossed with light red or purple, only intermediates between the two parents were obtained. This case

is unlike the situation reported earlier in A. andreanum in which white by red crosses gave red and coral pink progeny (Kamemoto & Nakasone, 1963). In some crosses of white by very light yellowish green to white, the F_1 progeny segregated into white, white tinge, pink, dark pink, and red. Although the data are not detailed enough to determine the inheritance of spathe color, the last situation is indicative of genetic interaction which can be explained in terms of the biosynthetic pathway for flavonoids as given by Harborne (1967).

The inheritance for spadix color appeared very similar to that of spathe color. Generally the spadix colors breed true. In Group I, the brownish spadix of A. ramonense and A. trianae was dominant to the yellow green spadix of A. littorale, but the segregation in F_2 's was not observed. Genetic interaction was also apparently observed in the spadix. In some crosses, a yellow by yellow spadix gave only red spadices, which can also be explained similarly as for the spathe. Taxonomically, the characters of spathe and spadix color, in consideration of the possible genetic interactions, should be used cautiously.

Leaf

Three characters of the leaf are of general taxonomic value: shape, texture, and petiole placement. The leaf shape was a rather stable character, and hybrids were usually intermediate in shape between parents with minor leaf variations. Interestingly, when a small cordate leaved species was crossed with a pedately parted leaved species, the resulting hybrid was palmately lobed. In a triploid obtained from a cross between A. ellipticum and A. hookeri, the hybrid

had a shallowly cordate leaf which appeared more like the species of Group VI. The only exception found to the taxonomic value of leaf shapes was in Group I. In this group, leaves in crosses segregated from ovate, elliptic to obovate, and the apex and base from acute to obtuse.

Several species especially in Group V had velvety leaves and often had crystalline markings along the veins. When velvety leaved species were crossed with leathery leaved species, the resultant intermediate had a leathery leaf with a sheen. The crystalline markings also tended toward intermediacy on crossings.

Peltate leaves were observed in a single species, A. forgetii. This plant was not selfed due to unavailability of suitable spadices. Peltate leaved plants were not observed in any of the crosses among open lobed species. In several crosses between peltate and open lobed species, the segregation was as follows: 3/4 fused-peltate, 28; 1/2 - 1/4 fused, 13; and open lobed, 20. With dominant epistasis and the peltate character considered as dominant, the suggested ratio of the above cross would be 2:1:1 with $\chi^2 = 1.535$ which is nonsignificant. Although leaf shape and velvety texture are apparently rather good taxonomic characters, peltation is a very poor character.

Conclusion

Three general conclusions can be made from the data presented. Chromosomal inheritance of B chromosomes was irregular unlike the inheritance of A chromosomes, and B chromosome accumulation was not a factor. Hybrid fertility and the included morphological characters

support the integrity of the six morphological groups which were constructed earlier except possibly for the division of Groups V and VI. The third conclusion is that self-fertilization in Anthurium is a derived condition.

THE TAXONOMY OF SECTION TETRASPERMIUM

General Taxonomic Considerations

Section Tetraspermium is a small section of only four species (Engler, 1905). This section is a natural one and very distinct. Anthurium scandens and A. trinerve could not be crossed with any other species. These two species are also distinctively based on the chromosome number of $2n = 24$. Living specimens of A. margaricarpum were not available, so this species could not be studied as the other two species have been.

Emasculation and pollination treatments, pollen morphology, close visual observation, and consideration of the anatomical work of Campbell (1905) indicated that self-fertilization is the probable mode of reproduction in A. scandens and A. trinerve. Table XIX shows the sizes and relative frequencies in percent of well and poorly developed pollen. The naturally occurring specimens (see Table XX) had a relatively low frequency of aberrant (poorly developed) pollen. Even in the 7N polyploids A328 & A329 (Figure 61), where aberrant pollen might be expected due to meiotic disorders, pollen was well developed. In the autotetraploids obtained spontaneously in A. scandens ssp. pusillum had much more aberrant pollen than the naturally occurring tetraploid (Figure 60). In both of the autotetraploids the aberrant pollen was

TABLE XIX.
 SIZE AND RELATIVE FREQUENCY OF LARGE AND SMALL POLLEN
 IN THE SECT. TETRASPERMIUM

Taxon	Accession No.	Large		Small	
		Size (in microns)	%	Size (in microns)	%
<u>A. scandens</u>	A174	19-24	99.6	7-10	0.4
<u>ssp. scandens</u>	A201	17-22	95.4	7-14	4.6
	A328	19-26	99.8	10	0.2
	A329	17-24	99.2	10-12	0.8
<u>A. scandens</u>	A211	12-17	98.4	5-10	1.6
<u>ssp. pusillum</u>	4N of A211	14-22	74.8	7-10	25.2
<u>A. trinerve</u>	A100	17-26	99.2	14	0.8
	4N of A100	17-26	88.6	7-17	11.4
	A275	17-22	99.6	7-12	0.4

TABLE XX.

COUNTRY OF ORIGIN FOR THE LIVING SPECIMENS OF THE SECT.

TETRASPERMIUM AT THE UNIVERSITY OF HAWAII

Taxon	Accession No.	Origin
<u>A. scandens</u> ssp. <u>scandens</u>	A174	Panama
	A201	Trinidad
	A328	Mexico
	A329	Mexico
<u>A. scandens</u> ssp. <u>pusillum</u>	A211	Costa Rica
<u>A. trinerve</u>	A100	Cultivated
	A238	Panama
	A275	Panama

probably due to multivalent formation at meiosis. If directional selection favored the development of well developed pollen as indicated by the pollen found in natural species, then self-fertilization rather than a form of apomixis would be indicated. A high degree of self-fertilization would obviously lead rather quickly to the virtual elimination of plants which form aberrant pollen according to the principles given by Crow and Kimura (1970). Generally apomixis would not favor pollen of any particular type, unless pollination was required (without fertilization) in which case well formed pollen would be favored (Stebbins, 1951; Fryxell, 1957). Cross-fertilization was not being considered, since as indicated above, no hybrids of any type were observed.

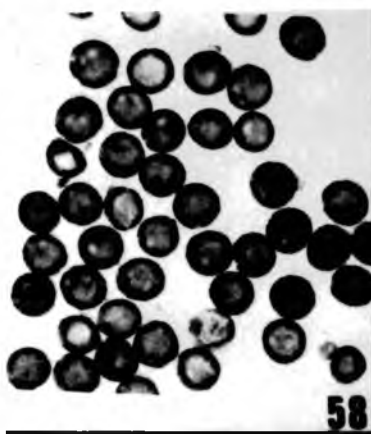
Unlike most Anthurium species, A. scandens and A. trinerve had an overlapping period when the flower was simultaneously receptive and releasing pollen if observed closely. When the events as traced by Campbell (1905) are considered in conjunction with the three above factors, self-fertilization is indicated as the mechanism of reproduction. Self-fertilization was considered as the mode of reproduction of these taxa when species and subspecies delimitations were determined.

Chromosome counts were determined for each of the species in Sect. Tetraspermium except for A. margaricarpum for which no material was available. Also, no previous chromosome count was reported for A. margaricarpum. The chromosome counts of the plants available for study are shown in Table II. Anthurium scandens ssp. pusillum was determined to be $2n = 24$ (Figure 67). Anthurium scandens ssp. scandens

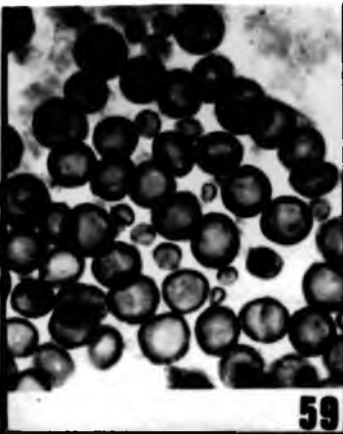
Plate VI. Pollen morphology, somatic chromosome and leaf structure of
Anthurium scandens and A. trinerve.

Figure:

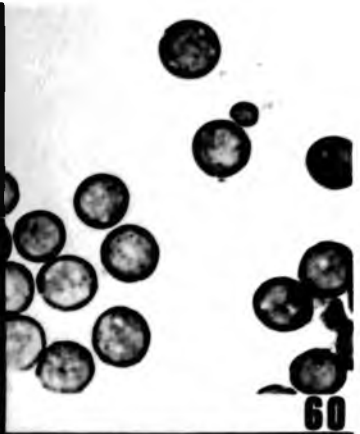
58. Pollen morphology of A211, A. scandens ssp. pusillum (400X).
59. Pollen morphology of 4N of A211 (400X).
60. Pollen morphology of A201, A. scandens ssp. scandens (400X).
61. Pollen morphology of A328 (7N), A. scandens ssp. scandens (400X).
62. Pollen morphology of A100, A. trinerve (400X).
63. Pollen morphology of 4N autotetraploid of A100, A. trinerve (400X).
64. Somatic chromosomes of A. scandens ssp. scandens, $2n = 48$ (1100X).
65. Somatic chromosomes of A. scandens ssp. scandens, $2n = 84$ (1100X).
66. Somatic chromosomes of A. trinerve, $2n = 24$ (1100X).
67. Somatic chromosomes of A. scandens ssp. pusillum, $2n = 24$ (1100X).
68. Leaf hypodermis of A. trinerve (160X).
69. Leaf with enlarged epidermis of A. scandens (160X).



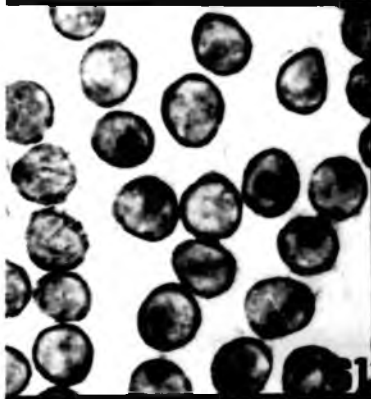
58



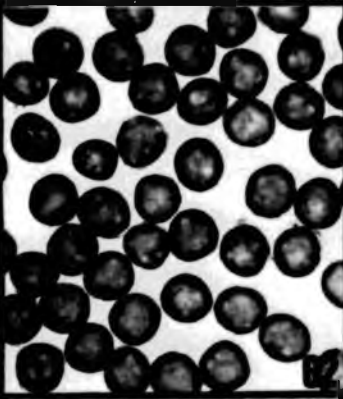
59



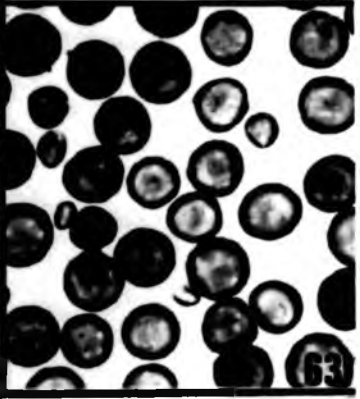
60



61



62



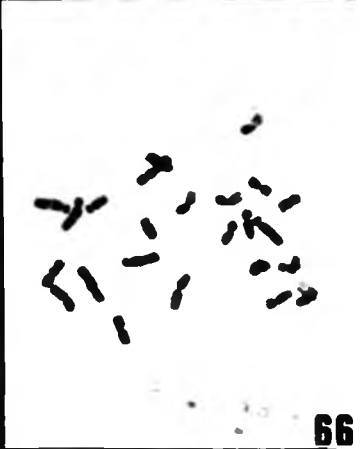
63



64



65



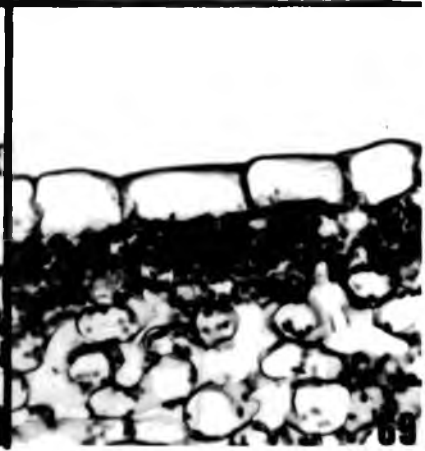
66



67



68



69

includes the chromosome number of 48 (Figure 64), and also a Mexican representative (A328, A329) with 84 chromosomes (Figure 65) A. trinerve has $2n = 24$ (Figure 66). If n is considered to be 12, then clearly 48 represents a tetraploid and 84 represents a heptaploid. Considering the genus as a whole $n = 12$ is quite unique and apparently occurs only in the two species indicated above. Thus chromosomally these two species seem to represent a distinct taxa.

The geographical distributions of the species within the Sect. Tetraspermium provided valuable clues, but must be considered in relationship to their respective elevations. Their distributions especially in Brazil were difficult to assess due to a lack of herbarium specimens for the interior regions. The range of the elevations where the various taxa occur are: A. scandens ssp. scandens, ca. 0-2700 m; A. scandens ssp. pusillum, ca. 600-2500 m (with only 3 of 52 specimens below 1200 m); and A. trinerve, ca. 0-1800 m (with only 2 of 22 specimens over 1000 m).

The geographic distributions for each of the species are given in Figure 70 for South America, Figure 71 for the northern part of Central America, and Figure 72 for the southern part of Central America. A figure for the West Indies is not included since only A. scandens ssp. scandens occurs in this region. Only one specimen (the type) was seen for A. margaricarpum which is probably endemic to Ecuador. Anthurium scandens ssp. scandens occurs from mid Mexico to southern Brazil in addition to being in the West Indies, and has the widest range of the examined taxa. Anthurium scandens ssp. pusillum has a comparatively restricted distribution being found from Honduras to

Plate VII.

Figure:

70. Geographic distribution of the species of Sect. Tetra-
spermium in South America.



Plate VIII.

Figure:

71. Geographic distribution of the species of Sect. Tetra-
spermium in the northern part of Central America (from
left to right, Mexico, Guatemala, British Honduras, El
Salvador and Honduras).

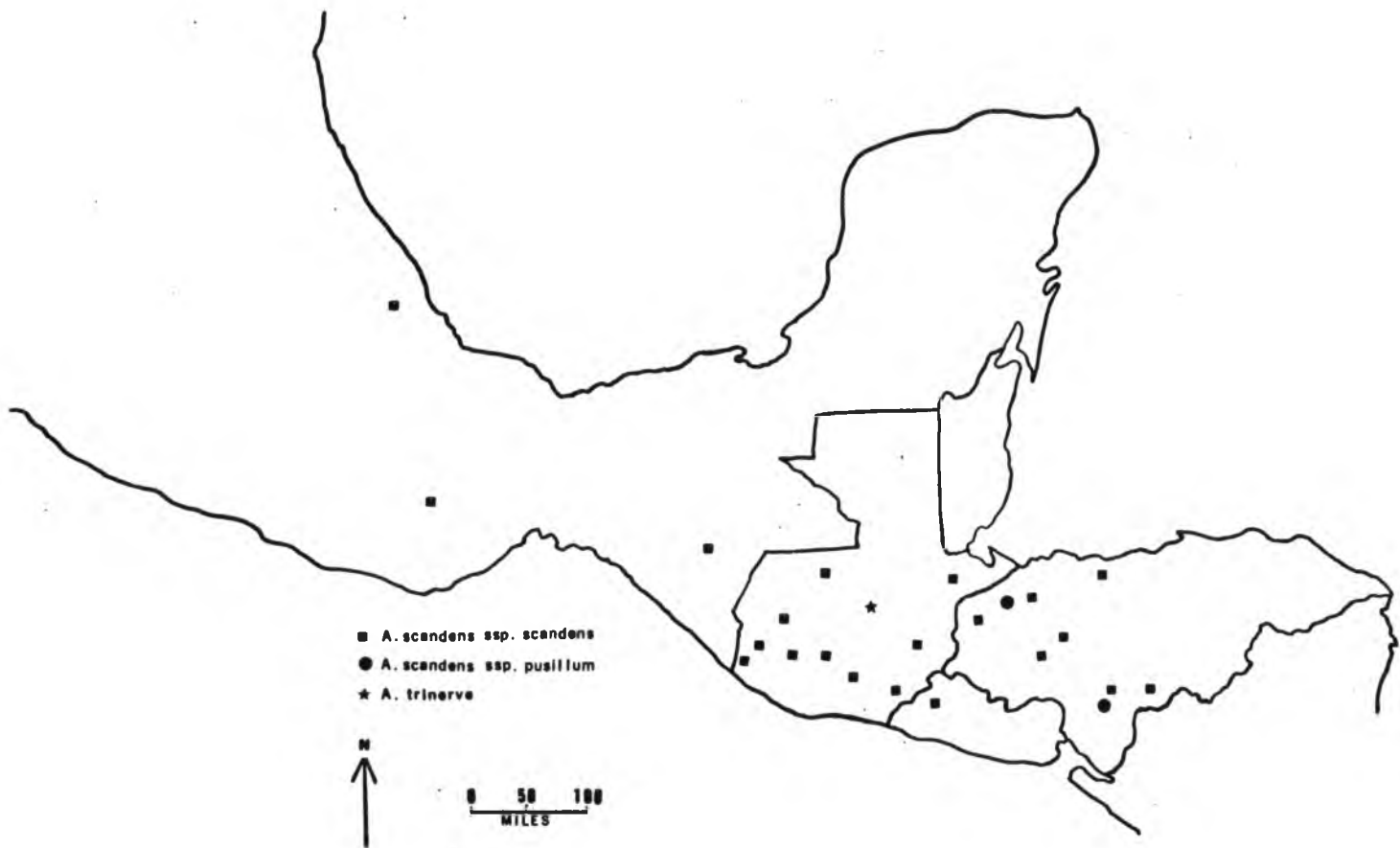


Plate IX.

Figure:

72. Geographic distribution of species of Sect. Tetraspermium in the southern part of Central America (from left to right, Nicaragua, Costa Rica and Panama).

Columbia. However as can be seen in Figure 72, the majority of the specimens examined are from Costa Rica. Subspecies pusillum also seems to be more restricted in elevations occurring generally about 1200 m while ssp. scandens is common at all elevations up to 2700 m. Anthurium trinerve occurs from Guatemala southward to northern Peru and Brazil, being somewhat more limited in distribution than A. scandens ssp. scandens and tending to be found at the lower elevations.

Perhaps the most interesting feature which deserves emphasis is the relationship between A. scandens ssp. scandens and A. scandens ssp. pusillum. Subspecies pusillum occurs over only a small restricted area of ssp. scandens and only at upper elevations. Using Stebbin's terminology (1971), evidently A. scandens forms a mature polyploid complex where the diploids are more restricted, and the polyploids more widespread. As a polyploid complex evolves, the diploids become more restricted and are gradually eliminated.

Anatomically, the leaf structure is different in A. scandens and A. trinerve with the latter having a hypodermis (Figure 68) while the former has none (Figure 69). Although no hypodermis is present in A. scandens, the epidermal cells are greatly enlarged and resemble the hypodermis of A. trinerve. These determinations were made on only four plants. The extent of the inter- and intraspecific variation of the leaf structure definitely needs further investigation. At present the above evidence tends to support the separation of these two species.

Recently A. scandens (Aubl.) Engl. and A. trinerve Miq. of Sect. Tetraspermium have been considered conspecific (Standley, 1944;

Jonker-Verhoef & Jonker, 1953; Matuda, 1954; Standley & Steyermark, 1958). Standley suggested that A. trinerve should be reduced to synonymy under A. scandens (Standley, 1944) which was done by Matuda in 1954. When Matuda made the new combination A. scandens var. trinervis Matuda, he indicated A. trinerve as a synonym; but in an included photograph, the plant shown was not A. trinerve as Engler has interpreted Miquel's description. The basis for Standley's suggestion was that peduncle length alone is not worthy of specific recognition and that no other differences occurred between the two (Standley, 1944; Standley & Steyermark, 1958). Although Engler's key suggested that the main difference was peduncle length, the description of Engler, if read carefully, does not indicate peduncle length as a main difference (Engler, 1878, 1905).

Recent authors have tended to treat A. scandens and A. trinerve as conspecific. Even though A. scandens is quite variable, distinction from A. trinerve can be made on the basis of berry shape, spathe and spadix shape and leaf structure as follows:

	<u>A. scandens</u>	<u>A. trinerve</u>
Berry shape	Depressed globose	Apiculate obovate
Spathe	Lanceolate to oblong-lanceolate, usually reflexed	Ovate-lanceolate to ovate, erect or slightly spreading
Spadix	Thin, cylindrical to slightly attenuate	Thick, cylindrical or attenuate
Leaf blade	Upper surface sparsely or not punctate, hypodermis absent	Upper surface not punctate hypodermis present.

Some of the problems in trying to separate these two species undoubtedly originated as the result of comparing the leaves of the tetraploid A. scandens with the diploid A. trinerve. If the diploids alone are compared the size difference is tremendous.

Self-fertilized plants generally present a problem taxonomically. Since populations are not formed in the usual manner, this must be taken into consideration for the taxonomic treatment of the group (Stebbins, 1957; Davis & Heywood, 1963). Recognition of all of the local variants (or pure lines) in A. scandens and A. trinerve would result in a long list of species or varieties. Generally the taxonomy of such groups depends on the group involved (Davis & Heywood, 1963). In A. scandens, a spontaneous tetraploid from ssp. pusillum was obtained which appeared much like the tetraploids of the wild. This spontaneous tetraploid was obtained from only a relatively small amount of seed from the diploid which evidently indicates a high rate of "mutation." Although the diploid can be separated from the tetraploid, it cannot be done so with the same degree of distinctiveness as between the species A. scandens and A. trinerve. For the degree of relationship indicated above, the taxonomic level of subspecies seems most appropriate for the diploid and polyploid forms.

Taxonomic Revision

Anthurium sect. Tetraspermium Schott, Prodr. 436-437, 1860.

Plant epiphytic. Caudex elongate, scandent or erect, emitting many roots from the nodes, covered with fibrous remains of cataphylls, internode more or less elongated. Blade subcoriaceous, lanceolate,

ovate to elliptic, apex acute to acuminate, base cuneate to obtuse, margin entire, pale green beneath, punctate sparsely on upper surface or not, black dotted densely beneath, primary lateral veins numerous uniting to form a collective vein 4-6 mm from the margin. Petiole terete or convex, front flat or grooved, dilated at the base, geniculate at the apex and slightly dilated. Peduncle terete, slender or thick. Spadix cylindrical to attenuate, thin to moderately thick, apex obtuse, white, whitish-green, or bluish-green to purple, sessile or short stipe. Spathe linear- to ovate-lanceolate or ovate, apex acuminate or cuspidate, white or green (then sometimes with purple towards the center), erect or reflexed. Berry depressed globose or apiculate ovate, white to pearly or light lavender to dark purple, ovules two or more per locule.

Type species: Anthurium scandens (Aubl.) Engl.

Distribution: Common in humid forests, West Indies and southern Mexico to southern Brazil. Sea level-2700 m.

KEY TO THE SPECIES

Berries depressed globose; spathe soon reflexed or caducous;
 spadix whitish-green or purplish-pink; blade upper surface
 punctate or not.

Internode long; spathe soon reflexed; spadix cylindrical to
 slightly attenuate, in fruit 5-50 mm long; petioles
 1-6 cm long. 1. A. scandens.

Internode short; spathe caducous; spadix attenuate in
 fruit 15 cm long; petiole 15-20 cm long. .2. A. margaricarpum.

Berries apiculate obovate; spathe remaining erect; spadix cylindrical-
 attenuate, bluish-green to purple or white; blade upper surface
 not punctate 3. A. trinerve.

1. Anthurium scandens (Aubl.) Engl., Mart. Fl. Bras. 3:78. 1878.

Plant epiphytic. Caudex elongate, scandent emitting many roots
 from the nodes, covered with fibrous remains of cataphylls, internode
 0.5-4.0 cm long. Blade subcoriaceous, elliptic to ovate-lanceolate,
 apex acute to acuminate, base acute to obtuse, margin entire, 2-16 cm
 long, 1-7 cm wide, pale green beneath, upper surface punctate sparsely
 or not, lower surface densely black dotted, primary lateral veins num-
 erous uniting to form a collective vein 4-6 mm from the margin. Peti-
 ole semiterete, narrow to wide grooved or sometimes flat, 1-6 cm long,
 1-3 mm wide, dilated at the base, geniculate at the apex and slightly
 dilated. Peduncle terete, slender, 2-8 cm long, 1 mm wide. Spadix
 cylindrical to slightly attenuate, thin, apex obtuse, in anthesis 2-30
 mm long, in fruit 5-50 mm long, whitish-green or purplish pink,

sessile or nearly so, with 5-60 flowers per spadix. Spathe lanceolate to oblong-lanceolate, apex acuminate to cuspidate, 3-30 mm long, 2-8 mm wide, green or pale green, soon reflexed. Berry depressed globose, 5-8 mm in diameter, dark violet or pale violet to almost white, usually 0-2 seeds per locule.

A. scandens var dolosum (Schott) Engl. and A. scandens var. violaceum (Swartz) Engl. are indistinguishable taxonomically (Standley & Steyermark, 1958). A close observation, indicates that all the named varieties are not also really distinguishable; or if distinction is made, the number of varieties becomes enormous. The species, however, can be divided into two subspecies for the reasons already given above. The two can be differentiated by the following key.

KEY TO THE SUBSPECIES OF A. SCANDENS

Spadix 16-60 flowered, 7-30 mm long in anthesis; blade

upper surface punctate or not, 4-16 cm long. .1a. ssp. scandens.

Spadix 5-12 (16) flowered, 2-10 mm long in anthesis; blade

upper surface punctate, 2-7.5 cm long. . . .1b. ssp. pusillum.

1a. Anthurium scandens ssp scandens

Dracontium scandens Aubl., Hist. Pl. Gui. Franc. 2: 836. 1775.

Pothos violacea Swartz, Prodr. 32. 1788.

Dracontium repens Descourt., Fl. Antill. 7: t 499. 1829.

Anthurium violaceum Schott, Melet. 22. 1832.

Anthurium violaceum forma latifolia Kunth, Enum. Pl. 3: 68. 1841.

Anthurium violaceum forma angustifolia Kunth, Enum. Pl. 3: 68.

1841.

Anthurium leucocarpum Schott, Oesterr. Bot. Wochenbl. 7: 53.
1857.

Anthurium dolosum Schott, Oesterr. Bot. Z. 8: 179. 1858.

Anthurium rigidulum Schott, Oesterr. Bot. Z. 8: 180. 1858.

Anthurium virgosum Schott, Oesterr. Bot. Z. 9: 100. 1859.

Anthurium scandens var. violaceum Engl., Mart. Fl. Bras. 3: 78-
79. 1878.

Anthurium scandens var. dolosum Engl., Mart. Fl. Bras. 3: 78.
1878.

Anthurium scandens var. leucocarpum Engl., Mart. Fl. Bras. 3:
79. 1878.

Anthurium scandens var. virgosum Engl., Mart. Fl. Bras. 3: 79.
1878.

Anthurium scandens forma angustifolia Engl., Bot. Jahrb. Syst.
25: 355. 1898.

Anthurium scandens var. ovalifolium Engl., Bot. Jahrb. Syst. 25:
357. 1898.

Anthurium scandens var. sodiroi Engl., Bot. Jahrb. Syst. 25:
357. 1898.

Anthurium scandens var. latifolium K. Krase, Notizbl. Bot. Gart.
Berlin-Dahlem 11: 606. 1932.

Plants epiphytic. Caudex elongate, scandent emitting many roots from the nodes, covered with fibrous remains of cataphylls, internode 0.5-4 cm long. Blade subcoriaceous, elliptic to ovate-lanceolate, apex acute to acuminate, base acute to obtuse, 4-16 cm long. 1.5-7 cm wide, pale green beneath, upper surface punctate sparsely or not,

lower surface densely black dotted, primary lateral veins numerous uniting to form a collective vein 4-6 mm from the margin. Petiole semiterete, narrow to wide grooved or sometimes flat, 1-6 cm long, 1-3 mm wide, dilated at the base, geniculate at the apex and slightly dilated. Peduncle terete, slender, 2-8 cm long, 1 mm wide. Spadix cylindrical to slightly, thin, apex obtuse, in anthesis 7-30 mm long, in fruit 10-55 mm long, whitish green or purplish pink, sessile or nearly so, with 16-60 flowers per spadix. Spathe lanceolate to oblong-lanceolate, apex acuminate to cuspidate 6-24 mm long, 2-8 mm wide, green or pale green, soon reflexed. Berry depressed globose, 5-8 mm in diameter, usually pale violet to almost white, sometimes dark violet, usually 1-2 seeds per locule.

TYPE: FRENCH GUIANA: Drawing by Plum. in Amer. Nascentium Icon. tab. 74. 1703 (HOLOTYPE: P, BM).

Distribution: Common in humid forests on trees or rocks and rarely in exposed dry situations, West Indies and southern Mexico to southern Brazil. Sea level-2700 m.

Representative specimens:

BOLIVIA: LA PAZ: Coroico, Oct-Nov 1912, O. Ruchtein 3663 (US); LA PAZ OR COCHABAMBA: Coripati in the region of Yungas, 22 Jun 1894, A. M. B. Lectae 2307 (K, US). BRAZIL: BAHIA: Forests of Rio Gron-gogy Basin, 100-500 m, 1 Oct-30 Nov 1915, H. M. Curran 237 (US); SANTA CATARINA: Ibirama, 100 m, 26 Oct 1953, R. Klein 685 (F). BRITISH GUIANA: ESSEQUIBO: Pakaraima Mountains, 11 Nov 1951, B. Maguire & D. B. Fanchawe 32579 (US). COLOMBIA: CAQUETA: Between Sucre and La Portada, 1200-1350 m, 5 Apr 1940, J. Cuartrecasas 9152 (US); HUILA:

Guadalupe, 1000-1300 m, 20 Mar 1940, E. P. Arbelaez & J. Cuartrecasas 8404 (F, US); ?: 1760-1808, J. C. Mutis 53 (US). COSTA RICA: CARTAGO: Turrialba on the Rio Reventazon, 30 Jan 1957, M. C. Carlson 3437 (F); SAN JOSE: Vicinity of Escazu on Cerro de Piedra Blanca, 31 Jan 1924, P. C. Standley 33973 (US); Probably near the border of Cartago & San Jose, Feb 1895, H. Pittier 9227 (K, US). CUBA: ORIENTE: Gran Piedra near Santiago, 1000 m. Mar 1949, B. Clemente 6474 (US). DOMINICAN REPUBLIC: SAMANA: Samana Peninsula, Vicinity of Samana, Sea level-200 m, 25 Apr 1921, W. L. Abbott 1418 (US). ECUADOR: PINCHINCHA: W of Santa Domingo de los Colorados, 300 m, 17 Oct 1961, P. C. D. Cazalet & T. D. Pennington 5271 (US). EL SALVADOR: SANTA ANA: Volcan de Chingo, 1777 m, 2 Mar 1968, A. Molina R. & E. Montalvo 21900 (F). GUATEMALA: ALTA VERAPAZ: Vicinity of Coban, 1260-1440 m, 26 Mar-15 Apr 1939, P. C. Standley 69239; IZABAL: Vicinity of Livingston, 16 Apr 1940, J. A. Steyermark 39532 (F); HAITI: NORD: Vicinity of Dondon, 400 m, 8 Jan 1926. E. C. Leonard 7963 (US). HONDURAS: INTIBUCA: Vicinity of Yamaranguila, 12 Apr 1956, A. Molina R. 6548 (F, US). JAMAICA: ST. ANN: Moneaque, 400-600 m, 15 May 1850, R. C. Alexander 1702 (F, K). MEXICO, VERACRUZ: Fortin de Las Flores?, Feb 1883, E. Kerber 297 (US); NICARAGUA: JINOTEGA: Vicinity of Jinotega, 1030-1300 m, 19 Jun-9 Jul 1947, P. C. Standley 9595 (F); MANAGUA: Vicinity of Las Nubes, S of Managua, 800-900 m, 28 Jun 1923, W. R. Maxon, A. D. Harvey & H. T. Valentine 7504 & 7509 (US). PANAMA: CHIRIQUI: Above El Boquete, 1300-1560 m, 5 Mar 1911, H. Pittier 3028 (US). PERU: CUZCO: Provincia Convencion, 1700 m, 28 Jul 1943, C.

Vargas C. 3463 (F); Provincia Quispicanchi, Marcapata Valley between Chaupichaca & Mamabamba, 19 Feb 1929, A. Weberbauer 7845 (F, US).
 PUERTO RICO: Luguillo, 6 Jul 1885, Engler 1505 (maybe Sintenis 1505) (F, US). TRINIDAD: Brazil-Talparo Road, 25 Jan 1948, N. W. Simmonds 257 Duplicate (K). VENEZUELA: BOLIVAR: Vicinity of Deborah, N of Trumeremo, 600-650 m, 5-8 Feb 1961, J. A. Steyermark 89149 (US);
 MONAGAS: S side of Rio Caripe, 850 m, 17 Apr 1945, J. A. Steyermark 62146 (F).

This subspecies includes a diverse group of specimens representing primarily the superstructure of a polyploid complex. Although counted specimens include two tetraploids and two heptaploids, these cannot easily be separated morphologically. The examined herbarium specimens also show this great overlapping diversity. The two tetraploids counted were from Trinidad and Panama while the two heptaploids were from Mexico. Whether this indicates geographic correlation with the polyploidy levels is not at present known. No taxonomic recognition, therefore, is given to the cytological variants which appear morphologically similar.

1b. Anthurium scandens ssp. pusillum R. D. Sheffer, sp. nov.

Plantae pusillae. Lamina 2-7.5 cm longus, 1-4 cm lata, supra punctis sparsis majoribus, infra densis minoribus. Spadix cylindricus, 2-10 mm longus, fructifer 5-15 mm longus, pauciflorus 5-12 (-16).
 Baccae depresso globosae, loculis 0-2 spermis.

Plants epiphytic. Caudex elongate, scandent emitting many roots from the nodes, covered with fibrous remains of cataphylls, internode

0.5-2.5 cm long. Blade subcoriaceous, elliptic to ovate-lanceolate, apex acute to acuminate, base acute to obtuse, 2-7.5 cm long, 1-4 cm wide, pale green beneath, upper surface punctate sparsely, lower surface densely black dotted, primary lateral veins numerous, uniting to form a collective vein 4 mm from the margin. Petiole semiterete, narrow to wide grooved or sometimes flat. 1-5 cm long, 1-2 mm wide, dilated at the base, geniculate at the apex and slightly dilated. Peduncle terete, slender, 2-3 cm long, 1 mm wide. Spadix cylindrical to slightly attenuate, thin, apex obtuse, in anthesis 2-10 mm long, in fruit 5-15 mm long, whitish-green or purplish-pink, sessile or nearly so, with 5-12 (-16) flowers per spadix. Spathe lanceolate to oblong-lanceolate, apex acuminate to cuspidate, 3-11 mm long, 1-5 mm wide, green or pale green, soon reflexed. Berry depressed globose, 5-8 mm in diameter, usually dark violet, sometimes pale violet, usually 0-2 seeds per locule.

TYPE: COSTA RICA: CARTAGO: SE of Tapanti, Rio Grande de Orosi, 1400 m, 16 Apr 1967, R. W. Lent 830 (HOLOTYPE: F!).

Distribution: Common in humid forests on trees or rocks and rarely in exposed dry situations, Honduras to Colombia. 600-2500 m.

Representative specimens:

COLOMBIA: EL VALLE: La Cumbre, 1700-2200 m, 11-18 Sep 1922, E. P. Killip 11338 (US); Vicinity of Rio Digua, 900-1180 m, J. Cuatrecasas 15076 (F). COSTA RICA: CARTAGO: N of Cartago along Rio Reventado, 1460-1650 m, 26 Feb 1926, P. C. Standley & J. Valerio 49504 & 49620 (US); Cerro de La Carpintera, 1500-1850 m, Feb 1924, P. C. Standley 34228 (US); SE of Tapanti, Rio Grande de Orosi, 1400 m, 16

Plate X.

Figure:

73. Photo of holotype of A. scandens ssp. pusillum ($\frac{1}{2}X$).



FLORA OF COSTA RICA

Anthurium scandens (Aubl.) Engler

Epiphytic herb. Flowers green. Fruit pale blue-violet, fleshy. No tubers present. Growing about 20 m. up on host tree. Disturbed primary forest, hillside overlooking Rio Grande de Oroqui, about 3 km. S.E. of Tapantí. 16 April, 1967

1649939

FIELD MUSEUM OF
NATURAL HISTORY

Prov. Cartago

Alt. 1,400 meters

Collected by Roy W. Lent

No. 830

Apr 1967, R. W. Lent 830 (F); ?, Aug 1875, M. Endress 156 (K);
 HEREDIA: N of San Jose, 17 May 1966, D. Nicolson 4006 (US); SAN JOSE:
 Escazu, 31 Jan 1924, P. C. Standley 32510 (US); La Palma area, 1500 m,
 27 May-1 Jun 1968, W. C. Burger & R. G. Stolze 5342 (F). HONDURAS:
 MORAZAN: Cerro de Uyuca along trail from Las Flores to La Labranza
 1600-1750 m, Oct-Dec 1948, P. C. Standley 14092 (F); SANTA BARBARA: S
 Montana Santa Barbara, 2350 m, 7 Apr 1951, P. H. Allen, R. Armour &
A. Chable 6115 (F). NICARAGUA: JINOTEGA: E of Jinotega, 1300-1500
 m, 5 Jul 1947, P. C. Standley 10925, 1200-1500 m, 3 Jul 1947, P. C.
Standley 10648 (F). PANAMA: CHIRIQUI: Vicinity of Bajo Mona, 1500
 m, 18 Jul 1940, R. E. Woodson, Jr. & R. W. Schery 570 (F). VENEZUELA:
 ?, 1800-2000 m, Dec 1924, A. Allart 492 (US).

The specimens representing this subspecies were consistently labelled as A. scandens (usually var. violaceum). These specimens were probably considered as juvenile forms or poorly grown specimens. This subspecies may represent one of the diploids upon which the polyploid complex has been built; however other diploids of this complex have yet to be identified.

2. Anthurium margaricarpum Sodiro in Anales Univ. Centr. Ecuador 15: 292 & 293. 1902.

Plant epiphytic. Caudex elongate, scandent or erect, internode short. Blade subcoriaceous, narrow oblong-lanceolate, apex short acuminate, base narrowed, 20-35 cm long, 8-10 cm wide, lower surface black dotted densely. Petiole convex, flat, 15-20 cm long, geniculate at apex. Peduncle slender, twice petiole, marked with striates.

Spadix attenuate upwards, in fruit 15 cm long, short stipe. Spathe wide linear, apex short acuminate, 6-8 cm long, 1 cm wide, green with purple towards the center. Berry depressed globose, white to pearly.

TYPE: ECUADOR: A. Sodiro. (HOLOTYPE: B, as photo US!)

Distribution: In dense tropics, Ecuador. Known only from the type collection.

Anthurium margaricarpum evidently was placed in Sect. Tetraspermium by Sodiro (1902) due to the 2 ovules per locule. Anthurium margaricarpum seems to be more morphologically like the other species of Group I in Table IV which also have 2 ovules per locule than A. scandens or A. trinerve. The correct placement of these other species into appropriate sections is at present unclear, as explained before. Anthurium margaricarpum is, therefore, left in Sect. Tetraspermium for the present.

3. Anthurium trinerve Miq., *Linnaea* 17: 66-67. 1843.

Anthurium brachyspathum C. Koch & Bouche in Koch, *Allg. Gartenz*
25: 233. 1857.

Anthurium trinerve var. obtusum Engl. *Bot. Jahrb. Syst.* 25: 357-
358. 1898.

Anthurium trinerve var. angustifolium Krause, *Bot. Jahrb. Syst.*
54: 123. 1916.

Anthurium scandens var. trinervis Matuda, *Anal. Inst. Biol. Univ.*
Nac. Mexico 25: 189. 1954.

Anthurium codajasi Barroso, *Arch. Jard. Bot. Rio de Janeiro* 15:
97. 1957.

Plant epiphytic. Caudex elongate, scandent emitting many roots from the nodes, covered with fibrous remains of cataphylls, internode 0.5-4 cm long. Blade subcoriaceous, lanceolate to oblong-lanceolate or sometimes ovate, apex acute to acuminate, base acute, 11-24 cm long, 2.5-10 cm wide, pale green beneath, upper surface not punctate, lower surface densely black dotted, primary lateral veins numerous uniting to form collective vein 4-6 mm from the margin. Petiole semiterete, somewhat grooved to flat, 2.5-13 cm long, 3-6 mm wide, dilated at the base, geniculate at the apex and slightly dilated. Peduncle terete, slender to moderately thick, 3-11 cm long, 2-4 mm wide. Spadix cylindrical or attenuate, moderately thick, apex obtuse, in anthesis 2-6 cm long, in fruit 3-9 cm long, bluish green to purple or white, sessile or nearly so. Spathe ovate-lanceolate or ovate, apex acuminate or acute, 1-5 cm long, 1-2.5 cm wide, pale yellowish green to white, erect or slightly spreading. Berry apiculate obovate, 5-7 mm in diameter, white or sometimes light lavender, usually 2-5 seeds per locule.

TYPE: SURINAM: Miquel. (HOLOTYPE: U, not seen)

Distribution: Common in humid forests on trees or sometimes rocks, Guatemala southward to mid Brazil. Sea level-1800 m.

Representative specimens:

BRAZIL: ?; Around the Rio Negro, property of San Gabriel de Cachoeira, Jan-Aug 1852, R. Spruce 2266 (K). BRITISH GUIANA: ESSE-QUIBO: Pomeron district, Moruka River, 20 Sep 1921, J. S. De La Cruz 1155 (US), 16 Aug 1921, J. S. De La Cruz 1241 (US). COLOMBIA:

CALDAS: Santa Cecifia, 800 m, 26 Nov 1945, K. von Sneidern 5021;
 META: Villavicencio, Jan 1899, T. A. Sprague (K). COSTA RICA: LIMON:
 Vicinity of Guapiles, 300-500 m, 12-13 Mar 1924, P. C. Standley 37463
 (US); PUNTARENAS: Along the interamerican highway, 9°9' N X 83°19' W,
 26 Jan 1967, W. Burger & G. Matta 4670 (F); CARTAGO-SAN JOSE: Cala-
 manca, 100 m, Feb 1895, Pittier & Conduz 9235 (US); ?, Estrella Valley,
 50 m, 3 Jan 1925, A. Alfaro (US). FRENCH GUYANA: Riviere Camopi, 200
 m, 13 Feb 1968, Oldeman & Sastre 236 (US). GUATEMALA: Rio Tatin near
 Rio Dulce, 28 Mar 1939, C. L. Wilson 390 (F). PANAMA: BOCAS DEL
 TORO: Vicinity of Chiriqui Lagoon, 21 Oct 1940, H. von Wedel 1290 (F),
 10 Feb 1941, H. von Wedel 2046 (F), 26 Feb 1941, H. von Wedel 2171
 (f); Vicinity of Nievécita, Sea level to 50 m, 8-19 Aug 1938, R. E.
Woodson, Jr., P. H. Allen & R. J. Seibert 1873 (F). PERU: LORETO:
 Above Pongo de Manserichi, along the Rio Santiago in dense forest,
 200 m, 6 Dec 1931, Y. Mexia 6233a (F, K); SAN MARTIN: E Tingo Maria,
 625-1100 m, 30 Oct 1929-19 Feb 1930, H. A. Allard 20455 & 21888 (US).
 NICARAGUA: ZELAYA: SE Cerro San Isidro, Sea level to 65 m, 10 Mar
 1966, G. R. Proctor, G. C. Jones & L. Facey 27085 (F). SURINAME:
 BROKOPONDO: S Afobaka, 12 Mar 1964, R. A. Florschütz & P. J. M. Maas
2306 (US), Feb 1965, J. van Donselaar 2110 (F). VENEZUELA: AMAZONAS:
 Along Rio Casiquiare between Piedra Lais and Cano Pamoni, 150 m, 1 Apr
 1953, B. Maguire & J. J. Wurdack (US).

F. Miquel's description is vague. Essential characters (berry
 shape, spathe and spadix shape, and leaf structure) needed for differ-
 entiation are not adequately described. Miquel's original type

materials could not be located. Even Engler and Schott apparently did not see these specimens. Evidently the first worker to give a list of specimens for A. trinerve was Engler (1878). His descriptions (Engler, 1878, 1879 & 1905), although brief, provide a basis for distinguishing between A. trinerve and A. scandens.

Anthurium trinerve is somewhat variable, especially in spathe and leaf size. Adequate numbers of specimens, however, have not been seen to determine if infraspecific taxa should be recognized. This is especially true considering that A. trinerve is self-fertilizing and probably forms many pure lines in nature. At present no infraspecific taxa are therefore recognized.

GENERAL DISCUSSION

Distinct morphological groups were constructed which are generally geneticaly distinct, as indicated by crossabilities. The chromosome data and hybrid analysis also support the presented division into groups. The array of gametic chromosome numbers for each group was: Group I, 12-24-42, 14,15; Group II, 10-20, 15; Group III, 15-30; Group IV, 15-30; Group V, 15-30 (+ B chromosomes); and Group VI, 15-30-45. Chromosome numbers within the groups are consistent, which would also tend to support these groups. Only interspecific crosses within the groups gave fertile hybrids except for crosses between Groups V and VI, but these two groups are also closely related

morphologically. The analysis of taxonomic characters indicated that the morphological characters used for the key are generally good characters.

Relationships of species can perhaps be clarified through gametic basic chromosome number changes (Figure 74). The basic chromosome numbers are 5, 6, 7 and 15 with six presented earlier as the basic number for the genus from consideration of the chromosome numbers of related genera. Chromosome numbers based on six were found only in Group I. Among the morphological characters which were analyzed, characters of the berry were the most consistent with perhaps leaf shape second. On the basis of berry characters, Group I is the most primitive group since the general evolutionary tendency in Araceae has been a reduction in the number of ovules (Arber, 1925). If the monocot leaf is a modification of a bladeless petiole (Cronquist, 1968), and in aroids the tendency has been for "the elaboration of replacement organ" (Arber, 1925), then the expected sequence for the development of the leaf would be from small elliptic, to large elliptic, lanceolate, or oblanceolate, to cordate, and finally to pedately parted. This factor again would tend to indicate that Group I is the most primitive and by implication important for an understanding of the evolutionary origin of the genus.

Within Group I, A. trinerve is the most primitive species examined. Anthurium trinerve has the greatest number of seeds, and therefore is the most primitive condition. If the reduction in number of flowers is also an evolutionary tendency, then A. trinerve is more primitive than A. scandens. The berry shape perhaps also supports the

Plate 11

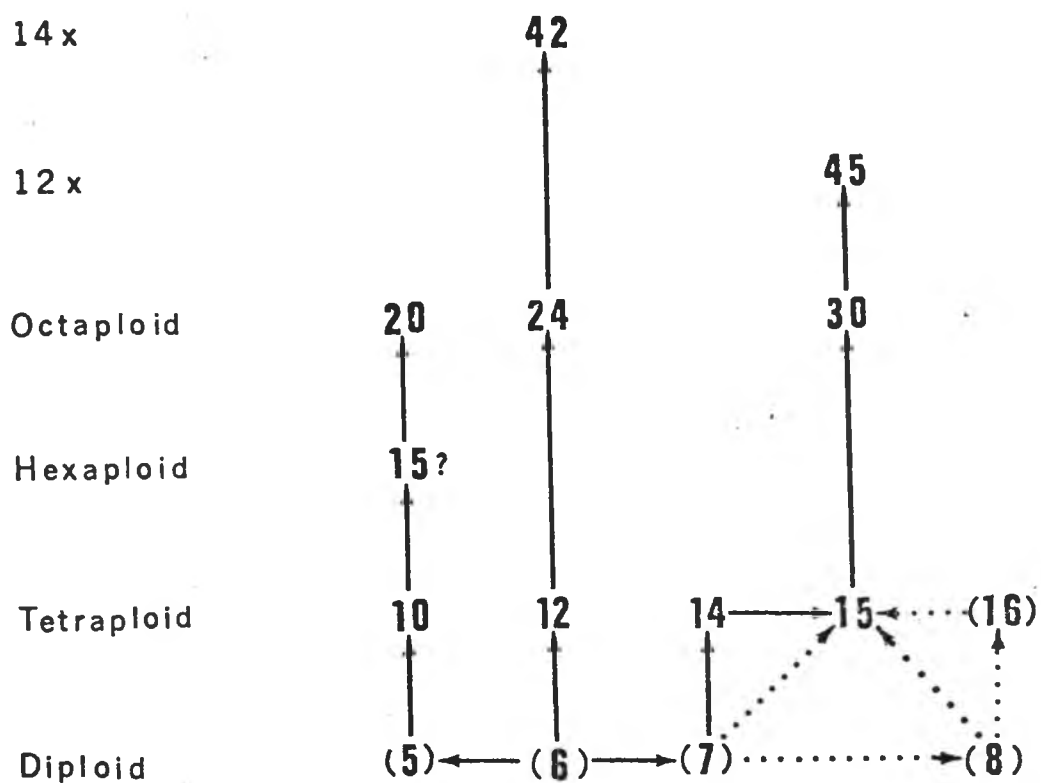


Figure 74. A possible mode of transition in gametic chromosome numbers during the evolution of *Anthurium* species. Six is considered as the basic number of the genus. Numbers in parenthesis are hypothetical chromosome numbers, and dashed lines indicate hypothetical relationships.

more primitive condition of A. trinerve (apiculate obovoid) over A. scandens (subglobose). Subglobose berries only occur in Group I. If subglobose berries were the most primitive, then the filling of the apical depression of the berry would have had to occur several times to explain the existing species.

In Group I to obtain $n = 14$ from $n = 12$, the most likely mode would be if movement would have occurred from 6 to 7. If movement occurred from 12 to 14, then $n = 13$ would also be expected. No species was observed with $n = 13$. In A. acutangulum, A. allenii, A. chiriquense, A. ramonense and A. trianae, 15 probably arose by way of 14. Crossing readily occurred among these species indicating a rather recent increase in chromosome number. The other species of this group with $n = 15$, but such a number would represent a hexaploid. Morphologically A. scolopendrinum and the other species seem different. Few representative species of this group were available for study and perhaps two diverse lines may be present. Since 15 could also arise as indicated for Group I, some species may have originated in this manner.

The placement of the species of Group III into the system is somewhat difficult. Most of the species of Anthurium are based on $n = 15$ and perhaps originated through this group considering the leaf shape. Group III has the lanceolate or oblanceolate type leaves much like Groups I and II. In a cross within Group III, a shallow cordate leaved hybrid was obtained much like some of the species of Group VI. This group can perhaps then be considered as the origin of the similar Groups V and VI. Group IV is easily placed in reference to Group VI,

in consideration of the hybrid obtained between them. Considering this hybrid and the ontogeny of the pedately parted leaf. Multiples of 3 or 5 seem unlikely chromosomally and from consideration of the berry. Fifteen may originate from 14 as indicated in Group I, but why an aneuploid with 15 chromosomes should become so well established would be unclear. However, if movement occurred from 7 to 8, then a hybrid of 15 could be formed by amphidiploidy (Note must be made that chromosome numbers based on 8 were not observed). A hybrid of $n = 15$ with hybrid vigor would explain why perhaps 15 became so prevalent.

The previous analysis is hypothetical. With increased data the evolutionary relationships within Anthurium should be clearer. The pivotal groups are Groups I, II, and III, but data are perhaps most needed in Group III in order to better place the origin of $2n = 30$.

SUMMARY

Chromosome numbers, sexual compatibilities and morphological data were collected for 63 Anthurium species. The resulting hybrids were analyzed both chromosomally and morphologically. The species relationships within Sect. Tetraspermium were analyzed taxonomically, especially to clarify the recent dispute about the status of A. scandens and A. trinerve. An attempt was made to consider all the data presented to elucidate the evolutionary relationships among the species.

Chromosome numbers of 38 of the 63 species were newly determined. Generally the present work confirmed existing chromosome counts when these were available for comparison. In a few instances conflicting counts were obtained. The most common somatic chromosome number was 30, but counts ranged from $2n = 20$ to 90. B chromosomes were found frequently in Group V and varied in number from one to three. Four polyploid series were evident: 20-40, 24-48-84, 28-56 and 30-60-90-ca. 124. Most species are part of the polyploid complex based on 30.

Sexual compatibility studies involved 1600 cross- and self-pollinations of 56 species. These pollinations included 292 different cross-combinations, 29 different selfs (including sibling and clonal pollinations). In total, 321 combinations were attempted. Three hundred thirty fruiting spadices yielded 220 seedling populations of which 139 were evaluated both morphologically and chromosomally. Six morphological groups were constructed using primarily the characters considered as important by Engler (1905). These groups were constructed as an aid in understanding the species relationship.

Generally the genetic integrity of these six groups was confirmed with the possible exception of Groups V and VI. Since these groups were constructed upon the tenets that Engler indicated for his sectional categories, Engler's basic understanding of the natural relationships within Anthurium was therefore upheld. Groups V and VI were more closely related to each other than to any other group, and the characters used in the division of these two groups were not as distinctive as those used to divide the other groups. Nevertheless in Anthurium crossabilities tended to follow morphologic distinctness.

A series of observations were made on the hybrids for an understanding of hybrid fertility and morphology. Although few of the hybrid progenies were analyzed for fertility, all of the progenies were analyzed morphologically. Chromosome transmission was regular, except for B chromosomes which were apparently preferentially transmitted. Hybrid fertility and the analysis of morphological characters (berry, inflorescence, and leaf) supported the integrity of the six groups. Genetically the data indicated that self-fertilization is a recessive character. An argument for consideration of self-fertilization as a derived condition in Anthurium was presented.

A taxonomic revision was prepared for Sect. Tetraspermium based upon herbarium specimens, chromosome counts, mode of reproduction, and morphological characters of living plants. Although a part of Group I, A. scandens and A. trinerve could not be crossed with any of the other species which suggested genetic distinctness. These two species with A. margaricarpum form Sect. Tetraspermium. Self-fertilization was the probable mode of reproduction of A. scandens and A. trinerve.

The dispute over whether A. scandens and A. trinerve were separate species or conspecific was investigated. Anthurium trinerve was found to easily be distinguished from A. scandens on the basis of berry shape, spadix shape, and leaf shape. Chromosome numbers of $2n = 24$ for A. trinerve and $2n = 24, 48$ and 84 for A. scandens were determined. Anthurium scandens was divided morphologically into two subspecies pusillum ($2N$) and scandens ($4N, 7N$).

Through a synthesis of the presented data, a possible mode of chromosome number changes and evolutionary pathway was proposed. Six was considered as the basic number of the genus. Anthurium trinerve was indicated as the most primitive species on the basis of chromosome number, leaf shape, and berry characters. Although no species were observed with $n = 5, 6$ or 7 , movement among the basic numbers was considered to have occurred at this level to adequately explain the observed chromosome numbers. A proposal was made that $n = 15$ was commonly of hybrid origin and that perhaps a species with $n = 8$ was responsible. However $n = 8$ or its polyploids were not observed in Anthurium.

APPENDIX

LIST OF HERBARIUM SPECIMENS EXAMINED

A. scandens ssp. scandens (296 Specimens)

WEST INDIES (66)

CUBA: ORIENTE: Sierra Maestra, 1000 m, 28 Oct 1916, Ekman 8098 (US); Gran Piedra near Santiago, 1000 m, Mar 1949, B. Clemente 6474 (US).

DOMINICAN REPUBLIC: BARAHONA: 700 m, Jul 1910, M. Fuertes 488 (F, US); Barahona, 100 m, Dec 1909, H. von Turckheim 2743 (K); SW of Barahona, 27 Jul 1950, R. H. Howard (US); Vicinity of Paraiso, Sea level-800 m, 28 Jan-18 Feb 1922, W. L. Abbott 1609 (US); Forested slopes SE of Polo, 1100 m, 21-25 Aug 1946, E. S. Howard & R. A. Howard 8520 (US); DISTRITO NACIONAL: Santo Domingo, 1857, R. Shomburgr (K); DUARTE: Villa Riva, Sea level-100 m, 11-19 Jan 1912?, W. L. Abbott 565 (US); SANTIAGO: P. Diego de Ocampo, 1200 m, 2 Sept 1948, J. Batista 1722 (US); P. Diego de Ocampo, 1220 m, 15 Apr 1950, J. Jimenez 2020 (US); San Jose de Las Matas, growing on trees, 600 m, 24 Aug 1929, E. J. Valeur 85 (US); SAMANA: Samana Peninsula, Vicinity of Laguna, 100-500 m, 20 Dec 1920, W. L. Abbott 346 (US); Samana Peninsula, Vicinity of Samana, Sea level-200 m, 25 Apr 1921, W. L. Abbott 1418 (US); EL SEIBO: South shore of Samana Bay, 25 Feb 1928, G. S. Miller, Jr. 1004 (US); LA VEGA: Bona, Cordillera Central, 200 m, E. L. Ekman H 16470 (US); Loma Campana, 1036 m, 31 Dec 1947, H. A. Allard 18243a & 18247 (US); Vicinity of Piedra Blanca, 200-500 m, 17 Jan 1946, H. A. Allard 14692 (US), 29 Nov 1945, H. A. Allard 13822 (US), 19 Jan 1948, H. A. Allard 18956 (US); ?: Jan-Mar 1871, H. Brummel,

C. C. Parry & C. Wright 533 (US); ?: 1-7 Feb 1923, W. L. Abbott 2666 (US).

HAITI: L'ARTIBONITE: Vicinity of Kalacroix, 700 m, 11 Dec 1925, E. C. Leonard 7963 (US); NORD: Vicinity of Dondon, 400 m, 8 Jan 1926, E. C. Leonard 8680 (US); Vicinity of Marmelade, on tree, 800 m, 18 Dec 1925, E. C. Leonard 8122 (F, US); Vicinity of Plaisance, on tree along Marmelade trail E of Plaisance, 400 m, 27 Jan 1926, E. C. Leonard 9307 (US); ?: Vicinity of Port de Paix, on tree along La Comp Road, 22 Jan 1929, E. C. Leonard & G. M. Leonard 12281 (US); Miragoane and vicinity, epiphyte on trees in woods, 9 Sep 1927, W. J. Eyerdam (US); ?, climbing on tree, 525 m, 8 Aug 1903, G. V. Nash 281 (F); ?, 1000 m, 14 Aug 1924, E. L. Ekman 1467 (US).

JAMAICA: MANCHESTER: Devon, 600 m, 4 Mar 1952, G. R. Proctor 6308 (US); Vicinity of Mandeville, 600-900 m, 26-30 Apr 1910, J. Crawford 781 (US); Blue Mountains?, Morces Gap and vicinity, 1500 m, 12 Jul 1903, G. E. Nichols (F, US); 1175-1500 m, 6 Mar 1920, W. R. Maxon & E. P. Killip 715 (F, US); 1500 m, Mar 1920, W. R. Maxon & E. P. Killip 1072 (F, US); ST. ANDREW: Catherine Peak, 1200 m, 23 Jan 1888, Eggers 3599 (US); Cinchoma, Blue Mountains, leeward slopes, 1200 m, 13 Feb 1915, J. A. Harris & J. V. Lawrence C15171 (US), 9 Mar 1915, J. A. Harris & J. V. Lawrence C15389 (US), 11 Mar 1915, J. A. Harris & J. V. Lawrence C15436 (F); Blue Mountains above Cinchoma, 1500 m, 15 Dec 1958, J. G. Hawkes, J. P. Hjerting & R. N. Lester 2275 (K); Gordon Town, J. Hart 539 (US); Mt. Horeb, climbing on mossy tree trunks, 1375 m, 14 May 1952, G. R. Proctor 6692 (US), 1500 m, 2 Apr 1958, A. D. Skelding 4458 Duplicate (K); ST. ANN: Moneaque, 400-600 m, 15 May

1850, R. C. Alexander 1702 (F, K); Border of PORTLAND & ST. THOMAS: Lower eastern ridge of Mossman's Peak, on trunk of forest tree, 1600-1700 m, 30 Jun 1926, W. R. Maxon 9643 (US); ?, Mar 1867, Lusebach (K); ?, 23 Jul 1897, A. Fredhelm 3264 (US); ?, J. H. Hart (F).

PUERTO RICO: Aibonito, 600-800 m?, 12 Mar 1916, J. A. Stevenson 5044 (US); Florida, 1842-1849, F. Ruge (US); Luguillo, 6 Jul 1885, Engler 1505 (maybe Sintenis n.1505) (F, US); Monte Montoso, mountain forest, 13 Feb 1915, N. C. Britton & J. F. Cowell 4138 (US); Naquabo, Rio Icacose and adjacent hills, 465-720 m, 30 Jul-5 Aug 1914, J. A. Shafer 3562 (F, US); Ponce, 400-600 m, 31 Dec 1902, A. A. Heller 6357 (F, US); Vicinity of Utuado, 500-700m?, 15-20 Mar 1906, N. L. Britton & J. F. Cowell 1031 (US); Yauco, 100-300 m?, 1880, A. P. Garber 92 (K); ?, 28 Jun 1901, R. F. Griggs & L. M. Underwood 415 (US); ?, Feb 1838, Villian 4038 (K).

TRINIDAD: Brazil-Arena Road, on felled trees, 31 Mar 1959, N. W. Simmonds & R. S. Cowan 1407 (US); Brazil-Talparo Road, 25 Jan 1948, N. W. Simmonds 257 Duplicate (K); Cumaca Road, 175 m, 2 Jan 1948, N. W. Simmonds 272 Duplicate (K); ?, 12 Jan 1911, W. E. Broadway 3951 (K); Mount Tamana, on forest trees, 18 Apr 1920, N. W. Britton, E. G. Britton & T. E. Hazen 1937 (US); ?, 10 Jul 1925, W. E. Broadway 5725 (F).

CENTRAL AMERICA (135)

COSTA RICA: Alajuela: La Ventolera, on the southern slope of the Volcan de Poas, 1700 m, 17-18 Feb 1924, P. C. Standley 34583 & 34649 (US); San Ramon, NE on the Alto de Acosta, 1935, A. M. Brenes

20386 (F); Vicinity of Santa Clara, 200 m, Feb 1896, J. D. Smith 6810 (US); Santa Clara, Jul 1899, H. Pittier 13462 (US); Zarcero, 25 Aug 1937, A. Smith H217 (F); Zarcero, 1400 m, 1 Feb 1938, A. Smith H243 (F); Region of Zarcero, 2000 m, 13 Mar 1938, A. Smith H474 (F); CARTAGO: Cerro de la Carpintera, on tree, 1500-1850 m, Feb 1924, P. C. Standley 34226 (US); Cartago, 1300 m, Oct 1887, J. J. Cooper 5965 (K); Cartago, 1500 m, 18 Mar 1925, H. E. Stork 1217 (F); Dulce Nombre, 1400 m, 27 Feb 1924, P. C. Standley 35830 (US); Dulce Nombre, on tree, 1400 m, 27 Feb 1924, P. C. Standley 35905 (US); Vicinity of Orosi, on tree in forest, 30 Mar 1924, P. C. Standley 39943 (US); Peralta, Jun-Jul 1923, H. E. Stork 494 (US); W of Tapanti, N bank of the Rio Grande de Orosi, in remanent forest on a steep hill, 30 Apr 1967, R. W. Lent 903 (F); Tucurrique, 635-700 m, 1899, A. Conduz 13314 (US); Turrialba, on the Rio Reventazon, 30 Jan 1957, M. C. Carlson 3437 (F); ?, found on trees, Dec 1887, J. J. Cooper 185 (US); ?, on tree, 1425 m, Feb 1924, P. C. Standley 33343 (US); ?, 8-9 Feb 1926, P. C. Standley & J. Valerio 47318 (US); ?, 1931, R. Torres 350 (F); GUANACASTE: El Arenal, 485-600 m, 18-19 Jan 1926, P. C. Standley & J. Valerio 45327 (US); La Tejona, on tree, 600-600 m, 25 Jan 1926, P. C. Standley & J. Valerio 46021 (US); LIMON: Hamburg Finca on the Rio Reventazon below Cairo, on tree, 55 m, 19 Feb 1926, P. C. Standley & J. Valerio 48864 & 48925 (US); PUNTARENAS: Steep forested slopes above Golfito along the trail to the television tower 8°38' N X 83°10' W, epiphyte in forest, 100-300 m, 27-28 Jan 1967, W. Burger & G. Matta 4708 (F); SAN JOSE: Vicinity of Escazu on Cerro de Piedra Blanca, on tree, 31 Jan 1924, P. C. Standley 33973 (US); Cerro Gallito, 2000 m, 3 Feb 1935, M. Valerio

1128 (F); Vicinity of El General, on tree in a woods, 825 m, Feb 1936, A. F. Skutch 2580 (US); 675-900 m, 14 Apr 1962, A. F. Skutch 5425 (F); Low hills above Rio Raquita, 5-50 m, 15 Aug 1936, C. W. Dodge & V. F. Goerger 9882 (F); Vicinity of San Isidro, 730 m, 3 Mar 1966, A. Molina R., W. C. Burger & B. Wallenta 18303 (F); Vicinity of San Isidro, Jul 1938, J. M. Orozco 168 (F); Vicinity of Santa Maria de Dota, 1500 m, 1890, H. Pittier 2445-2488 (US); 1500-1800 m, 14-26 Dec 1925, P. C. Standley 41563-41729 (US); 1500-1800 m, 26 Dec 1925 to 3 Jan 1926, P. C. Standley & J. Valerio 44051 (US); Vicinity of San Jose, on tree, Feb 1924, A. Alfaro 36022 (US); 1150 m, Feb 1924, P. C. Standley 33314 & 34770 (US); San Pedro de Montes de Oca, 1200 m, 2 Feb 1924, P. C. Standley 32792 & 36116 (US); ?, 1160 m, Jul 1935, M. Valerio 1354 (F); Probably near the border of Cartago & San 11 Dec 1939, J. A. Steyermark 33055 (F); QUEZALTENANGO: Between Finca Pirineos and Finca Soledad, 1300-1400 m, 5 Jan 1940, J. A. Steyermark 33491 (F); SAN MARCOS: Volcan Tajumulco, epiphyte in tree, 9 Mar 1940, J. A. Steyermark 37394 (F); 11 Mar 1940, J. A. Steyermark 37542 (F); SUCHITPERQUEZ: Vicinity of Finca Alvidas, on slopes of Volcan Zunil, 2 Feb 1940, J. A. Steyermark 35454 (F); Between Finca El Naranjo and upper slopes of Volcan Santa Clara, 1250-2650 m, 23 May 1942, J. A. Steyermark 46608 (F); ?, 4 Apr 1902, O. F. Cook & R. F. Griggs 442 (US); ?, Jan 1907, H. Pittier 1864 (US); ?, 29 m, 12 Dec 1928, F. Mortor 265 (F).

HONDURAS: ATLANTIDA: Vicinity of La Ceiba, on slopes of Mt. Cangrejal, 200 m, 16 July 1938, T. G. Yuncker, J. M. Koepper & K. A. Wagner 8500 (F); Lancetilla, 60 m, 12 Jul 1934, T. G. Yuncker 4557 (F); Tekam 20-600 m, 6 Dec 1927-20 Mar 1928, P. C. Standley 52735 &

54124 (F, US); COPAN: Vicinity of Paraiso, on tree trunk, 12 May 1919, S. F. Blake 7367 (US); COMAYAGUA: Vicinity of Siguatepeque, 1350 m, Jun-Aug 1936, T. G. Yuncker, R. F. Dawson & H. R. Youse 5980 (F, K); Valibrea, 1585 m, 7 Apr 1945, J. V. Rodriguez 2779 (F); Yojoa, 500 m, 17 Apr 1945, J. V. Rodriguez 2880 (F); CORTES: Near the shore of Lake Yojoa, epiphyte on tree, 700 m, 29 Jul 1934, T. G. Yuncker 4836 (F); 30 Jul 1934, T. G. Yuncker 4880 (F): ?, 20 m, 27 Aug 1955, A. Molina R. 5673 (F); EL PARAISO: Between Rio Los Almendros and Chichicaste, 15 Mar 1963, A. Molina R. 11397 (F); Emila?, 22 Feb 1952, M. C. Carson 2563 (F); INTIBUCA: Vicinity of Yamaranguila, 12 Apr 1956, A. Molina R. 6548 (F, US); MORAZAN: Near Hoya Grande, 1550 m, 14 July 1946, L. O. Williams & A. Molina R. 10037 (F); Lower slopes of Cerro de Uyuca, 1530-1600 m, 22 Feb 1947, P. C. Standley & A. Molina R. 4319 (F); Cortes or Atlantida?: 12 Mar 1929, W. A. Schipp 78 (F, US); ?, 1 Sep 1929, W. A. Schipp S-20 (F).

MEXICO: CHIAPAS: SE of Comitán, creeping on fallen log, 1530 m, 15-20 Apr 1949, M. C. Carlson 1820 (F); Ocozocoautla, 1130 m, 12-13 May 1949, M. C. Carlson 2103 (F); Ocozocoautla, 825 m, 23 Mar 1949, M. C. Carlson 1553 (F); OAXACA: Vicinity of Tuxtepec, 20 m?, Jul 1940-Feb 1941, G. Martinez-Calderon 118 (US); ?, 1850-2450 m, 22 May 1921, C. Conzatti 4137 (US); VERACRUZ: Cordoba, Aug 1936, E. Matuda 838 (F); Cordoba, M. Bourgeau 2170 (K); Vicinity of Cordoba, on branches of large trees, 4 Aug 1947, F. A. Barkley, J. B. Paxson & C. M. Rowell, Jr. 17M663 (F); Fortin de Las Flores ?, Feb 1883, E. Kerber 294 & 297 (US); Orizaba, 13 Mar 1867, E. Cossor 409 (K); Jalapa, 3000 m, Jun-

Oct 1840, H. Galeotti 6052 (K); SE of Jalapa, epiphyte on trees and rocks, 3 Aug 1947, F. A. Barkley, C. M. Rowell & G. L. Webster 2600 (F); Veracruz to Orizaba, F. Muillen 1132 (K); ?, on trees, Jan 1912, C. A. Purpus 5764 (F, US); ?, Schnee (US); ?, May 1841, Liebmann N915796 Duplicate (F, US); ?: 1867, Minadon (K); C. Hohr 577 (US).

NICARAGUA: JINOTEGA: Vicinity of Jinotega, on tree, 1030 m, 19 Jun-9 Jul 1947, P. C. Standley 9595 (F); MATAGALPA: Between Matagalpa and Jinotega in cloud forest area, 1300-1500 m, 8-15 Jan 1963, L. O. Williams, A. Molina R. & T. P. Williams 23329 & 23455 (F); N Sta. Maria de Ostuma, 1300-1500 m, Feb 1963, L. O. Williams, A. Molina R. & T. P. Williams 24931 (F); MANAGUA: S Managua, casa Colorada and Vicinity, 850 m, 27 Jun 1923, W. R. Maxon, A. D. Harvery & A. T. Valentine 7360 (US); 14-25 May 1947, P. C. Standley 8418 (F); S. Managua, Las Nubes and vicinity, 800-900 m, 28 Jun 1923, W. R. Maxon, A. D. Harvey & H. T. Valentine 7504 & 7509 (US).

PANAMA: BOCAS DEL TORO: Rio Cricamola, 10-15 m, 12-16 Aug 1938, R. E. Woodson, Jr., P. H. Allen & R. J. Seibert 1880 (F); CANAL ZONE: Barro Colorado Island, 21 Aug 1927, L. A. Kenoyer 194 (US); ?, 29 Sep 1909, D. D. Gaielard 091340 (US); CHIRIQUI: Above El Boquete, 1300-1560 m, 5 Mar 1911, H. Pittier 3028 (US); Vicinity of El Boquete, 1160 m, 24 Jun 1938, M. E. Davidson 734 (F, US); Locality of Volcan de Chiriqui, 2100 m, 12 Feb 1938, M. E. Davidson 913 (F); ?, 28 Jun-2 Jul 1938, R. E. Woodson, Jr., P. H. Allen & R. J. Seibert 925 (F); COCLE: Vicinity of El Valle in the foothills of Cerro Pilon, 900 m, 5 Oct 1967, M. Correa & J. Duke 14690 (3) (US); DARIEN: Along Rio Balsa, 26

Jul 1967, J. A. Duke 13502 (US); S of Cerro Pirre, Cerro Campamento,
J. A. Duke 15651 (US).

SOUTH AMERICA (95)

BOLIVIA: COCHABAMA: Vicinity of Cochabamba, 1600 m, 20 Feb
 1929, J. Steinbach 8867 (F); Region of Yungas, 1830 m, 1885, H. H.
Rusby 2427 (US); LA PAZ: Coroico, Oct-Nov 1912, O. Ruchtein 3663,
3664 & 4517 (US); LA PAZ: On the road to Tipuani, Feb 1920, O. Buch-
tien 5341 (US); PANDO?: Santa Rosa, 2000 m, 1892, O. Kuntze (F);
 SANTA CRUZ: Vallecito, epiphyte on mossy logs in forest, 1300 m, Nov
 47, M. Cardenas 4001 (F, US); LA PAZ OR COCHABAMA: Coripati in the
 region of Yungas, 22 Jun 1894, A. M. B. Lectae 2307 (K, US); BRAZIL:
 BAHIA: Ilheus, 24 Mar 1965, R. P. Belem & M. Magalhaes 507 (US); For-
 ests of Rio Grongogy Basin, 100-500 m, 1 Oct-30 Nov 1915, H. M. Curran
237 (US); MINAS GERAIS: Caete, 5 Jun 1934, M. Barreto 923 (F, US);
 Road to Sao Miguel, on huge tree, 20 Nov 1930, Y. Mexia 5327 (F, US);
 PARANA; 24 Sep 1908, P. Dusen 6587 (US); 13 Sep 1914, P. Dusen 15537
 (US); PERNAMBUCO: Palmares, epiphyte in forest, 13 Jan 1952, E. Henz
52227 (US); SANTA CATARINA: Brusque, 40-50 m, 23 Feb 1952, L. B.
Smith 5768 (US); Ibirama, 100 m, 26 Oct 1953, R. Klein 685 (F);
 Itajai, 15 m, 26 Jul 1955, R. Klein 1478 (US); ?, 30 Aug 1947, B. Rod-
riques C1840 (US).

BRITISH GUIANA: ESSEQUIBO: Pakaraima Mountains, epiphyte on
 tree, 11 Nov 1951, B. Maguire & D. B. Fanchawe 32579 (US).

COLOMBIA: AMAZONAS: Loretoyaca River, 100 m, Oct 1946, R. E.
Schultes & G. A. Black 8455 (US); ANTIOQUIA: Angostura, base of tree

in brushy fence row, 2150 m, 12 Mar 1944, F. R. Fosberg 21630 (US); Jerico, Dec 1940, B. Daniel 2586 (US); Vicinity of La Union, 2700 m, 21 Aug 1948, F. A. Barkley & W. Johnson 18C849 (US); Medellin, Oct 1945, J. D. Ponages & B. Daniel 3811 (US); On the road between Medellin and Rionegro, 2500 m, 1 Apr 1949, F. A. Barkley, J. Guardiola & R. Barriga 520 (US); CALDAS: 1700-1900 m, 16 Feb 1946, K. von Sneider 5043 (F); CAQUETA: Between Sucre and La Portada, 1200-1350 m, 5 Apr 1940, J. Cuatrecasas 9152 (US); CAUCA: 1600-1800 m, F. C. Lehmann-iana 5362 (F) & B. Perpetual P5362 (K); CHOCO: Quibdo, along Rio Atrato, epiphyte, 60 m, Apr-May 1931, W. A. Archer 1873 (US); Yuto, along Rio Atrato, climbing in trees, 70 m, 2 Apr 1958, J. Cuatrecasas & M. Llano 24137 (US); Peak over Rio Curundu, 600 m, 8 Mar 1968, J. H. Duke 15334(1) (US); CUNDINAMARCA: Vicinity of Bogota, 1919, B. Ariste-Joseph (US); Pacho, 1800 m, Oct 1948, L. Uribe 1826 (US); Sasaima, 1300 m, 10-12 Jul 1960, H. Garcia-Barriga 17241 (US); Tequendama, along Rio Bogola above falls, 2400 m, 25 Jul 1949, O. Haught 6553 (US); GUAJIRA: S Garraipia, small epiphyte growing with bromeliads and orchids, 30 Jul 1944, O. Haught 4271 (US); Serrania La Macuirra, 670 m, 11-12 Apr 1964, C. Saravia T. & M. E. de Saravia 3590 (US); HUILA: Balsillas, epiphytic herb, 2000-2100 m, 3-6 Aug 1917, H. H. Rusby & F. W. Pennell 740 (US); Guadalupe, 1000-1300 m, 20 Mar 1940, E. P. Arbelaez & J. Cuatrecasas 8404 (F, US); META: Sierra de La Macareva, on rocks in forest, 21 Dec 1949, W. R. Philipson & J. M. Idrobo 1834 (US); Villa-vicencio, epiphyte growing in dense shade, 1230 m, Mar 1948, C. Lausleae 5880 (K); NORTE DE SANTANDER: Tapata, N of Toledo in Culaga Valley, 1500-2100 m, 3-8 Mar 1927, E. P. Killip

& A. C. Smith 20163 (US); SANTANDER: Mesa de Los Santos, subscandent herb among rocks in open, 1500 m, 11-15 Dec 1926, E. K. Killip & A. C. Smith 15170 (US); Vicinity of Surata, scandent herb on tree trunk, 1700 m, 4-10 Jan 1927, E. P. Killip & A. C. Smith 16753 (US); VALLE: La Cumbre, 1800-2100 m, 14-19 May 1922, F. W. Pennell & E. P. Killip 5738 (US); La Cumbre, 1500-1700 m, 11-16 Jul 1922, T. E. Hazen 11844 (US); Palmira, Nov 1942, R. E. Schultes (US); Vicinity of Rio Cali and Rio Pichinde, 2270-2320 m, 17 Oct 1944, J. Cuatrecasas 18185 (F); 2250-2350 m, 24 Jul 1946, J. Cuatrecasas 21657 (F); Zarzel, Cauca Valley, 970-1050 m, 21 Jul 1922, F. W. Pennell, E. P. Killip & T. E. Hazen 8413 (US); VAUPE: Along Rio Pacoa, 7-12 Feb 1952, R. E. Schultes & I. Cabrera 15271 (US); ?, Bitaco Valley, 1500-2600 m, H. F. Winters 9923 (US); Forest of Solota, 1400-1800 m, May 1897, 8903 (F); ?, 1760-1808 J. C. Mutis 53 (US).

ECUADOR: BOLIVAR: Atio de Telimbela, 1500 m, 18 Nov 1943, M. A. Solis 6915 (F); PINCHINCHA: W of Santo Domingo de los Colorados, on tall trees, 300 m, 11 Mar 1961, P. C. D. Cazalet & T. D. Pennington 5271 (US), 17 Oct 1961, P. C. D. Cazalet & T. D. Pennington 5052 (K, US); Along road between Santo Domingo to Quininade, 300 m, 4 Sep 1949, M. A. Solis 13736 (F); ?c 15 Jul 1920, I. Holmgren 850 (US).

PERU: CUZCO: Provincia Convencion, 1700 m, 28 July 1943, C. Vargas C. 3463 (F); Provincia Quispicanchi, Marcapata Valley between Chaupichaca & Mamabamba, 19 Feb 1929, A. Weberbauer 7845 (F, US); JUNIN: Chanchamayo Valley, 1200 m. epiphyte, Nov 1924-1927, C. Schunke 322 (F), 1500 m, Jul 1929, C. Schunke 373 & 374 (F); Sam Ramon, 1400-1700 m, 8-12 Jun 1929, E. P. Killip & A. C. Smith 24880

(US); LORETO: Rio Huallaga Canon below Rio Santo Domingo, 1230 m, 3 Jun 1923, J. F. Macbride 4249 (F); ?, Toulir, 1800 m, 14 Oct 1957, R. Hirsch P2219 (F); ?, 1230 m, 27 Aug-1 Sep 1923, J. P. Macbride 5746 (F).

VENEZUELA: ANZOATEQUI: NE of Bergantin, epiphyte, 500 m, 20 Feb 1945, J. A. Steyermark 61044 (F, US); BOLIVAR: Auyan Tepui, epiphyte in dense clump on tree trunk, 1800 m, 7 May 1964, J. A. Steyermark 93523 (F, US); Chimanta, epiphyte on tree trunk in densely forested area, 1700-1850 m, 23 Jun 1953, J. A. Steyermark 75954 (F); Vicinity of Deborah, N of Tumeremo, epiphyte on tree, 600-650 m, 5-8 Feb 1961, J. A. Steyermark 89149 (US); Ptari-tepui mountain, on steep forested slopes, 2130 m, 4 Nov 1944, J. A. Steyermark 59848 (F, US); W. Soledad, 600 m, Aug 1953, H. Gines 3912 (US); CARABOBO: S of Borburata, epiphyte on tree, 750 m, 28 Mar 1966, J. A. Steyermark & C. Steyermark 95233 (US), 1 Apr 1966, J. A. Steyermark & C. Steyermark 95423 (F); COJEDES: Sucre, Jan 1942, F. Tamayo 2126 (US); DELATA AMACURO: Rain forest between La Margarita and Puerta Miranda, epiphyte on tree, 80-100 m, 23-24 Nov 1960, J. A. Steyermark 87736 (US); DISTRITO FEDERAL: El Junquito, scandent on tree trunks, 1925 m, E. P. Killip & E. Rohl 37197 (US); MIRANDA: Vicinity of Los Teques, 1000-1800 m, 26-28 Apr 1945, J. A. Steyermark 62146 (F); ?, 1854-1835, A. Fendler 1347 (K).

A. scandens ssp. pusillum R. D. Sheffer (62 Specimens)

CENTRAL AMERICA (59)

COSTA RICA: ALAJUELA: Vicinity of Fraijanes, on tree in wet forest, 1500-1700 m, 12-13 Feb 1926, P. C. Standley & R. Torres R.

47562 (US); Colimas de San Pedro of San Ramon, 31 Jan 1934, A. M. Brenes (F); La Pena de Zatcero, epiphyte on forest tree, 1450 m, 6 May 1938, A. Smith H507 (F); Zarcero, epiphyte in low branches of trees in shade, 9 Jan 1938, A. Smith H59 (F); CARTAGO: N of Cartago, along the Rio Reventado, on tree, 1460-1650 m, 26 Feb 1926, P. C. Standley & J. Valerio 49504 (US); Vicinity of Cartago, on tree, 1425 m, Feb 1924, P. C. Standley 33401 (US); Cerro de la Carpintera, on tree, 1500-1850 m, Feb 1924, P. C. Standley 34228, 34323 & 34406 (US); La Estrella, on tree, 26-27 Mar 1924, P. C. Standley 39519 & 39536 (US); El Muneco, S of Navarro, on tree, 1400 m, 8-9 Feb 1924, P. C. Standley 33786 & 33903 (US); Santa Cruz de Turrialba, 1400 m, Jan 1941, J. Valerio 1331 (F); SE of Tapanti, along Rio Grande de Orosi, 1400 m, 16 Apr 1967, R. W. Lent 830 (F); ?, 1400 m, 4 Aug 1924, R. T. Rojas 109 (US); ?, 1400 m, 15 Feb 1926, R. T. Rojas 205 (F); CARTAGO?: 1830 m, 7 Mar 1928, H. E. Stork 1143 (F); 3 Apr 1925, H. E. Stork 1363 (F); GUANACASTE: Le Tejona, N of Tilaran, on tree in wet forest, 600-700 m, 25 Jan 1926, P. C. Standley & J. Valerio 46055 & 46072 (US); HEREDIA: Volcan Barba, common epiphyte in cool, wet woodland pasture, 2000 m, 26 May 1965, W. H. Hatheway 1383 (F, US); Volcan Barba, N of San Jose, epiphyte, 17 May 1966, D. Nicolson 4006 (US); Cerro de las Caricias, N of San Isidro, on tree, 2000-2400 m, 11 Mar 1926, P. C. Standley & J. Valerio 52465 (US); Cerro de Las Lajas, N of San Isidro, on tree, 2000-2400 m, 7 Mar 1926, P. C. Standley & J. Valerio 51536 (US); Yerba Buena, NE of San Isidro, on tree in wet forest, 2000 m, 22-28 Feb 1926, P. C. Standley & J. Valerio 49086, 49092 & 50157 (US); PUNTARENAS: S of San Vito de Java, 1530 m, 22 Mar 1967, P. H. Raven 20874 (F), Aug 1967, P.

H. Raven 21851 (F); SAN JOSE: Above Escazu, on Cerro de Piedra Blanca, on trees, 31 Jan 1924, P. C. Standley 32510 (US); La Hondura, on tree in forest, 1300-1700 m, 2-4 Mar 1924, P. C. Standley 36335 (US), 16 Mar 1924, P. C. Standley 37624 & 37700 (US); La Palma, on tree, 1600 m, 3 Feb 1924, P. C. Standley 32951 & 33050, 17 Mar 1924, P. C. Standley 38054; NE of San Jeronimo, above the La Hondura Valley, common epiphyte on trunks and branches in open or protected areas, 27 May-1 Jun 1968, W. C. Burger & R. G. Stolze 5342 (F); Laguna de la Chonta, NE of Santa Maria de Dota, on tree in wet forest, 2000-2100 m, 18 Dec 1925, P. C. Standley 42193 (US); Las Nubes, on tree, 1500-1900 m, 20-22 Mar 1924, P. C. Standley 38794 (US); San Francisco de Guadalupe, 100 m, Jul 1894, H. Pittier (US); Santa Domingo de Vera Blanca, 2200 m, 22 Feb 1937, M. Valerio 1601 (F); Zurgui, on trees, 2000-2500 m, 13 Feb 1926, P. C. Standley & J. Valerio 48295 (US); SAN JOSE?: Tapanti, 1300 m, 15 Jul 1937, M. Valerio 1611 (F); ALAJUELA-HEREDIA: Palmira, epiphyte in pasture tree, 1900 m, 22 Dec 1937, A. Smith A748 (F); Vara Blanca de Sarapigui, between Poas and Barba volcanoes, on logs in open, 1650 m, Mar 1938, A. F. Skutch 3665 (K, US); ?, Aug 1875, M. Endress 156 (K); ?, 28 Apr 1946, J. A. Echeverria (F).

HONDURAS: MARAZAN: Cerro de Uyuca, Vicinity of drainage of the Rio Yeguaré, at about 87° W X 14° N, epiphyte in cloud forest, 2000 m, 2 Jan 1949, L. O. Williams & A. Molina R. 14933 (F); Cerro de Uyuca, along trail from Las Flores to La Labranza, 1600-1750 m, Oct-Dec 1948, P. C. Standley, 14092 (F); SANTA BARBARA: Montan Santa Barbara, scandent epiphyte, 2350 m, 7 Apr 1951, P. H. Allen, R. Armour & A. Chable 6115 (F).

NICARAGUA: MATAGALPA: Santa Maria de Ostuma, between Montagalpa and Jinotega, in cloud forest area, 1300-1500 m, 8-15 Jan 1963, L. O. Williams, A. Molina R. & T. P. Williams 23454 (F), 20-24 Feb 1963, L. O. Williams, A. Molina R. & T. P. Williams 25061 (F); JINOTEGA: Vicinity of Fina San Roque, E of Jinotega, chiefly in dense wet mixed forest, 1300-1500 m, 5 Jul 1947, P. C. Standley 10925 (F); Region of Las Mercedes, E of Jinotega, chiefly in dense wet mixed virgin cloud forest, 1200-1500 m, 3 Jul 1947, P. C. Standley 10648 (F).

PANAMA: CHIRIQUI: Vicinity of Bajo Mona, 1500 m, 18 July 1940, R. E. Woodson & R. W. Schery 570 (F); Boquete District, Locality Bajo Chorro, rain forest, 1830 m, 26 Jan 1938, M. E. Davidson 162 (F); Humid forest between Alto de las Plamas and the top of Cerro de la Horqueta, 2100-2268 m, 18 Mar 1911, H. Pittier 3259 (US).

SOUTH AMERICA (3)

COLOMBIA: VALLE: La Cumbre, 1700-2200 m, 11-18 Sep 1922, E. P. Killip 11338 (US); Vicinity of Rio Digua, 900-1180 m, 19-28 Aug 1943, J. Cuatrecasas 15076 (F).

VENEZUELA: ?, 1800-2000 m, Dec 1924, A. Allart 492 (US).

A. trinerve Miq. (63 SPECIMENS)

CENTRAL AMERICA (32)

COSTA RICA: ALAJUELA: Quesada, roadside on tree in open exposure, 650 m, 11 Mar 1940, A. Smith P2528 (F); NE of Quesada, epiphyte in dense wet secondary forest, 550 m, 17 Feb 1966, A. Molina R., L. O. Williams, W. C. Burger & B. Wallenta 17276 (F); CARTAGO: N of

Cartago, along the Rio Reventado, on tree, 1460-1650 m, 26 Feb 1926, P. C. Standley & J. Valerio 49516 (US); Vicinity of Pejivalle, on tree, 900 m, 7-8 Feb 1926, P. C. Standley & J. Valerio 47232 (US); LIMON: Below Cairo on the Rio Reventazon, 55 m, 19 Feb 1926, P. C. Standley & J. Valerio 48927 (US); Vicinity of Guapiles, on tree, 300-500 m, 12-13 Mar 1924, P. C. Standley 37463 (US); Moin, 29 Mar 1936, M. Quiros 547 (F); Drainage area of Rio Reventazon, 15 m, 23 Oct 1951, P. J. Shank & A. Molina R. 4379 (F); PUNTARENAS: Region of Osa, area between Rio Espuinas and Palmar Sur de Osa, common in tops of large trees, 30 m, 16 Mar 1950, P. H. Allen 5472 (F, US); W of Rincon de Osa, Osa Peninsula, 8°42' N X 83°31' W, 30 m, 4-7 Jun 1968, W. C. Burger & R. G. Stolze 5530 (F); Along the inter-american highway, 9°9' N X 83°19' W, 26 Jan 1967, W. Burger & G. Matta 4670 (F); N. Y. Sandwith 39 (K); Pomeran district, Moruka River, 20 Sep 1921, J. S. De La Cruz 1155 (US), 16 Aug 1921, J. S. De La Cruz 1241 (US); ?, 22 Aug 1937, N. Y. Sandwith 1165 (K); W. Parking (K); ?, Jan 1889, Spruce (K).

COLUMBIA: ANTIOQUIA: Vicinity of Villa Arteaga, 15 Apr 1948, G. Guteirrez & F. A. Barkely 18C610 (US); CALDAS: Santa Cecifia, 800 m, 26 Nov 1945, K. von Sneidern 5021 (F); CHOCO: Near Halipad in Raphia swamp on Rio Truando, 40 m, 1 Apr 1968, J. A. Duke (US); Quibdo, Rio Atrato, 60 m, Apr-May 1931, W. A. Archer (US); META: Extreme NE Cordillera La Macarena, 600-1300 m, 30 Dec 1959-5 Jan 1951, J. M. Idrobo & R. E. Schultes 881 (US); Villavicencio, Jan 1899, T. A. Sprague (K); VALLE: Cisneros, 300-500 m, 5 May 1939, E. P. Killip 35557 (US); Sabaletas, on highway from Buenaventura to Cali, 25 m, 4-6 Jun 1944,

E. P. Killip & F. Cuatrecasas 38851 (US); VAUPES: 200 m, 4 Nov 1944, P. A. Allen 3314 (US); ?, Chajal, 13 Jun 1951, R. R. Casteneda 2719 & 2728 (F).

FRENCH GUYANA: Riviere Camopi, 200 m, 13 Feb 1968, Oldeman & Sastre 236 (US).

PERU: LORETO: Above Pongo de Manserichi, along the Rio Santiago in dense forest, 200 m, 6 Dec 1931, Y. Mexia 6233a (F, K); SAN MARTINE: E of Tingo Maria, on tree limb, 625-1100 m, 30 Oct 1949-19 Feb 1950, H. A. Allard 20455 & 21888 (US).

SURINAME: BROKOPONDO: S of Afobaka, forest along Sara Creek, 12 Mar 1964, R. A. Florschütz & P. J. M. Maas 2306 (US), Feb 1965, J. van Donselaar 2110 (F).

VENEZUELA: AMAZONAS: Along Rio Casiquiare between Piedra Lais and Cano Pamoni, 150 m, 1 Apr 1953, B. Maguire & J. J. Wurdack (US); BOLIVAR, Alto Rio Paragua, 1 Jul 1944, F. Cardona 1067 (US); ?, Tabay, 2300-2400 m, 30 Aug 1930, Gehriger 383 (F).

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