Chromosome Variation in Araceae: V. Acoreae to Lasieae
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Source: *Kew Bulletin*, Vol. 28, No. 2 (1973), pp. 199-210
Published by: Springer on behalf of Royal Botanic Gardens, Kew
Stable URL: http://www.jstor.org/stable/4119780
Accessed: 12/08/2011 09:53

Chromosome variation in *Araceae*: V*

ACOREAE TO LASIEAE

C. J. Marchant†

Summary. Somatic chromosome numbers are reported for six tribes of the *Araceae* and for miscellaneous genera which were not included earlier in the series. While much chromosome diversity is evident in the family, the chromosome data do not support completely the major *Araceae* classifications of either Hutchinson (1959) or Engler (1920). Evolutionary relationships in the family are considered from the viewpoint of known basic chromosome numbers and suggestions are made concerning the taxonomic positions of some critical genera especially in the proposed *Arophyteae* of Bogner (1972).

Introduction

This is the last of a series of five papers describing karyotypes of miscellaneous genera in the *Araceae*. The purposes of this chromosome survey of an entire family were set out in the introduction to the first paper (Marchant, 1970) and the very diverse karyotypes and basic numbers, with occasional intraspecific diversity, have become apparent (Marchant, 1970, 1971a & b, & 1972). The cytological examination of genera is far from complete, there being some 54 genera not available at Kew, but it is hoped that these data for a little over 50 per cent. of the total genera will provide a stimulus for further work at the same comparative level.

The present paper deals with the first six tribes in the classification of Hutchinson (1959), most of which are considered by him to be the more primitive in the family. There are also a number of miscellaneous additions from tribes already treated in this series. These plants have had their chromosomes counted since the results of the survey first began to be published.

Materials and methods

Materials and methods were both as previously described (Marchant, 1970). Voucher specimens are deposited in the Kew Herbarium.

Results

Acoreae

Acorus calamus L. has a curiously mixed record of chromosome numbers accorded to it by numerous authors (listed in Table 1). These range from $2n = 18$ ($x = 9$) to $2n = 24$ ($x = 12$) and $2n = 36$, 44 and 48 ($x = 11$ or 12). The majority, with $2n = 36$, correspond with my own count of $2n =$ c. 36 very small chromosomes (Fig. 1/A, p. 202). It is important that chromosomes of other species in the genus should be counted to help verify the correct basic number. The most likely explanation seems to be that widespread European $2n = 36$ plants, which are sterile, are triploids based on $x = 12$ (Palmgren, 1943) in the same chromosome series as $2n = 24$ and 48. The

Accepted for publication 2 October 1972.
* Continued from Kew Bull. 26: 404 (1972).
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TABLE 1. List of chromosome counts in the *Araceae*, tribes *Acoreae* to *Lasieae*.

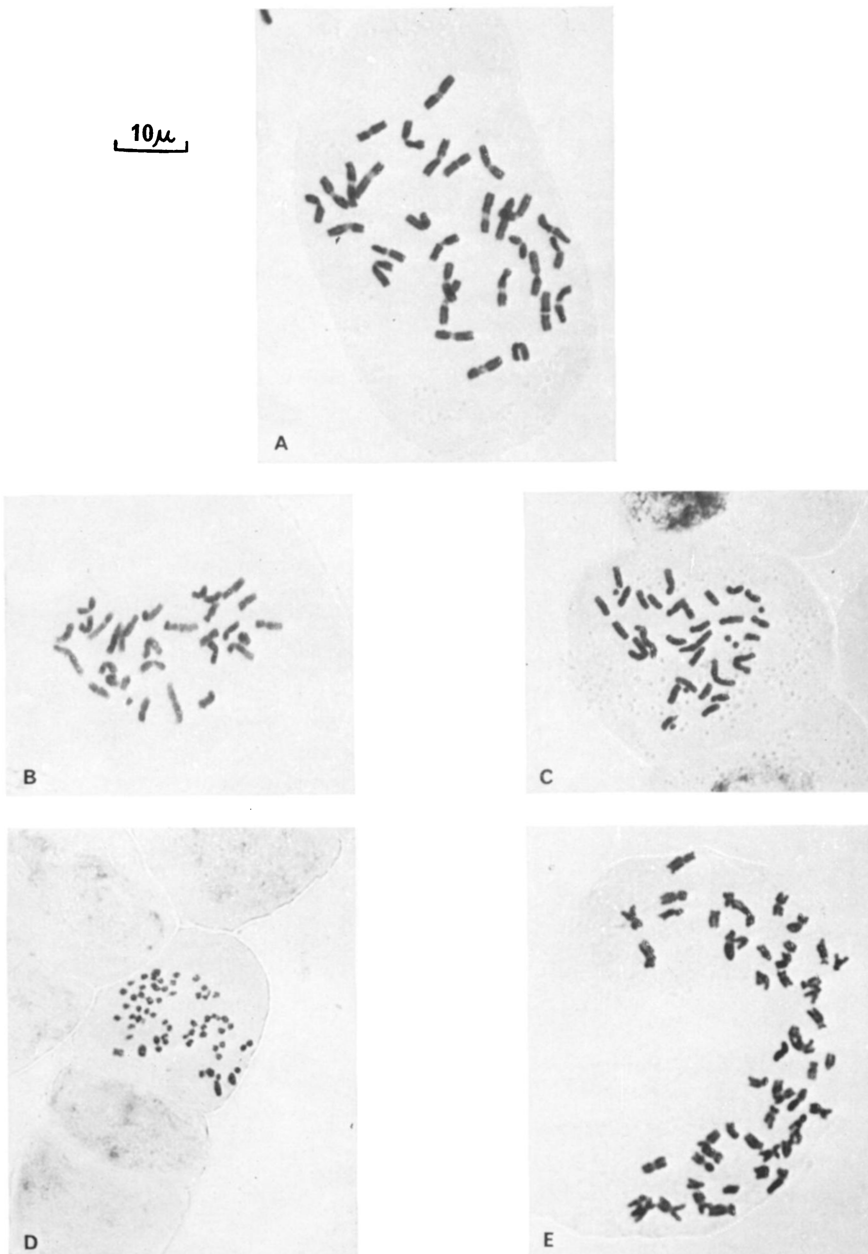
Name	Kew Entry No.	Cytology Accession No.	Origin	Chromosome No. (2n)	Basic No. (x)	Size S M or L (small, medium or large)	PREVIOUS COUNTS: Name	PREVIOUS COUNTS: Chromosome No. (2n)	PREVIOUS COUNTS: Author	PREVIOUS COUNTS: Date
Tribe **Acoreae**										
Acorus calamus L.		65.560	R.B.G., Kew	c. 36	6, 9	S	*A. calamus*	18	Matsuura & Suto	1935
Acorus calamus L.		65.817	R.B.G., Kew	c. 36				18	Dudley	1937
Acorus calamus L.		65.1010	Staines Moor, Middlesex, England	c. 36				24, 36, 48	Wulf	1940
								36	Palmgren	1943
								24	Varaama in Löve & Löve	1948
								18	Delay	1951
								36	Löve & Löve	1957
								36	Wulf & Hoffman	1957
								36	Jones	1957
								36	Wulf & Fritz	1958
								24, 36	Kozlowski	1960
								36	Skalinska *et. al.*	1961
								44	Larsen	1969
							A. asiaticus	44	Ito	1942
Tribe **Oronteae**										
Lysichiton americanum Hulten & St. John		65.520	R.B.G., Kew	28	7	S	*L. americanum*	28	Löve & Kawano	1961
Orontium aquaticum L.		65.549	R.B.G., Kew	26	13	L	*O. aquaticum*	24	Delay	1950
								28	Huttleston in Darlington & Wyllie	1955
								26	Cave	1967
Tribe **Spathiphylleae**										
Spathiphyllum commutatum Schott		64.556	R.B.G., Kew	c. 30	15	M				
S. floribundum (Linden & André) N. E. Br.	340.66	69.790	Seed, ex Saarbrücken Bot. Garden	60			*S. floribundum*	60	Pfitzer	1957
S. friedrichsthalii Schott	401.64	69.792	*L. M. Mason*	30						
S. × *hybridum* N. E. Br. (*S. cannifolium* × *S. patinii*)		69.791	R.B.G., Kew	30						
S. wallisii Regel		64.496	R.B.G., Kew	30						

TABLE 1. (contd.) List of chromosome counts in the *Araceae*, tribes *Acoreae* to *Lasieae*.

Name	Kew Entry No.	Cytology Accession No.	Origin	Chromosome No. (2n)	Basic No. (x)	Size S M or L (small, medium or large)	PREVIOUS COUNTS Name	PREVIOUS COUNTS Chromosome No. (2n)	PREVIOUS COUNTS Author	PREVIOUS COUNTS Date
Tribe **Anthurieae**										
Anthurium acutum N. E. Br.	442.64	68.1639	R.B.G., Kew	30	15	S				
A. crystallinum Linden & André		63.1715	R.B.G., Kew	30 + 2f			*A. crystallinum*	34	Mookerjea	1955
								30 + 0–2f	Pfitzer	1957
A. gracile (Rudge) Lindl.	579.62	63.2278	S. Cent. America *L. Siedal*	40	20		*A. gracile*	30	Gaiser	1927
A. harrisii (Graham) G. Don	687.61	69.103	*L. M. Mason*	30 + 5f	15					
A. imperiale Miq. ex Schott		61.230	R.B.G., Kew	30 + 2f						
A. lucidum Kunth	4676.66	68.1643	Costa Rica, *Lankester*	c. 124						
A. microphyllum (Hook.) G. Don	434.59	65.150	R.B.G., Kew	30 + 1f						
A. scolopendrinum (W. Ham.) Kunth	699.58	63.2280	cult. ex Chelsea Parks Dept.	40	20					
A. scandens (Aubl.) Engl.							*A. scandens*	c. 48	Gaiser	1927
var. *violaceum* (Sw.) Engl.	598.60	62.469	*Lankester*	45–47	15			24	Pfitzer	1957
A. signatum C. Koch & Mathieu	2809·66	68.1642	R.B.G., Kew	30 + 1f	15		*A. signatum*	34	Mookerjea	1955
A. undatum Schott	671.62	65.188	*L. Siedal*	c. 60 + 1B						
A. undatum Schott	671.62	68.1641	*L. Siedal*	60						
Anthurium sp.	434.59	65.473	*Lankester*	c. 124						
Tribe **Dracontieae**										
Dracontium foecundum Hook. f.	568.63	65.208	Trinidad, *Jermy*	26	13	M				
Symplocarpus foetidus (L.) Salisb.		69. 456	R.B.G., Kew	60	15	S	*S. foetidus*	30	Ito	1942
Tribe **Lasieae**										
Cyrtosperma johnstonii (Bull) N. E. Br.		62.1733	Solomon Islands	c. 26	13	S	*C. senegalense* Bogner	26	Mangenot & Mangenot	1962
Cyrtosperma johnstonii (Bull) N. E. Br.		69.67	R.B.G., Kew Dept.	26						
Urospatha sagittifolia (Rodsch.) Schott	167.62	68.1411	*Bleher*	52	13	M				
Urospatha sp.	500.65	69.703	*Bleher* 124	52						
Tribe not specified by Hutchinson (1959)										
Microculcas marattioides Peter	032.69 ·350	69.785	Tanzania, E. Usambaras, *Bogner* 247	34	17	L				

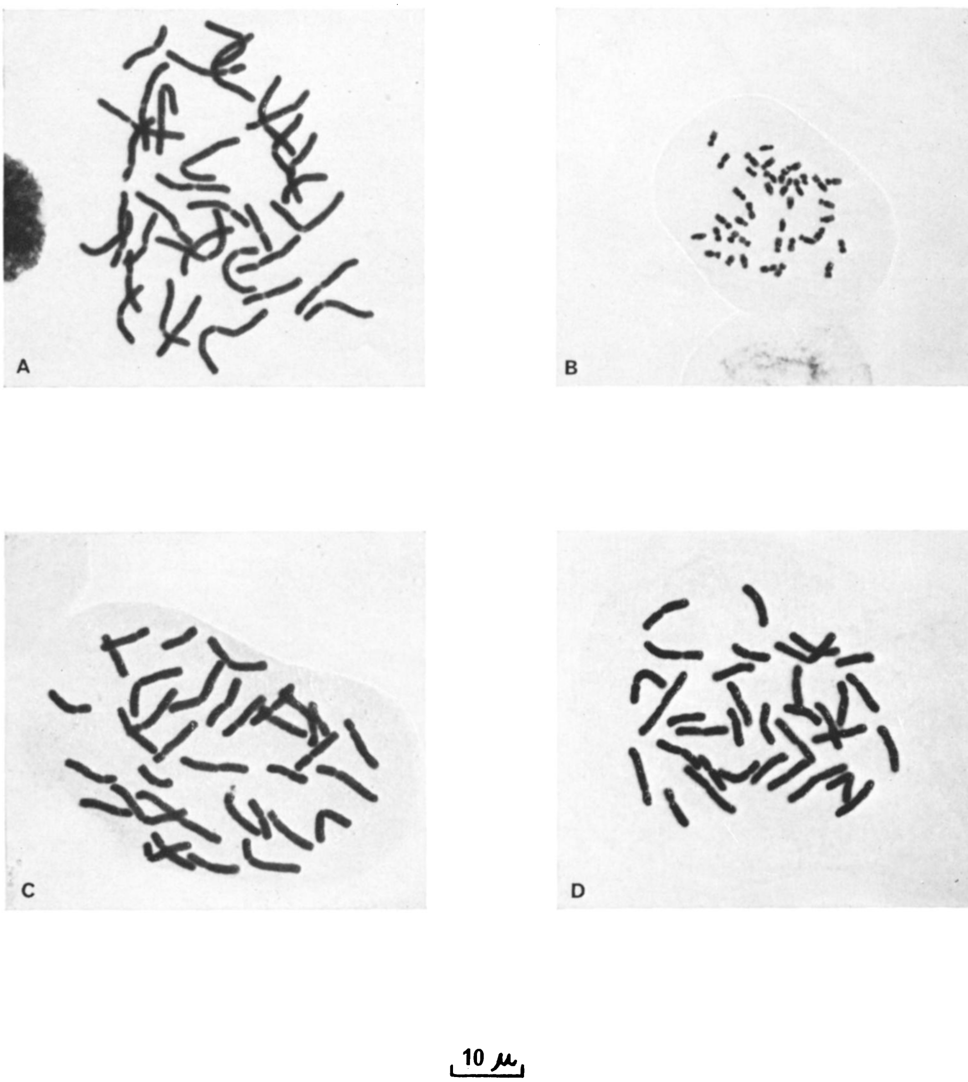
FIG. 1. Mitotic chromosome complements in some *Araceae*. **A,** *Acorus calamus* (2n = ca. 36); **B,** *Lysichiton americanum* (2n = 28); **C,** *Orontium aquaticum* (2n = 26); **D,** *Spathiphyllum wallisii* (2n = 30); **E,** *Anthurium microphylla* (2n = 30 + 1f); **F,** *Urospatha* sp. (2n = 52).

PLATE 14



Somatic chromosome complements from root tips in the tribes *Spathiphylleae*, *Anthurieae*, *Dracontieae* and *Lasieae*. **A,** *Spathiphyllum* × *hybridum*, 69.791 (2n = 30); **B,** *Anthurium signatum*, 68.1642 (2n = 30 + 1f); **C,** *A. harrisii*, 69.103 (2n = 30 + 5f); **D,** *Symplocarpus foetidus*, 69.456 (2n = 60); **E,** *Urospatha sagittifolia*, 68.1411 (2n = 52).

PLATE 15



Somatic chromosome complements from root tips in the tribes *Stylochitoneae*, *Pothoeae* and *Colocasieae*. **A,** *Microculcas marattioides*, 69.785 (2n = 34); **B,** *Arophyton humbertii*, 70.64 (2n = 38); **C,** *Gonatopus boivinii*, 70.27 (2n = 34); **D,** *Zamioculcas zamiifolia*, 70.30 (2n = 34).

counts of $2n = 44$ by Larsen (1969) for *Acorus calamus* in Thailand and by Ito (1942) for *A. asiaticus* Nakai apparently have a distinct basic number of $x = 11$.

Oronteae

A specimen of *Lysichiton americanum* Hulten & St. John had $2n = 28$ small chromosomes (Fig. 1/B) in agreement with the $2n = 28$ report of Löve & Kawano (1961). In contrast in the same tribe, *Orontium aquaticum* L. (Fig. 1/3) has $2n = 26$ and large chromosomes agreeing with Cave (1967). However, Delay (1951) reports $2n = 24$, and Huttleston (in Darlington & Wyllie, 1955) $2n = 28$.

Spathiphylleae

Three species of *Spathiphyllum* Schott and a hybrid have chromosome numbers based on $x = 15$, all with $2n = 30$ medium-sized chromosomes (Fig. 1/D, p. 202) except the tetraploid *S. floribundum* (Linden & André) N. E. Br. with $2n = 60$. The hybrid, *S.* $\times$ *hybridum* N. E. Br., also has $2n = 30$ (Plate 14/A) but its parental species were not available for examination and comparison. An interesting and distinctive cytological feature in *Spathiphyllum* is the pericentric region of heterochromatin in several chromosomes of the complement (Plate 14/A). Such pericentric heterochromatin has been reported in the insect, *Drosophila* (Hannah, 1951) but is not commonly so clearly visible and this is the first example observed in the *Araceae.*

Anthurieae

The genus *Anthurium* Schott clearly has a base number of $x = 15$, usually with $2n = 30$ or $2n = 60$ small chromosomes. However, there are two species (*A. gracile* (Rudge) Lindl. and *A. scolopendrinum* (W. Ham.) Kunth) with $2n = 40$. There are also two polyploids with $2n =$ c. 124 ($x = 15$), *A. lucidum* Kunth and *Anthurium* sp., not previously recorded. The most extensive list of previous chromosome counts is that of Gaiser (1927) who cites approximate counts for about 37 species, all of them based on $x = 15$. In addition to their counts of $2n = 30$ and 60, Sharma & Bhattacharya (1966) cite two species with $2n = 28$, but their poor karyotype illustrations cast doubt on the accuracy of these numbers. Other authors cite $2n = 34$ (Mookerjea, 1955) for *A. crystallinum* Linden & André and *A. signatum* C. Koch & Mathieu and $2n = 24$ (Pfitzer, 1957) for *A. scandens* (Aubl.) Engl. Such aneuploid variation is almost certainly due in this case to the presence of B-chromosomes, ranging from 1 to 5 in number, which I have recorded in five species with $2n = 30$ chromosomes (Plate 14/B & C and Fig. 1/E, p. 202) and in one $2n = 60$ species. However, in the two species recorded as $2n = 40$ there is no evidence for the presence of B-chromosomes and the basic number difference seems to be a shift in the A-chromosome complement, possibly an upward trend to $x = 20$.

Dracontieae

Two of the four tribal genera had their chromosomes counted. *Dracontium foecundum* Hook. f. had $2n = 26$ medium sized chromosomes, no previous counts being available for comparison. *Symplocarpus foetidus* (L.) Salisb. has two previously recorded ploidy levels with numbers of $2n = 30$ (Ito, 1942) and 2n = 60 (Mulligan, 1965). My own result of 2n = 60 small chromosomes (Plate 14/D) verifies the higher level of polyploidy already recorded in the northern collection of Mulligan (*l.c.*).

Lasieae

Only two of the seven genera in this largely tropical tribe were studied. Two accessions of *Cyrtosperma johnstonii* (Bull) N. E. Br. had 2n = 26 small chromosomes in accord with a previous count of 2n = 26 for *C. senegalense* (Schott) Engl. by Mangenot & Mangenot (1962). These indicate a basic number of x = 13, a base which appears again in *Urospatha* Schott in two species, *U. sagittifolia* (Rodsch.) Schott and *Urospatha sp.* both with 2n = 52 medium sized chromosomes (Plate 14/E and Fig. 1/F). No previous counts are available.

Tribe not specified by Hutchinson (1959)

A relatively recently described genus, *Microculcas* Peter had a chromosome count showing 2n = 34 large chromosomes in *Microculcas marattioides* Peter (Plate 15/A). This is an interesting link with the 2n = 34 large chromosomes in *Zamioculcas* Schott (Plate 15/D), with which there is considerable morphological affinity.

Additional results throughout the family

During the course of this long-term survey a number of counts have accumulated for additional species not already included in earlier papers of the series. They are presented in Table 2 and discussed below.

Pothoeae

Pothos chapelieri Schott from Madagascar has 2n = 24 small chromosomes with a base number of x = 12. This is in accord with 2n = 24 in *P.* aff. *scandenti* L. reported previously (Marchant, 1970).

Calleae

Pycnospatha soerensenii S. Y. Hu has 2n = 26 (x = 13). This is a very different basic number from the only other member of this tribe, *Calleae*, which, in *Calla palustris* with 2n = 72 (Marchant, 1970), has x = 9 (or possibly 6).

Stylochitoneae

Some members of this group of genera from tropical Africa and Madagascar, were discussed in Paper 1. Further counts for *Arophyton tripartitum* Jumelle and *A. humbertii* Bogner, are 2n = 38 with small chromosomes (Plate 15/B) indicating a secondary basic number of x = 19. This basic number was also recorded in *A. tripartitum* previously with 2n = ca. 76 (Marchant, 1970), but it is not in agreement with 2n = 40 (x = 10 or 20) in *A. buchetii* Bogner (Marchant, *l.c.*). There may well be simple duplication (tetrasomy), or two B-chromosomes in the latter species, but this has not been established. It is of interest that two other genera of the tribe, *Carlephyton madagascariense* Jumelle with 2n = 108 (Marchant, 1970), *C. glaucophyllum* Bogner with 2n = 54 (Table 2) and *Colletogyne perrieri* Buchet have a base of

TABLE 2. Additional counts from tribes covered in earlier parts (Marchant, 1970, 1971a, 1971b and 1972).

Tribe **Pothoeae**										
Pothos chapelieri Schott	677.67	70.958	Madagascar, *Bogner* s.n.	24	12	S				
Tribe **Calleae**										
Pycnospatha soerensenii S. Y. Hu	094-71-01039	71.1584	Thailand, Makam Village, Makam-Dist. Province Chantaburi, *Bogner* 395	26	13	?		26	Larsen	Unpub.
Tribe **Stylochitoneae**										
Arophyton tripartitum Jumelle var. *tripartitum*	129.69 00982	69.714	Madagascar, Presqu 'Ile de Masoala, Mont Ambato, *Bogner* 272	38	19	S	*A. rhizomatosum* (S. Buchet) Bogner	38	Kress in Bogner	1972
A. humbertii Bogner	639.69 .5825	70.64	Madagascar, 38 Reserve Naturelle No. 12 (Massif du Marojezy), *Bogner* 163	38						
A. crassifolium (Buchet) Bogner (*Humbertina crassifolia* Buchet)	639.69 .5826	70.63	Madagascar, Massif de l'Ankarana, 20–30 m. (type locality), *Bogner* 278	54	9					
Colletogyne perrieri Buchet	711.67	69.96	Madagascar, Montagne des Français, *Bogner* 165	54	9					
Carlephyton glaucophyllum Bogner	719.67	69.658	Madagascar, Reserve Naturelle No. 12, Massif de l'Ankarana, *Bogner* 167	54	9	S	*C. diegoense*	c. 108	Kress in Bogner	1972
Zamioculcas zamiifolia (Lodd.) Engl.	630.67	70.30	Tanzania, limestone formation between Kange & Amboni (Tanga Prov.) *Bogner*, s.n.	34	17	L				
Zamioculcas zamiifolia (Lodd.) Engl.	494.67	70.28	Usambara mountains, Tanzania, *Bogner*, s.n.	34						
Tribe **Dieffenbachieae**										
Gonatopus boivinii (Decne.) Hook. f.	301.68	70.27	Tanzania, near Kwamtili, East Usambaras, *Bogner* 219	34	17	L				
Tribe **Colocasieae**										
Xanthosoma brasiliense (Desf.) Engl.	797.58	69.97	Dominica, *Campbell*	26	13	M				
Tribe **Areae**										
Arum cyrenaicum Hruby			Cyrenaica, Gebel Akhdar, *L. Boulos*	56	7	S				

$x = 9$ but it would be premature to suggest, without further research that the $x = 19$ of most *Arophyton* species is in some way derived from a combination of $x = 10$ as in *A. buchetii* and $x = 9$ in related *Carlephyton*. Further study is needed in this group.

Two further counts of $2n = 34$ in *Zamioculcas zamiifolia* (Lodd.) Engl. confirm my earlier citation for this genus (Marchant, 1970). *Microculcas marattioides* described above with a closely similar karyotype and the same chromosome number, appears to be closely related on this basis and should be included in the same tribe. In the same way *Gonatopus boivinii* (Decne.) Hook. f. with $2n = 34$ large chromosomes (Plate 15/C) and *Heterolobium petiolulatum* Peter cited previously (Marchant, 1971a) seem to belong in the *Stylochitoneae* and not the *Dieffenbachieae*.

A count of $2n = 54$ was reported previously (Marchant, 1972) for *Humbertina crassifolia* Buchet. Bogner (1972) has decided to move this species to the genus *Arophyton* as *A. crassifolium* (Buchet) Bogner. This involves a change of tribe, for the genus *Humbertina* was placed in the *Areae* by Hutchinson (1959). This change is in better agreement with the basic number of $x = 9$ which, though rare in the *Areae* (only *Typhonium* and a few *Cryptocoryne* spp.), is common in the *Stylochitoneae*. However, at the generic level the switch to *Arophyton* does introduce yet another basic number ($x = 9$) to an already confused mixture of $x = 19$ and $x = 10$ or 20 (Marchant, 1970). It seems to me that $2n =$ c. 76 in *A. tripartitum* Jumelle is $x = 19$, in accord with *A. humbertii* and *A. rhizomatosum*. This is probably a secondary basic number derived at some point in evolution from combining $x = 9$ with $x = 10$ in other species.

Colocasieae

The count of $2n = 26$ for *Xanthosoma brasiliense* (Desf.) Engl. accords with my earlier report of $2n = 26$ for three other species of the genus (Marchant, 1970).

Areae

A specimen of *Arum cyrenaicum* Hruby from Cyrenaica has $2n = 28$ small chromosomes in accord with the basic number ($x = 7$) of my previous counts for the genus (Marchant, 1972) and with those of other authors.

Discussion

In this final chapter of this series tabulating mitotic karyotypes and basic numbers in the *Araceae* I intend to make some attempt to relate the cytological data to existing taxonomic classifications. It is impossible without a specialist knowledge to suggest profound changes in arrangement, though these may well be necessary in this poorly understood family. Instead I will indicate instances where widely separated genera have similar karyotypes or where cytological data support or contradict changes suggested by taxonomists.

I would first like to correct a misconception in Paper 1 (Marchant, 1970) where I erroneously concluded that *Scindapsus pictus* Hassk. ($2n =$ ca. 110) had a base number of $x = 10$. This is a poor numerical interpretation of the facts. In accord with chromosome data from other sources cited in that paper it now seems much more likely that the base number is x = 7 and the specimen of *S. pictus* with 2n = ca. 110 would then be 16-ploid.

In the *Richardeae*, the genera *Nephthytis* Schott and *Anchomanes* Schott, both with 2n = 40, have extremely similar chromosome size and karytotype agreeing with Hutchinson's classification. However, it seems much more logical to separate *Homalomena*, again with x = 10 but with small chromosomes, as Engler (1920) has done.

The genus *Protarum* Engl. in the *Areae*, with 2n = 28 seems to relate chromosomally to *Alocasia* Neck. (2n = 28) in the *Colocasieae*, as Bogner (unpublished) suggests on morphological grounds.

As has already been mentioned above, the genera *Zamioculcas* and *Gonatopus* are separated by Hutchinson in the *Stylochitoneae* and *Dieffenbachieae* respectively, while *Microculcas* was not placed by him in a tribe; yet each has x = 17 large chromosomes and closely similar karyotypes. So far, in Hutchinson's *Dieffenbachieae*, *Dieffenbachia* Schott is the only other genus recorded with x = 17 and is clearly not closely related morphologically to *Gonatopus*. It therefore seems logical to remove *Gonatopus* from the *Dieffenbachieae* and put it with *Microculcas* and *Zamioculcas*. These three would fit best in Engler's subfamily *Pothoideae*, tribe *Zamioculcaseae*.

From the chromosome data cited in this paper, and from the conclusions of Bogner (personal comm.) it appears that *Zamioculcas*, *Gonatopus* and *Microculcas* should be removed as a group from the *Stylochitoneae* as defined by Hutchinson (1959), while *Humbertina* must be included in the genus *Arophyton* and in the tribe *Arophyteae*; the latter genus seems misplaced in the *Stylochitoneae* by Hutchinson. Several of the genera now included by him in the *Stylochitoneae* were not known at the time of Engler's publication (1920) and have since been assigned to the tribe *Arophyteae* Lemée (formerly *Synandrodieae* Buchet). The *Arophyteae* would fit neatly next to the *Stylochitoneae* of Engler's subfamily *Aroideae*.

It is clear that neither of the major classifications of the *Araceae* are adequate to circumscribe the family. Whereas Hutchinson's treatment of the family is too simple, with too many genera lumped into too few groups at the tribal level, Engler (1920) goes to the opposite extreme with a breakdown into many small and diversified units. However, Engler's system, using floral characters, vegetative morphology and anatomy as criteria, was much more broadly based than that of Hutchinson who relies solely on floral structure. This is borne out also by the comprehensive pollen morphological study of Thanikaimoni (1969) which also supports Engler's system.

Amongst the chromosomal information accumulated in this investigation there is much diversity; yet extreme assymetry (telocentrics) is absent and strict metacentrics are rare. On the basis of the kind of karytotypes encountered in those genera contrasted by taxonomists as primitive or derived it is hard to formulate any obvious evolutionary trends. This inadequacy of chromosome information serves only to emphasize our present-day lack of knowledge of chromosomes as evolutionary indicators over a broad spectrum of genera, as for example in a family.

Some insight can be gained from the consecutive organization of the basic numbers of the various genera, as indeed has already been done by Larsen (1969) using the data available at that time. Now that just over 50 per cent. of the genera of the *Araceae* have been studied cytologically I agree with Larsen (*l.c.*) that x = 7 is the most common basic number. This is followed

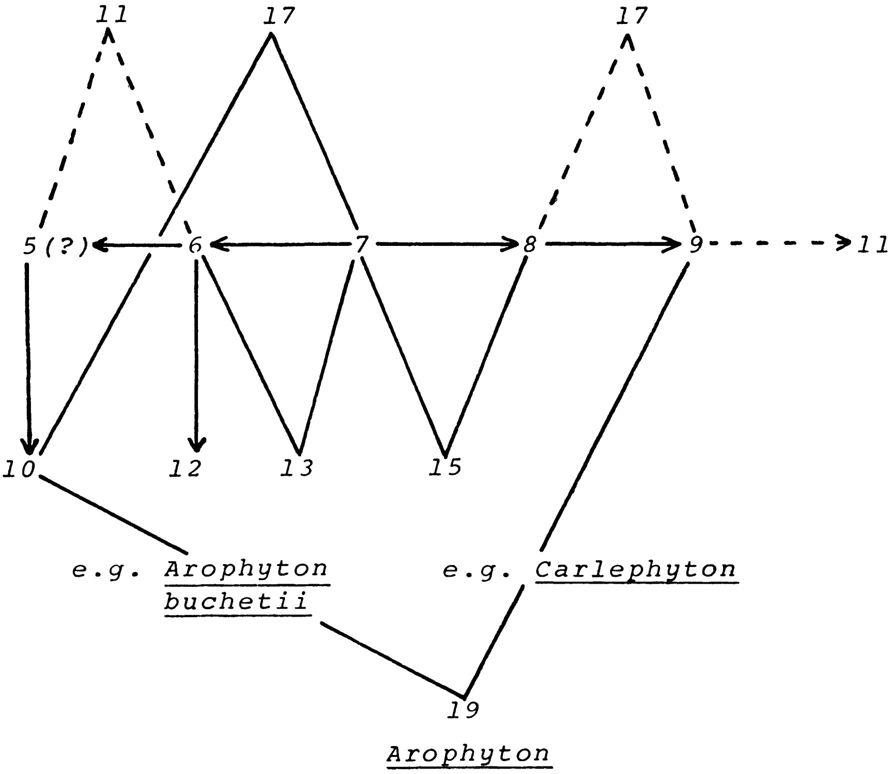


FIG. 2. Possible basic number relationships and direction of their evolution in the *Araceae*. Dotted lines indicate very uncertain derivations.

in frequency by x = 13. My diagram in Figure 2 (above) reflects the considerations of Larsen for basic number evolution in *Araceae*, while at the same time I have incorporated several higher, secondary, basic numbers. The relationships suggested are only tentative and some alternatives are indicated by broken lines.

Obviously my own survey of Araceous chromosomes, despite its range, is incomplete in terms of coverage of the whole family and in terms of representation within some individual groups. Nevertheless, it has helped to resolve differences in chromosome numbers published by previous authors and gives no support to the claims of widespread intraspecific and intraplant aneusomaty and aneuploidy by A. K. Sharma and his associates (Sharma & Das, 1954; Mookerjea, 1955; Sharma & Mukhopadhyay, 1965; Sharma & Bhattacharya, 1966). I believe this contribution of chromosome numbers to be important in fostering a deeper knowledge of the family through a cooperative multidisciplinary approach. It is intended to encourage a wider interest in, and investigation and interpretation of the phylogeny and evolution of the *Araceae*.

ACKNOWLEDGEMENTS

The technical assistance of Miss C. A. Brighton and the photographic processing of the illustrations by Mr. T. Harwood is gratefully acknowledged.

I would also like to thank Mr. J. Bogner for his continuing interest in this work and for supplying plant material, and Dr. L. Boulos for the material of *Arum cyrenaicum* Hruby.

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