STATISTICAL ANALYSIS OF BILATERAL SYMMETRY
IN PLANT ORGANS

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SUMMARY. Certain organs of several species of plants express bilateral symmetry. An attempt is made to understand the laws operating in the expression of this kind of symmetry and the relationship between the substructures.

1. INTRODUCTION

As Sinnott (1937) puts it '...morphology, far from being the hopelessly static discipline which some would have us believe, therefore, touches so intimately the central problem of biology that it may still be described by Darwin's words, in a famous passage of the 'Origin' as the 'very soul' of natural history'. Further, morphology does not end with the presentation of facts in the form of data as is common today, but our task is to gain knowledge of those laws which are operative in the structure and behaviour of the various members of plant kingdom.

The aim of the present studies is to assess the totality of structures relating to plant organs, to find suitable classification for them and to test statistically the various hypotheses regarding their occurrence in Nature. A broader aim envisaged is to explore the relationship between the important characteristics like yield, colours and the classified structures, and to find the selection process of structures by Nature. Further questions of interest would be to create artificially the possible structures and study the relationship between yield and structure.

In this paper observations on clockwise and counter-clockwise situations, i.e. left- and right-handedness of plant organs in a few species are described. Many of these variations were not known till recently. It is worth mentioning that none of these observations demanded the use of any serious equipment, not even a hand lens.

2. PRESENTATION OF DATA

In this section the various situations in plant organs where bilateral symmetry occur are explained. Data on brief or continuous observations made on the members of a few families are also presented.

2.1. *Morphology of asymmetry in plant organs.*
Asymmetry in morphological structures is expressed in certain organs of many plant species. In this report, those situations where the asymmetry is manifested in the two complementary forms (bilateral symmetry) by identical organs of individual plants of the same species alone are considered. The proportions of such left-handed and right-handed leaves, flowers, stems, tendrils or fruits within a plant may be 1 : 1 as is the case observed in a majority of species, or may occur in different ratios.

In most plant species where the leaf arrangement is alternate, the single foliar spiral perceivable can be regarded as running clockwisely (left-handed) or counter-clock-

wisely. In grasses and some species of the family Scitamineae, though a single leaf is formed at each node, the leaves do not show a spiral mechanism. But they fall one over another in two vertical rows, which arrangement is known as distichous. In bananas, the two rows of leaves move spirally and both the spirals in all the known species and varieties of banana move counter-clockwisely. But in some Agavaceous species like *Cordyline rubra* where the foliar spirals (two per shoot) move either clockwise or counter-clockwise, both the kinds of shoots can be usually seen with in a plant. In most palms, the leaves are arranged in single, two, three, five or more numbers of spirals. Strikingly, the leaves of some individuals of each species veer clockwisely and the others counter-clockwisely (Davis, 1962a, 1964a, 1971a). The leaf-blade (lamina) while in bud rolls margin to margin in some families, and the rolling may take place along the upper surface (convolute) or lower surface (revolute). In most grasses, while the lamina of one leaf convolutes clockwisely, the next one moves counter-clockwisely, and this pattern is repeated continuously. But in Scitamineae and Araceae, the individual plants of many species do not show a regular pattern although their laminas convolute. However, in *Scindapsus officinalis*, the laminas exhibit not only clockwise and counter-clockwise convolution, but also another situation of involution (Davis, 1970). In *Cordyline rubra*, there exists a correlation between the direction of foliar spiral and the convolution of the lamina (Davis and Ghosh, 1969). In palm leaves, the numbers of leaflets on linear halves differ. In most pinnate type of palms, this difference between halves is statistically significant. In left-spiralled palms, the left half of the leaves bears more leaflets, and vice versa in right-spiralled palms (Davis, 1971b; Davis, et al, 1971). A similar situation is observable with the numbers of spines on the leaf margins of both the types of young *Agave sisalana* plants (Mitra, 1968).

Most (perhaps all) members of Malvaceae (Davis, 1964b), and Bombacaceae (Davis, 1966, 1967; Davis and Kundu, 1965; Davis and Ghosh 1970) and some of Sterculiaceae, Tiliaceae, Cochlospermaceae, Euphorbiaceae, Caricaceae, Linaceae, Plumbaginaceae, Theaceae, Palmae, Tropaeolaceae, Rutaceae and Oxalidaceae show bilateral symmetry of flowers. In a flower, all the petals twist (contort) clockwisely or counter-clockwisely. While in most species, the petals form a single rotating whorl, in the multipetalled variety of *Hibiscus rosasinensis* (Davis and Ghoshal, 1965) and some species of *Camellia*, there are five spirals of petals, all twisting one way or the other. This situation is like the arrangement of leaves in the Spiral Aloe (Koflor, 1965).

The fibres of a few species of plants move spirally. Some individuals of the same species have their fibres twisting clock-wisely and the others counter-clockwisely. While in the coconut the two kinds of palms occur fairly equally (Potch, 1911), in chestnut trees, a great majority of individuals twist counter-clockwisely (van Oye, 1926).

In some xerophytes, the individual stems veer either clockwisely or conversely. Thus, in *Euphorbia antiquorum*, the stem has three wings (or rarely four), and it twists either to the left or right. From each node, usually three off-shoots are produced which in turn show spiral mechanism. Some of these off-shoots twist like that of the

trunk, and the rest differently (Davis, 1968). In another species, *Euphorbia neriifolia*, there are five ridges and at each node it produces 0-5 off-shoots. Here again some off-shoots move like that of the trunk and the others unlike it. A somewhat similar condition exists in many plants with alternate phyllotaxy.

In the flowers of *Crescentia alata*, a peculiar variation was noticed. A flower has normally 5 stamens at five fixed positions. After examining over 75,000 flowers of a particular tree at Calcutta, it was found that at each position one of the four possibilities occurred : a fully developed stamen, a staminode, a stamen fully fused with the corolla, or nothing at all. Thus, 1025 forms are possible of which only 105 could be symmetrical forms, and the rest comprised pairs of mirror image forms. Usually the number of flowers falling under one type equalled more or less that of its mirror image form.

2.2(a). *Floral asymmetry* : *Malvaceae*. Of the two Deccan hemp flowers shown in Fig. 1, the one on the left has its petals twisting clockwisely (left-handed). When viewed apically, the inner margin of the petals of a left-handed flower curves
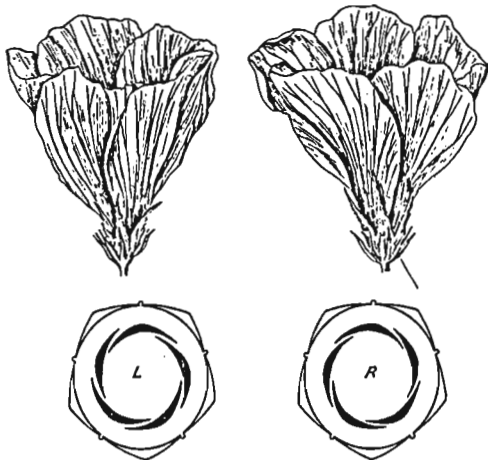

Fig. 1. Left and right-twisting flowers of Deccan hemp.

clockwisely towards the periphery. In the right-handed flower, the petals curve counter-clockwisely. Often it is possible to determine the spirality of a flower by examining a single petal. According to Rendle (1959), there exists a positive cor-

relation between the asymmetric nature of a petal and twisted aestivation. In *Sida cordifolia*, each petal shows two distinct steps at the distal margin, the half that moves out first is always shorter than the other. While in *Thespesia populnea* the stigmatic end twists in accordance with the aestivation of the corolla, in *Hibiscus rosasinensis*, the monadelphous staminal tube shows clear twisting, by which the spirality of the flower can be determined.

Available flowers from 463 plants of 34 species of the family Malvaceae were examined for their aestivation (Davis and Selvaraj, 1964) and the data presented in Table 1.

TABLE 1.   AESTIVATION OF FLOWERS OF MALVACEOUS SPECIES

species	no. of plants	petal-twist		$L+R$	χ^2
		left	right		
1. *Abutilon hirtum*	12	1301	1371	2672	1.8336
2. *Abutilon indicum*	9	315	222	537	16.1061
3. *Abutilon megapotamicum*	2	29	31	60	0.0667
4. *Abutilon ochenii*	1	2	4	6	0.6667
5. *Achania conzeitii*	2	168	156	324	0.4444
6. *Althaea rosea*	39	1445	1414	2859	0.3361
7. *Gossypium anomalum*	1	7	3	10	1.6000
8. *Gossypium arboreum*	5	683	649	1332	0.8679
9. *Gossypium barbadense*	26	663	627	1290	1.0047
10. *Gossypium davidsonii*	1	13	16	29	0.3103
11. *Gossypium herbaceum*	3	8	6	14	0.2857
12. *Gossypium hirsutum*	14	397	391	788	0.0457
13. *Gossypium laitense*	3	8	6	14	0.2857
14. *Gossypium thurberi*	1	3	0	3	3.0000
15. *Gossypium sp. (wild)*	2	62	67	129	0.1938
16. *Hibiscus cannabinus*	89	876	891	1767	0.1273
17. *Hibiscus esculentus*	60	255	254	509	0.0020
18. *Hibiscus hirtus*	6	30	34	64	0.2500
19. *Hibiscus indicus*	1	18	19	37	0.0270
20. *Hibiscus mutabilis*	4	72	84	156	0.9231
21. *Hibiscus rosasinensis*	55	16871	16047	32918	20.6263
22. *Hibiscus schizopetalus*	2	17	10	27	1.8148
23. *Hibiscus sabdariffa*	93	567	574	1141	0.0429
24. *Hibiscus tiliaceus*	3	291	300	591	0.1371
25. *Hibiscus tortuosus*	1	81	80	161	0.0062
26. *Hibiscus tricuspis*	1	14	13	27	0.0370
27 *Hoheria lvalli*	1	3	6	9	1.0000
28. *Malachra capitata*	6	8892	8883	17775	0.0046
29. *Malvastrum sp.*	2	27	32	59	0.4237
30. *Pavonia cari*	5	104	92	196	0.7347
31. *Pavonia odorata*	2	3	13	16	6.2500
32. *Sida cordifolia*	23	3187	3049	6236	3.0539
33. *Thespesia populnea*	6	2282	2394	4676	2.6826
34. *Urena lobata*	2	118	117	235	0.0043
total	463	38812	37855	76667	65.1951

2.2(b). *Bombacaceae*. The family Bombacaceae was formerly included under Malvaceae (Hooker, 1872). The 13 species of this family examined in India showed the two kinds of twisting of the corolla. The data relating to 41, 470 flowers are presented in Table 2.

TABLE 2. LEFT- AND -RIGHT TWISTING FLOWERS OF BOMBACACEAE

| species | no. of plants | aestivation of corolla | | | χ^2 |
		left	right	$L+R$	
Adansonia digitata	5	213	204	417	0.1942
Bombax anceps	2	93	94	187	0.0053
Bombax ceiba	27	19664	18826	38490	18.2448
Bombax insignis	2.	46	28	74	4.3784
Ceiba pentandra	8	804	771	1575	0.6914
Ceiba rosca	1	30	28	58	0.0690
Chorisia insignis	1	49	48	97	0.0103
Pachira acquatica	1	83	102	185	1.9510
Pachira cyathophora	2	87	78	165	0.4909
Pachira insignis	1	11	14	25	0.3600
Pachira longifolia	1	36	32	68	0.2353
Pseudobombax grandiflorum	1	27	39	66	2.1818
Salmalia insignis	2	39	24	63	3.5714
total	54	21182	20288	41470	32.3842

$$\chi_1^2 = 19.2726; \quad \chi_{12}^2 = 13.1116$$

2.3. *Euphorbia antiquorum*. The stem of a particular variety of *Euphorbia antiquorum* screws clockwisely or counter-clockwisely, and on account of this screwing habit perhaps this plant is called by the Tamils as "thirikalli" meaning the twisting cactus (Fig. 2). 1,500 main stems were examined at Coimbatore in January 1965 for

Fig. 2. Right- and left- spiralling stems of *Euphorbia antiquorum*.

their spirality. Two percent of these stems reversed from one direction to the other, a tenth of which reversing twice (left to right and again back to left) as may be seen from Table 3.

TABLE 3. *EUPHORBIA ANTIQUORUM* : NATURE OF MAIN STEM

type of stem-twist	observed	percentage
Left-handed	748	49.867
Right-handed	722	48.133
Left turned to right	20	1.333
Right turned to left	7	0.467
Left to right to left	3	0.200
Right to left to right	—	—
total	1500	100.000

50.88 per cent of the regularly twisting stems are thus, left-handers.

A further 200 main stems were collected at random from an adjoining locality. A stem had either three or four wings at the 'internodal' region. Of these plants, 58 bore four wings and the rest three each. The stem usually produces one off-shoot each from a wing from an 'internodal' region, and thus a four-winged stem may have four off-shoots. But this number may be reduced to 3, 2, 1 or nil. Similarly, a three-winged stem may have 3, 2, 1 or no off-shoots. Stems having no off-shoot were excluded. Very rarely a wing may produce more than one off-shoot. In Table 4, details are given on the number of off-shoots produced from the 200 main stems.

TABLE 4. *EUPHORBIA ANTIQUORUM* : NO. OF OFF-SHOOTS PER MAIN STEM

main stem	4-winged stems nos. of off-shoots					3-winged stems nos. of off-shoots				
	spiral no.	4	3	2	1	total	4	3	2	1	total
left	117	22	10	5	—	37	1	51	24	4	80
right	83	12	8	—	1	21	—	43	15	4	62
total	200	34	18	5	1	58	1	94	39	8	142

Like the main stems, the off-shoots also show bilateral symmetry by twisting either clockwisely or conversely. A smaller percentage of these off-shoots, however, did not show any twisting and they were accounted for as neutrals. 572 off-shoots were examined from the 200 plants and their spirality recorded. The data are given in Table 5.

TABLE 5. *EUPHORBIA ANTIQUORUM* : NATURE OF OFF-SHOOTS OF 200 PLANTS

main stem	off-shoots								
	left		right				neutral		
	total	%	total	%	total	%	total	total	%
left	243	71.27	72	21.11	26	7.62	341	100.00
right	66	28.57	145	62.76	20	8.67	231	100.00
	309	54.02	217	37.94	46	8.04	572	100.00

To examine whether the twisting of the off-shoots depends on that of the main stem, the data are split up for the 4-winged shoots and 3-winged shooots as seen in Table 6.

Table 6 : *EUPHORBIA ANTIQUORUM* : ASYMMETRY OF OFF-SHOOTS IN RELATION TO KIND OF MAIN STEM

spiral of main stem	off-shoots	nature of off-shoots			
		left	right	neutral	total
4-winged off-shoots (Total 198)					
	observed	100	16	12	128
left	percentage	78.13	12.50	9.38	100.00
	% on all shoots	29.32	4.69	3.52	37.53
	observed	13	47	10	70
right	percentage	18.57	67.14	14.29	100.00
	% on all shoots	5.63	20.35	4.33	30.31
3-winged off-shoots (Total 374)					
	observed	143	56	14	213
left	percentage	67.14	26.29	6.57	100.00
	% on all shoots	41.94	16.42	4.11	62.47
	observed	53	98	10	161
right	percentage	32.92	60.87	6.21	100.00
	% on all shoots	22.94	42.42	4.33	69.69

2.4. *Euphorbia neriifolia.* Fig. 3 shows two stem pieces of *Euphorbia neriifolia*, each beset with five rows of spines, the rows running right-handed in one and left-handed in the other. The stem grows in stages, and off-shoots are produced at the junction of the stem formed during different seasons, and such a junction simulates a node.

Off-shoots ranging from 0-5 are produced from each node. However, it may be mentioned that there is a bud in the axil of every leaf or leaf scar, and very occasionally some off-shoots are also produced from these 'extra-nodal' regions of the stem.

The main stem continues to grow, generally maintaining the original direction of twisting throughout. Exceptional shoots showing reversal of stem-twist were excluded. All the off-shoots from a 'node' do not necessarily show the same kind of spirality. An off-shoot of the first order usually maintains the spirality thereafter even though it may produce shoots of the second and further orders having different spirality.
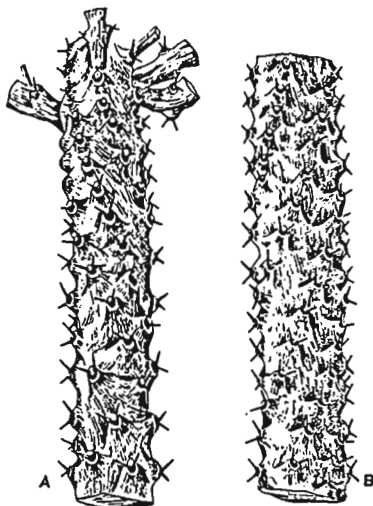
Fig. 3. Left- and right-spiralling stems of *Euphorbia neriifolia*

At the Central Arecanut Research Station, Vittal, Mysore, 36 different plants of *E. neriifolia* were observed in 1965 for the spirality of their off-shoots, and the data are presented in Table 7.

It may be seen from the data that 19 of the 36 plants bore excess left-handed off-shoots, 8 equality and 9 excess right-handed ones. On the totals, the left-handeds form 52.89 per cent, but the deviation from equality is not statistically significant, $\chi^2_{35} = 12.591$.

At Khandwa, Madhya Pradesh, 246 main stems of *E. neriifolia* each having a 'node' producing off-shoots ranging from 0-5 were examined. Of these, 140 or 56.91 per cent were left-handeds.

2.5. *Linum usitatissimum*. Linseed (*Linum usitatissimum*) is an economically important plant since its seeds yield the linseed oil, and the bast yields the fibre known as flax fibre of commercial importance.

TABLE 7. *EUPHORBIA NERIIFOLIA* : LEFT- AND RIGHT-
HANDED SHOOTS PER PLANT

plants	off-shoots				
	L	R	L+R	L−R	χ^2
1	10	10	20	—	—
2	19	15	34	4	0.471
3	9	8	17	1	0.059
4	4	5	9	− 1	0.111
5	6	6	12	—	—
6	15	14	29	1	0.034
7	11	10	21	1	0.048
8	6	8	14	− 2	0.286
9	10	9	19	1	0.053
10	8	5	13	3	0.692
11	12	7	19	5	1.316
12	8	8	16	—	—
13	9	8	17	1	0.059
14	11	6	16	5	1.470
15	10	5	15	5	1.667
16	11	6	17	5	1.470
17	9	9	18	—	—
18	21	14	35	7	1.400
19	9	8	17	1	0.058
20	12	13	25	− 1	0.040
21	6	9	15	− 3	0.600
22	8	5	13	3	0.692
23	6	3	9	3	1.000
24	5	7	12	− 2	0.333
25	6	4	10	2	0.400
26	4	3	7	1	0.143
27	6	7	13	− 1	0.077
28	6	5	11	1	0.090
29	2	4	6	− 2	0.666
30	7	7	14	—	—
31	1	3	4	− 2	1.000
32	5	5	10	—	—
33	3	3	6	—	—
34	14	17	31	− 3	0.290
35	6	6	12	—	—
36	16	15	31	1	0.032
	311	277	588	34	14.557

% lefts = 52.89 $\chi_1^2 = 1.966$ $\chi_{35}^2 = 12.591$

The primary stem continues to grow till it flowers when it produces a few
flower-bearing lateral shoots. But at an early stage, it produces a good number of

off-shoots almost from its base (Fig. 4). The single foliar spiral of the main stem can be determined from the leaves or the starting positions of the first-order off-shoots.
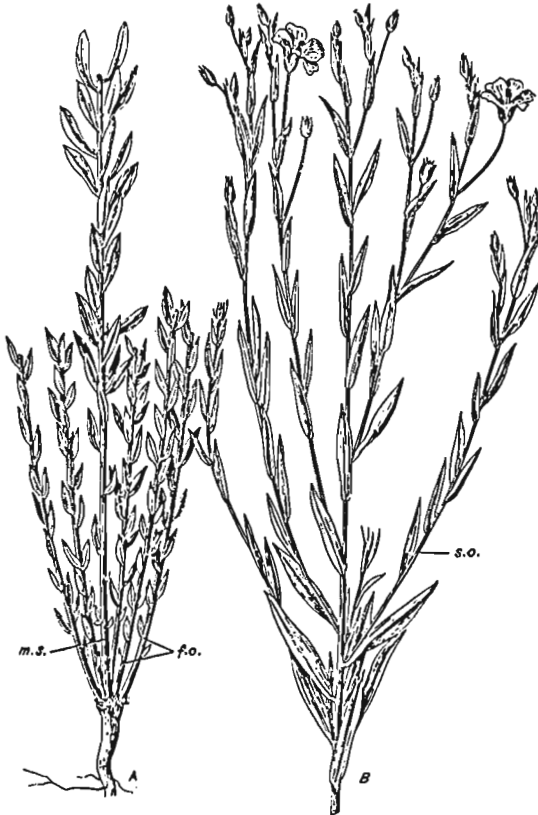

Fig. 4. Lower part of a plant (A) and a flowering shoot (B) of Linseed plant.

The off-shoots grow almost as fast as the primary stem and produce lateral flowering shoots at their apices. The spirality of the first and second order off-shoots was also determined. The number of fruits borne by each off-shoot was counted. In Tables 8 and 9, the data on the numbers of first order and second order off-shoots of 22 left-spiralled and 19 right-spiralled plants are given.

TABLE 8. *LINUM USITATISSIMUM* : FOLIAR SPIRAL OF MAIN STEM AND OFF-SHOOTS

(Main stem—Left-spiralled)

plant	spiral	I order branch	II order branch L	II order branch R	total	plant	spiral	I order branch	II order branch L	II order branch R	total
1	L	L	4	1		11	L	L	2	7	
		L	2	3				L	2	4	
		R	4	4				L	1	5	22
		R	1	4		12	L	L	2	3	
		R	2	3				R	2	3	
		R	3	5				R	3	2	15
		R	2	3	41	13	L	L	2	3	
2	L	L	4	2				L	2	3	
		L	2	3				L	3	3	16
		L	4	2		14	L	L	2	3	5
		R	2	3	22	15	L	L	2	4	
3	L	L	4	3				L	3	2	
		L	2	3	12			R	4	1	
4	L	L	2	3				R	2	3	21
		R	3	2		16	L	L	2	4	
		R	1	4				L	2	5	
		R	1	4	20			R	3	4	
5	L	L	3	3				R	5	4	29
		L	5	2		17	L	L	2	3	
		R	4	2				R	2	1	
		R	3	3				R	3	2	14
		R	2	3		18		L	3	5	
		R	3	2				L	1	4	
		R	2	3				R	2	3	
		R	3	2	46			R	2	3	23
6	L	L	1	5		19	L	L	4	2	6
		R	2	3	11	20	L	L	2	5	
7	L	L	4	4				L	2	3	
		L	3	2	13			R	2	3	17
8	L	L	1	4		21	L	R	1	4	
		L	1	4				R	3	2	10
		R	3	2	15	22	L	L	4	2	
9	L	R	2	3				L	2	4	
		R	2	3	10			R	2	3	
10	L	L	2	4				R	2	3	22
		L	2	4							
		L	5	3							
		R	3	2							
		R	3	3	31				**187**	**234**	**421**

main stem L = 22

I order off-shoots L = 38; R = 36 (total 74)

II order off-shoots L = 187; R = 234 (total 421)

TABLE 9. *LINUM USITATISSIMUM* : FOLIAR SPIRAL OF MAIN-STEM AND OFF-SHOOTS

(Main stem right-spiralled)

plant	spiral	I order branch	II order branch L	II order branch R		plant	spiral	I order branch	II order branch L	II order branch R
1	R	L	2	3		11	R	L	8	6
		R	4	1				L	2	3
		R	3	2	15			L	2	4
2	R	L	3	4				L	3	3
		L	1	4				R	4	5	40
		R	4	1		12	R	L	3	2
		R	1	5	23			R	4	2
3	R	R	2	3				R	2	3
		R	3	2	10			R	4	3	23
4	R	R	4	4		13	R	L	3	2
		R	2	3	13			L	3	3
5	R	L	3	3				R	3	3
		R	3	3				R	2	3	22
		R	2	3	17	14	R	R	3	2
6	R	L	4	4				R	3	2	10
		R	3	5		15	R	R	2	3
		R	5	1				R	2	4	11
		R	7	3		16	R	L	3	2
		R	4	4				L	3	4
		R	6	5	51			L	2	3
7	R	L	3	2				L	3	3
		L	2	3				R	3	4
		R	4	1	15			R	3	2
8	R	L	3	3				R	3	3
		R	2	3	11			R	3	2	52
9	R	L	1	4		17	R	R	2	3	5
		L	2	3		18	R	R	2	4	6
		R	4	3		19	R	L	3	2
		R	3	1				R	3	3
		R	2	3				R	3	2	16
		R	3	2	35						
10	R	L	3	2						
		L	1	4						
		R	4	4						
		R	3	2	23						

200   108

main stem R = 19;

I order off-shoots L = 24, R = 43; (Total 67)

II order off-shoots L = 200, R = 108 (Total 308).

2.6. *Cordyline rubra*. *Cordyline rubra* of Agavaceae has alternate leaves which are arranged in two spirals veering either to the left or to the right (Fig. 5).

Within a plant, the two types of spirals are usually seen on different shoots. The leaf blade shows clear convolution before unfolding, and this rolling may be clockwise or counter-clockwise (Davis and Ghosh, 1969).
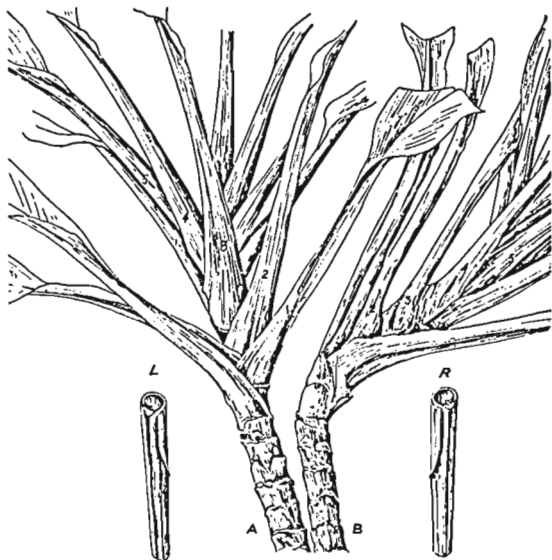

Fig. 5 Left- and right- handed shoots of *Cordyline rubra.*

43 shrubs of *Cordyline rubra* grown at the premises of the Indian Statistical Institute were examined in 1966 for the foliar arrangement in all their shoots. From 37 shoots of some of these plants, the convolution of the lamina of 519 leaves produced between September 1964 to April 1965 was recorded to find out whether the direction of convolution corresponded with the direction of the foliar spiral or not. 16 of the 37 shoots bore left-handed foliar spirals, and the rest, right-handed ones. The data are presented in Table 10.

TABLE 10. *CORDYLINE RUBRA* : FOLIAR SPIRAL AND PTYXIS

plant	shoot	spiral	convolution of consecutive leaves																						total L	R
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	L	R
I	1	R	L	L	R	R	L	R	L	R	R	R	R	R	L	R	R	R	R	R	R	R	R	L	L		7	17
	2	R	R	R	R	R	R	L	R	R	R	R	R	R	L	R	L	R	R	R	R	R	R	L			4	20
	3	R	R	R	R	R	L	R	R	R	L	R	R	R	R	R	R	L	R	R	R	R	R	L	L		5	17
	4	R	R	L	R	R	R	R	R	R	R	L	R	R	R	R	R	R	R								2	17
	5	R	R	L	L	L	R	R	L	R	R	R	R	R	L	L	R	R	R	R	R	R	R	R			6	18
	6	L	L	L	L	L	L	L	R	L	L	L	L	L	L	L	L	L	L	L							19	1
	7	L	R	L	L	L	L	L	R	R	L	L	L	L	L	L	L	L	L	L	L						18	3
II	1	R	R	L	R	R	R	R	L	L	R	R	R	R	R	R	L	R	L	R	L						5	13
	2	R	R	L	L	R	R	L	L	L	L	L	L	R	R	R	R										8	8
	3	R	R	R	R	R	R	L	L	R	R	R	R	R	R	R	R										2	14
	4	R	R	R	R	R	R	R	L	R	R	R	R	R	R	R	R	R	R								1	17
	5	L	L	L	R	R	R	R	R	L	L	L	L	L	L													9	5
	6	L	L	L	L	L	L	R	R	R	R	R	R	L	L	L	L	R	R								9	10
III	1	R	R	R	R	R	L	R	R	L	L	L	L	R	R													5	8
	2	R	R	L	R	R	R	R	R	L	L	R	R	L	L	R	R	R	R	R	R						6	15
	3	L	R	L	L	L	L	L	R	R	R	R	L	L	L	L	L										11	6
	4	L	L	L	L	L	L	R	R	L	L	L	L	L	L	L											12	2
	5	L	R	R	L	L	L	L Flowered																			4	2
	6	L	R	R	L	L	L	L	L	L	L	L	L	L	L												11	2
IV	1	R	R	R	R	R	L	L	R	R	R																2	8
	2	R	R	R	R	R	L	R	L	R	R	R	R														2	9
	3	R	R	R	R	R	L	R	R	R	R																1	8
	4	L	R	L	L	L	L	L	R	L																	6	2
	5	L	L	L	L	L	L	L	L	L																	9	—
	6	L	L	L	L	L	L	L	L																		8	—
V	1	R	L	R	R	R	R	R	L	R	R																2	7
	2	R	R	R	R	R	R	R	R	R	R																—	10
	3	L	L	L	L	L	L	L	L	L	L	L															11	—
	4	L	L	L	L	L	L	L	L	L	L																10	—
	5	L	L	L	L	L	L	L	L	L	L																10	—
	6	L	L	L	L	L	L	L	L	R	L	L															10	1
VI	1	R	R	R	R	R	R	R	L	L	R	R	L	R	R												3	10
	2	R	R	R	R	R	L	R	R	R	R	R															1	10
	3	R	R	R	R	R	R	R	R	R	R	R	R	R	R												—	13
	4	R	R	R	R	R	R	R	R	R																	—	9
	5	L	L	L	L	L	L	L	L	L	R	L	R														9	2
VII	1	R	R	R	R	R	R	R	R																		—	8

227 292
=519

21R+16L = 37

Plants I-III observed from 10.9.1964 to 9.4.1965

Plants IV-VII from 11.9.1964 to 31.12.1965.

2.7. *Scindapsus officinalis.* The leaves of *Scindapsus officinalis*, a tropical ornamental plant, are alternate and often arranged distichously. When young, the lamina rolls in one of three ways—two types of convolution (as in *Cordyline rubra*), and involution, where the two halves of a lamina roll along opposite directions over the upper surface (Fig. 6). The leaf sheath also overlaps one way or the other. Where the lamina rolls left-handed, the leaf sheath of the same leaf overlaps right-handed, and vice versa, if the lamina is right-handed. But when the lamina is involute, the sheaths of some leaves roll left-handedly and the others right-handedly.

R   I   L
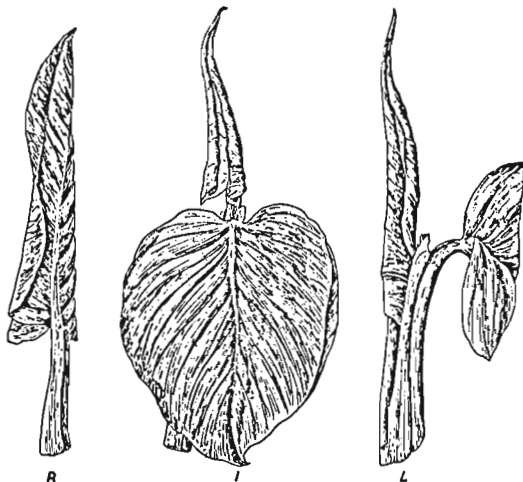
Fig. 6. *Scindapsus officinalis* leaves showing right-handed (R), involute (I) and left-handed (L) rolling of lamina.

50 shoots from three large *Scindapsus officinalis* plants creeping on mango trees at the premises of the Indian Statistical Institute were labelled and the type of ptyxis on the 627 leaves produced on them during 75 days commencing from the first of May 1965 were observed. The data are presented in Table 11.

Plant 3 produced equal numbers of lefts and rights while for plants 1 and 2, the lefts are more although the differences are not statistically significant. The occurrence of involute leaves seems to vary from plant to plant, plant 1 having the

273

TABLE 11. *SCINDAPSUS OFFICINALIS* : PREFOLIATION.
(L = Left, R = Right, I = Involute)

		L	R	I	total
Plant 1					
shoots	1 LRIIIIIIIIIIIIIIII I	1	1	18	20
	2 RLLRLR	3	3	—	6
	3 RIIILRLLIIRIIIIIL	3	3	10	16
	4 LILILLIIIIIIIIIRL	5	1	11	17
	5 LRLRLRLRRI	4	5	1	10
	6 RLRLILILILRLRIIIII	6	4	8	18
	7 LRIIILILIRLIIIL	5	2	9	16
	8 LRLRLIRIIIIILRIRL	5	5	7	17
		32	24	64	120
Plant 2					
	1 LRLLLLLRLRLRL	9	4	—	13
	2 RLRLILLRIILI	5	3	4	12
	3 LRLRLIIRLRLRRL	6	6	2	14
	4 LRLRLRLRLRLR	6	6	—	12
	5 LRLIILLRLRLRLR	7	5	2	14
	6 RLRLRLRLRIIII	4	5	5	14
	7 RLLLRLRLRLR	7	5	—	12
	8 RIILRIRLRIRILII	3	5	8	16
	9 LRLILILLILRLIIII	6	2	9	17
	10 RRLRLRLLL	5	4	—	9
	11 LRLRLRRIILIR	4	5	3	12
	12 LRLRLRLKLRLR	6	6	—	12
	13 LRLRL	3	2	—	5
	14 LIIRLRLILIIIIRRRLR	5	6	7	18
	15 LRLRIJLIILRLRLII	6	4	6	16
		82	68	46	195
Plants 3					
	1 LRLRLRLRLRL	6	6	—	12
	2 RLRIILRIIIIIJILRI	3	4	11	18
	3 LRLILRLRLRLRLRLR	8	7	1	16
	4 LLRILRLRLRLRLRL	8	6	1	15
	5 LRLRLRL	4	3	—	7
	6 LRLRRLRRLRRLRL	5	7	—	12
	7 RLRLRLRLRLR	5	6	—	11
	8 LLRLRLR	4	3	—	7
	9 LRLILRLIIRLRLI	6	4	4	14
	10 LRLRLILRRRIRIIRL	5	6	5	16
	11 LLRLILRRLILILRLRL	9	5	3	17
	12 LRRRLRLLRL	5	5	—	10
	13 RLRLRLRR	4	4	—	8
	14 RLRRIILRLI	3	4	3	10
	15 RLRLJLRLRLIRIRLII	6	6	5	17
	16 LRIIIIIIRJIIIRLR	2	4	9	15
	17 ILRIRLIIRILRLR	5	5	5	15
	18 LRLRLRL	4	3	—	7
	19 LRLRLRL	4	3	—	7
	20 RLRLILIRILIILRL	6	4	5	15
	21 LRLRLILRLL	6	3	1	10
	22 RRLRLRL	3	4	—	7
	23 RLRLRLRLRLRLII	6	6	2	14
	24 RLRLRLR	3	4	—	7
	25 RRRRLRRRIRIRL	3	2	2	13
	26 RRLRL	2	3	—	5
	27 RLRLLR	3	3	—	6
		127	127	57	311
	total for 3 plants	241	219	163	627

highest percentage (53.33%). Since the data were collected simultaneously from all the plants standing close to each other, one plant showing a very high percentage of involute leaves has to be regarded as a peculiarity of this individual plant.

2.8. *Arrangement of palm-perianth.* A palm flower usually possesses six perianth segments, generally all alike, which represent the sepals and petals of other flowers. The outer three segments may be called the sepals and the inner three, the petals. However, when the arrangement of the perianths of female flowers is carefully examined, it may be reasonable to consider that all the six perianth segments develop one after another forming a single spiral compressed into a whorl. In the female flowers of most species of palms, the aestivation of perianths vary considerably. When we consider the three inner perianths (petals), they either imbricate or twist regularly. In the imbricate flowers, one petal is completely exposed, the innermost petal is overlapped on both sides by the other petals. Thus the middle petal has its one half exposed and the other half overlapped by the outer petal. From the position of the exposed half of the middle petal, a flower may be regarded imbricate-right or imbricate-left (Davis and Kundu, 1966). Similarly, with the regularly-twisting corolla also, left-and right-handed types are observable (Davis, 1969b). Data on 9415 flowers from seven species of palms are presented in Table 12.

TABLE 12. AESTIVATION OF PETALS OF FEMALE FLOWERS IN 7 PALMS

species	corolla contorted		corolla imbricate		total
	lefts	rights	lefts	rights	
Areca catechu	320	275	1225	1219	3039
Areca triandra	9	6	182	206	403
Borassus flabellifer	25	38	143	143	349
Cocos nucifera	25	16	208	186	435
Phoenix paludosa	42	19	62	61	184
Phoenix sylvestris	384	253	1083	961	2681
Ptychosperma macarthurii	0	1	1195	1128	2324
	805	608	4098	3904	9415

It is obvious from data given in Table 12 that the left-handed flowers (left contortion plus left imbrication) are greater than the right-handed ones. The proportion of flowers having contorted corolla to those with imbricate corolla varies very greatly with species. The percetage of contorted flowers in *Areca triandra* was only 3.7, that in *Cocos nucifera* 9.4, *Borassus flabellifer* 18.0, *Areca catechu* 19.6, *Phoenix sylvestris* 23.8 and *P. paludosa* 33.7. In the case of *Ptychosperma macarthurii*, however, with the exception of a single flower, a population of 2,324 flowers had only imbricate corrolla.

When all the six perianth segments of a flower are considered as a single spiral as is more appropriate to do so since the individual members develop one after another, one may observe 14 different groups according to the way the margins of a perianth segment overlap. In one type, all the members twist regularly clockwise and in another, counter-clockwise. In the neutral patterns, the perianth cycles can be

divided into identical halves, one half exactly falling over the other half when folded along the diameter. Of the remaining patterns, two move clockwisely and the others counter-clockwisely. All these patterns are illustrated in Fig. 13 with the observed and expected frequencies inscribed for each perianth pattern.

3. Graph Theoretical Methods

Studies on the different morphological forms of plant organs described in the preceding sections lead to the combinatorial analysis of different possible structures of the same. These are facilitated by the use of one of the currently active fields of topology—'Graph Theory'. In this section a brief introduction to the theory as required for the present purpose is given and for other details the reader is referred to Berge (1962), Mac Mohan (1891), Polya (1962) and Ramanujacharyulu (1966).

3.1. *Graph Theoretic results*

3.1.1. A graph G is defined by a set X of points (n in number) and a set U of some pairs (m in number) of points from X. Each point of X is called a vertex and each pair (of points) in U is called an edge.

Example 1 : $X : \{a, b, c, d\}$ $U : \{(a, b), (c, d) (a, c), (a, d)\}$
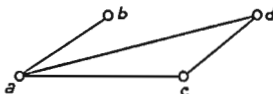
Fig. 7

The number m of edges can atmost be equal to $\frac{n(n-1)}{2}$. In a graph G, the vertices can be used to represent the locations or sites of interest in a flower and an edge corresponds to a particular situation between the two sites on the flower.

3.1.2. The complement $\overline{G}(X, U)$ of a graph $G : (X, U)$ is defined as a graph on the vertex set X, but an edge appears in $\overline{G}$ if and only if that edge did not appear in $G : (X, U)$.

Example 2 : For all our purposes we consider graphs on n vertices

$$a_i, \quad i = 0, 1, ..., (n-1) ;$$

and a set of edges which can be chosen from the following set

$$e_i = (a_i, a_{i+1}), \qquad i = 0, 2, ..., (n-1)$$

of edges, the suffixes being read under modulo n. These graphs are known as 'Restricted Random Graphs' under the assumption that a graph on these n vertices is chosen with the condition that a random number of edges e_i are randomly chosen from the set of n allowed edges of the polygon.
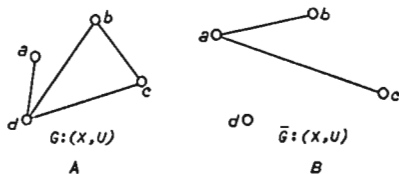
Fig. 8

3.1.3. Colouring.

3.1.3. *Colouring.* Let G be a polygon on n vertices. Let R be a set of s colours denoted by 1, 2, ..., s. A 'colouring' of the polygon is defined as assigning one and only one colour from the s colours to each edge independently. Thus there are s^n possible colourings.

3.1.4. *Cyclic rotation and patterns.* Consider a polygon G with vertices a_i, $i = 0, 1, ..., (n-1)$ and a colouring P_1 of its n sides. Let P_2 be another colouring of the polygon G. A 'cyclic rotation' of G is defined as a mapping of the vertices of the polygon G in which the vertex a_i is mapped to a_{i+j}; $i = 0, 1, ..., (n-1)$, where j is a fixed integer $0 \leqslant j \leqslant n-1$.

The two colourings P_1 and P_2 of G are said to be 'equivalent' of the same 'pattern' if given P_1 the colouring P_2 can be obtained by a cyclic rotation of the polygon.

Example 3 : Let G be a polygon of 4 sides and R a set of two colours black and white :
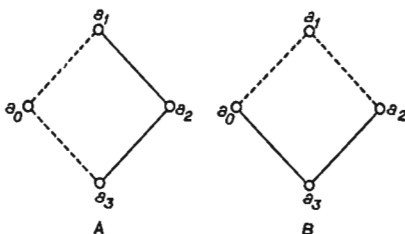
Fig. 9

In colouring P_1 by writing a_{i+1} in place of a_i we get colouring P_2. Thus, these are equivalent colourings or these are of same pattern. Two patterns are distinct if they are not equivalent colouring.

In other words, on a polygon a cyclic group is acting. One is interested in the number of distinct patterns. The solution is derived in Table 13.

TABLE 13. TABLE OF DISTINCT PATTERNS

s number of colours	polygon of n sides	3	4	5	6	7
	2	4	6	8	14	20
	3	11	24	51	129	315

The general formula for the number of distinct colourings to colour a polygon of n sides using s colours is as given below :

$$\frac{1}{n} (s^n + s + s + s^{d_2} + \ldots + s^{d_i} + \ldots + s^{d_{n-1}})$$

where d_i is the greatest common divisor between the integers n and i.

3.1.5. Evolution of restricted random coloured graphs : Now we consider the set of all possible coloured polygons which are s^n in number. Let all the graphs be given equal probability $\frac{1}{s^n}$ of being chosen. In other words consider the development of a coloured polygon by selecting a colour out of the s colours for each side with equal probability. After colouring all the n sides we say that a Restricted Random Coloured (RRC) graph has appeared. The probability that a particular pattern appears when an (RRC) graph is chosen can be computed by obtaining the number of members in that pattern class and multiplying it by $(1/s^n)$. This is obtained by Ramanujacharyulu (1966); however, it is given here for computational reference for values of $n = 3, 4, 5$ and 6 and $s = 2$.

A given pattern is an assignment of colours $1, 2, \ldots, s$ to the n cyclic edges $e_0, e_1, \ldots, e_{n-1}$. Hence let the pattern be represented by a cyclic sequence f of integers representing the colours on these edges in that order of the cycle edges. Let the sequence f be partitioned into $p(f)$ identical subsequences of length $l_{(f)}$ where $l = l_{(f)}$ is the least integer with this property. Then there are l equivalent colourings and the probability that an RRC graph is of observed pattern f is $l_{(f)}/s^n$.

Example 4 : $n = 4$ and 2 colours :
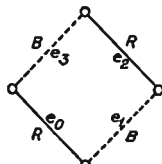
Fig. 10

In presenting the following patterns, only patterns with not more than $\binom{n}{2}$ edges in an n polygon are given as they can be obtained by complementation with respect to the polygon, the number of equivalent members in the corresponding complementary pattern classes are equal. A star on reference code denotes that the pattern is self-complementary.

A pattern $C_{n,m}$ with $P(n)$ equivalent members has a complementary pattern $\overline{C}_{n,n-m}$ and the same number $P(n)$ of equivalent members.

3.1.6. *RC-Patterns*: Consider once again the set of s^n possible coloured polygons of n sides in s colours.

In the above sections two colourings are said to be of the same pattern if one coloured polygon can be obtained by a cyclic rotation of the other coloured polygon.

However, this equivalence of two colouring can be defined in any required manner. In the foregoing examples as will be explained, we need the following definition of equivalence as well in case of two colourings.

The case of a polygon whose sides are coloured using two colours only in the same is that of a Restricted graph on the n cyclic vertices in which some of the cyclic edges appear (i.e. sides of one colour) and the others (sides of the other colour) do not appear.

These 2^n restricted graphs are derived from the coloured polygons. Two such graphs are said to be RC-equivalent if one graph can be obtained from the other by a cyclic rotation (R) or if one graph is complement of the other with respect to the polygon.

One is interested in the number of graphs which are not RC-equivalent. Let us call them 'RC-patterns'. The general formula for RC-patterns is not yet obtained and it is evaluated here for $n = 6$ as it is of immediate application. A self-complementary RC-equivalent pattern is called a 'neutral pattern' whereas among two RC-equivalent patterns other than self-complementary graphs, a classification of patterns into 'right' and 'left' is made in the following section viz., 3.2.2.

3.2. *Graph-theoretic approach for morphological studies*. Now we give below graph theoretic description of some of the morphological asymmetry mentioned in Section 2, which with the help of results of Section 3.1 is used to test various statistical hypotheses on the appearance of different structures in Section 4.

3.2.1. Let us consider *Euphorbia antiquorum* and *E. neriifolia* discussed in Sections 2.3 and 2.4. These can in general be described as follows. There are n rows of spines spiralling either to the right or left and at a branching point there are n buds and each bud may or may not develop into a full branch again. First of all one is interested in the total number of patterns and the various possible plant structures. For this purpose let us construct a graph whose vertices $a_0, a_1, ..., a_{n-1}$

TABLE 14. PATTERNS AND NUMBERS OF EQUIVALENT NUMBERS

PATTERN = P					$n = 3$
REFERENCE CODE = R	$c_{3,0}$	$c_{3,1}$			
NUMBER OF EQUIVALENT MEMBERS = $P(n)$	1	3			

P					$n = 4$
R	$c_{4,0}$	$c_{4,1}$	$c_{4,2}^{I}$	$*c_{4,2}^{II}$	
P(n)	1	4	4	2	

P					$n = 5$
R	$c_{5,0}$	$c_{5,1}$	$c_{5,2}^{I}$	$c_{5,2}^{II}$	
P(n)	1	5	5	5	

$n = 6$

P					
R	$c_{6,0}$	$c_{6,1}$	$c_{6,2}^{I}$	$c_{6,2}^{II}$	$*c_{6,2}^{III}$
P(n)	1	6	6	6	3

P					$n = 6$
R	$*c_{6,3}^{I}$	$*c_{6,3}^{II}$	$*c_{6,3}^{III}$	$*c_{6,3}^{IV}$
P(n)	6	6	6	2

represent the n interrow sites of the n buds which are circular at a branching point. Place an edge $(a_i, a_{i+1}) = e_i$ if and only if the bud between the sides a_i and a_{i+1} develops into a full branch. Now it is clear that all possible structures of the plant correspond to the restricted random graphs discussed in Section 3.1. Hence if we assume that all possible structures have an equal probability of appearance, then the probability that a particular structure with reference to code $C_{n,e}^1$ appears when a single structure is observed is given by the number of members in its equivalence class divided by 2^n. Tables of the required patterns and numbers are given in Section 3.1 for $n = 3, 4, 5, 6$.

It may be noted that if a bud has several possible states of development (which need not be measurable on an interval scale but only can be identified) which can be labelled by numbers $1, 2, ..., s$, then any structure of the plant corresponds to a polygon of n sides in which a side is coloured j where j is one of s colours depending on the state of development. It may be of use to have tables for these patterns and their probabilities of appearance.
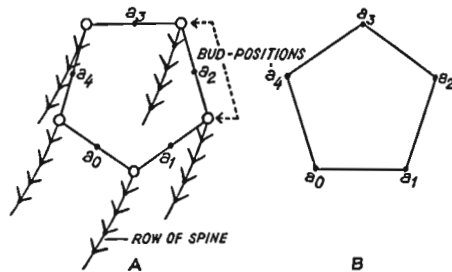

Fig. 11

3.2.2. Here we shall consider the arrangement of the perianth lobes of the areca fruits. As described in Section 2.8, each of these flowers has six perianths. On a fruit the two ends of a perianth lobe may be exposed, or only one end is exposed while the other is overlapped by an adjacent perianth, or else both the ends may be enclosed by the two neighbouring perianths. To understand the total number of patterns of development etc., we proceed as follows :

Consider the middle points of the perianths of a fruit. Let us construct a graph whose six vertices $a_0, a_1, a_2, a_3, a_4, a_5$ represent the six mid-points of the six perianths. Also choose a direction of orientation around the fruit, say, clockwise. An edge $(a_i, a_{i+1}) = e_i$ appears in the graph if and only if in the clockwise direction of movement the *second end of the perianth* whose mid-point is a_i is above *the first end of the perianth* corresponding to a_{i+1}. But the direction of orientation is arbitrary and

hence without insisting on the direction of orientation let us construct the graph. That is for a given fruit we follow either clockwise or counter-clockwise direction and for different fruits different directions of orientation can be used to draw the graph. Making the counting of structures independent of the direction of orientation brings us to consider two complementary patterns to be equivalent. Hence the number of distinct structures will be the number of RC-equivalent patterns studied in Section 3.1. As an example consider the following flower :

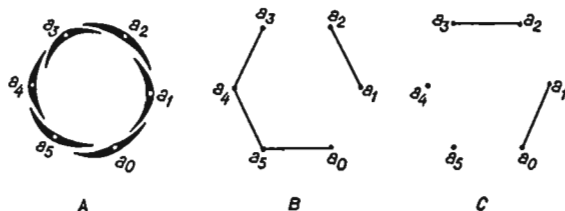*Example 5* : The two RC equivalent patterns arise because of two different orientations of the same flower in Fig. 12A.

Fig. 12

TABLE 15. TABLE OF RC-EQUIVALENT PATTERNS AND MEMBERS FOR $n = 6$

reference code	$C_{6\cdot0}$	$C_{6\cdot6}$	$C_{6\cdot1}$	$C_{6\cdot3}$	I $C_{6\cdot2}$	I $C_{6\cdot4}$	II $C_{6\cdot4}$	II $C_{6\cdot2}$	III $C_{6\cdot2}$	III $C_{6\cdot4}$
number of equivalent members	1	1	6	6	6	6	6	6	3	3

reference code.	I ${}^{\circ}C_{6\cdot3}$		II ${}^{\circ}C_{6\cdot3}$		III ${}^{\circ}C_{6\cdot3}$		IV ${}^{\circ}C_{6\cdot3}$	
number of equivalent members	6		6		6		2	

TABLE 16. LEFT, RIGHT AND NEUTRAL PATTERNS AND PROBABILITIES

pattern : classification	right	left	neutral
reference code	I $C_{6\cdot0}$; $C_{6\cdot1}$; $C_{6\cdot2}$; II III II $C_{6\cdot2}$; $C_{6\cdot3}$; $C_{6\cdot3}$;	I $C_{6\cdot6}$; $C_{6\cdot4}$; $C_{6\cdot4}$; II III III $C_{6\cdot4}$; $C_{6\cdot3}$; $C_{6\cdot3}$;	I $C_{6\cdot3}$; IV $C_{6\cdot3}$;
proportional probabilities	28	28	8

4. STATISTICAL ANALYSIS

In this section data on the morphology of various plant organs described under Section 2 are put to statistical analysis based on the theoretical results of Section 3. The tests are mainly to see whether a structure appears at random in nature, and on the inter-relationship of various organs of plants with regard to twisting (or coiling) and structure.

4.1. *Floral asymmetry in Malvaceae.* The null hypothesis taken is that the number of left- and right-handed flowers in each of the 34 species of Malvaceae is equal, the test statistic is $\frac{(L-R)^2}{(L+R)}$ which follows χ^2 with 33 d.f. under null hypothesis.

Of the 34 species, 19 have excess left-handed flowers, and of these, the χ^2 values for only three species show a significant difference from equality. None of the 15 species having excess right-handeds shows a significant difference. The χ^2 value for the overall population shows a significant difference from the expected even though the left-handeds form only 50.62 percent of the total flowers. This significance is brought about mainly by the figures for *Hibiscus rosasinensis* and *Abutilon indicum*. The former species alone accounts for 43.27 per cent of the total flowers studied, and the χ^2 value (20.6263) for this species largely affects the entire population, leading to a significant excess for the lefts. Ignoring this species, equality may be expected for the rest of the species. Since the excess of lefts over rights is persisting in the case of *H. rosasinensis* even with large samples, and during different seasons, this peculiarity requires to be investigated.

4.2. *Floral asymmetry in Bombacaceae.* Of the 41,470 flowers from the 13 species of Bombacaceae examined, 51.07 per cent were left-handed. But the difference between the two kinds of flowers is not statistically significant, the χ^2 value with 12 d.f. turning only to be 3.7562. However, the figures for *Bombax ceiba* show that this species produced significantly an excess of left-handed flowers like *Hibiscus rosasinensis* (Davis, 1966).

The data furnished in Tables 1 and 2 relating to the types of flowers in several species of Malvaceae and Bombacaceae discussed under the preceding two sub-heads are incomplete, since the recording of the individual flowers was not maintained in a chronological order which would have enabled to find out whether the time series would conform to the Bernoulli sequence, the lefts and rights being distributed randomly or not. This deficiency seems magnified when the data under Tables 10 and 11 are considered. However, while admitting that the data on floral asymmetry should have been more detailed, we do not consider that the detailed data would have shown a picture far different from what one expects in a Bernoulli sequence of trials. First of all, the data in Tables 1 and 2 relate to the arrangement of petals in the flowers of two specific families, while those in Tables 10 and 11 relate to the arrangement of leaves (on the stem) and the rolling of the immature laminae in two plants belonging to two far distant families. The parts of a flower and those of a leaf need not necessarily show similar phenomena. Further, from one of the species mentioned under Table 2 (*Ceiba pentandra*), the kind of twisting of flowers was recorded in the order of their occurrence on the several flower-bearing shoots. The data were plotted on a control chart for the proportions of the lefts. The control chart suggested that in the limited population sampled, the lefts and rights were about in equal numbers on each flower-bearing shoot (Davis and Kundu, 1965). In addition, all the flowers that bloomed in three large *Bombax ceiba* trees were examined during one season and their

twisting recorded. It was found that the lefts and rights were produced more or less in a 1 : 1 proportion throughout the blooming period (Davis, 1966). Thus, the nature of the data in Tables 1 and 2 seems to be unique.

4.3. *Euphorbia antiquorum*. Under the null hypothesis it is assumed that there is no dependence as regards the twisting between the main stem and off-shoots. Hence the following Table 17 gives the observed and expected value in a 2×3 table of main stem (L and R) against off-shoots (L, R and N). The symbol N denotes the neutral off-shoots which did not exhibit any twisting.

TABLE 17

| | main stem | off-shoots | | | total |
		L	R	N	
left	observed	243	72	26	341
	expected	184.21	129.37	27.42	
right	observed	66	145	20	231
	expected	124.79	87.63	18.58	
	Total	309	217	46	572

$\chi_5^2 = 18.76115 + 25.43766 + 0.07384 + 27.69520 + 37.55056 + 0.10900 = 109.62741$ i.e. the χ^2 value is very highly significant both at 5% and 1% levels, which clearly shows the dependence of the off-shoots on the main stem with regard to the screwing. Similar values for the data relating to the 4-winged stems and 3-winged stems as given in Table 6 were calculated and in each case the χ^2 value turns to be highly significant even at the 1 per cent level as shown below :

4-winged off-shoots $\chi^2 = 71.314$

3-winged off-shoots $\chi^2 = 147.984$

As may be seen below, with the limited data obtained on *Euphorbia neriifolia*, no serious resemblance of the main stem and their off-shoots was noticed with regard to the direction of twisting.

4.4. *Euphorbia neriifolia*. As has been mentioned in Section 3.2, the possible structures of this species with 5 buds correspond to Restricted Random Graphs on 5 vertices (Fig. 11). Table 18 gives the observed data and expected frequencies under null hypothesis that all structures are equally likely.

We shall test the hypothesis that there is dependency of the branches on the mainshoot with respect to twisting by exact treatment. The conditional probability distribution of the above table is 284!298!216!230!/514!174!124!110!100! This is cumbersome to evaluate and hence we use approximate χ^2 test using Yate's corrections.

$$\chi^2 = \frac{514(174.106 - 124.110) - \frac{1}{2} 514^2}{298.216.230.284} = 0.005550.$$

TABLE 18. *EUPHORBIA NERIIFOLIA* : NO. OF PLANTS
WITH GIVEN NUMBER OF OFF-SHOOTS

no. of off-shoots	no. of plants	expected frequency
0	16	7.594
1	30	37.970
2	52	75.940
3	54	75.940
4	30	37.970
5	11	7.594
total	243	243.008

χ^2 observed is 72.63. The upper 5% value of χ^2 with
5 degrees of freedom is 11.1 and is hence significant. Thus,
not all structures are equally likely for this species.

TABLE 19. *EUPHORBIA NERIIFOLIA* : LEFT-AND RIGHT-TWISTING PLANTS

no. of branches	left	expected frequency	right	expected frequency
0	9	4.218	5	3.374
1	41	21.090	39	16.872
2	30	42.180	22	33.734
3	33	42.180	18	33.734
4	16	21.090	19	16.872
5	6	4.218	5	3.374
total	135	134.976	108	107.960

1. Among the plants twisting to the left, χ^2 observed value is 32.21 and is significant
   enough to disprove the hypothesis that the number of branches is random or that
   all possible structures are equally likely.

2. Among plants twisting to the right, χ^2 observed value is 85.92 which is highly
   significant. Thus the data show that all structures are not equally likely.

   For the same species, Table 20 contains data on plants with 5 and 6 buds
   observed at Khandwa, Madhya Pradesh.

TABLE 20. *EUPHORBIA NERIIFOLIA* : RELATION BETWEEN
MAIN STEM AND OFF-SHOOTS

main stem	off-shoots		total
	left	right	
left	174	124	298
right	110	106	216
total	284	230	514

Table value at 5% level of χ^2 with 1 degree of freedom is 3.85 and hence the
observed χ^2 is not significant. Hence we cannot reject the hypothesis that the main
shoot and branches twist independently.

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4.5. *Linum usitatissimum* With *Linum usitatissimum*, no clear picture can be formed as to the dependence of the foliar spiral of the off-shoots with that of the primary stem. There is, however, a tendency for the first order off-shoots to show a preference to follow the foliar spiral of the primary stem. The second order off-shoots do not exhibit even this degree of affinity either with the first order off-shoots or with the primary stem.

4.6. *Scindapsus officinalis*. A perusal of the data given in Table 11 suggests that in the case of convolute leaves, there is a tendency for a leaf with left-handed convolution to be followed or preceded by one with right-handed convolution. To verify this, the type of each leaf in relation to its immediate older one was determined. The data are presented in Table 21.

TABLE 21. *SCINDAPSUS OFFICINALIS* : PTYXIS OF LAMINA

first leaf	second leaf			total
	left	right	involute	
left	20	155	44	219
right	150	21	34	205
involute	47	16	90	153
total	217	192	168	577

The hypothesis that the ptyxis of the first leaf and that of the second are statistically independent is rejected since the χ^2 value with 1 d.f. turns out to be 330.80. Therefore a left-handed lamina is generally followed or preceded by a right-handed one. However, in the case of involution, there is a greater chance for a leaf to be an involute if the immediate older one is already an involute. Data relating to the involutes were tested to see whether the involutes followed/preceded by a left-handed convolution were greater than those followed/preceded by a right-hander. It was found that the LI (left involute) or IL were occurring more frequently than the RI or IR, and statistically significantly. An involute leaf followed by another involute is significantly more than a left- or right-convolute leaf followed by an involute.

The state of the leaves of *Scindapsus officinalis* can also be represented by vertices 1, 2, ..., n on a line. Then join i to $i+1$ by an edge if i and $i+1$ are of different types of convolutions. Assuming that the convolution of a leaf is independent of the preceding or succeeding one, the null hypothesis becomes that all possible restricted graphs on these n labelled vertices on a line are equally likely and hence for a given graph the probability of its appearance can be evaluated. This work is deferred to a later paper.

4.7. *Arrangement of palm perianth*. Here let us consider the 316 fruits of *Areca catechu*. The possible arrangements of the six perianths are shown in Fig. 13 which give rise to the Restricted Random Graphs on six vertices described in 3.2.2.
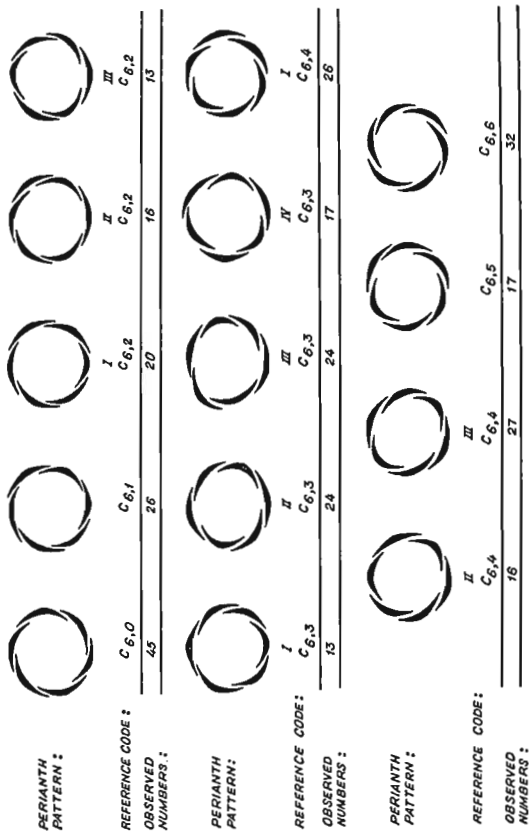
Fig. 13. The possible arrangements of the six perianth lobes in *Areca catechu* fruit.

Under the hypothesis that no specific pattern is preferred by Nature we obtain the expected numbers of observations as follows :

$$C_{6,0} \text{ and } C_{6,6} \qquad\qquad 4.83 \text{ each}$$

$$\left.\begin{array}{l} C_{6,1}; \ C'_{6,2}; \ C''_{6,2} \\[2pt] C'_{6,3}; \ C''_{6,3}; \ C'''_{6,3}; \ C''''_{6,3} \\[2pt] C'_{6,4}; \ C''_{6,4}; \ C_{6,5} \end{array}\right\} \qquad 25.98 \text{ each}$$

$$C'''_{6,3} \text{ and } C''''_{6,3} \qquad\qquad 14.40 \text{ each}$$

$$C'''_{6,3} \qquad\qquad 9.66$$

The χ^2 value computed as (observed—expected)²/expected summed over all patterns is 510.39 which is quite significant at 5% level compared to (22.36) the χ^2 value with 13 degrees of freedom. Hence in the course of evolution of perianths, certain structures are preferred by Nature. In another species of Areca (*A. triandra*) which has only 3.7 per cent fruits under the $C_{6,0}$ and $C_{6,6}$ perianth-combinations (Table 12), all patterns may occur as per expectation which would mean that no particular pattern is preferred by Nature. On the other hand, in *Ptychosperma macarthurii*, with only a single stray fruit under the patterns $C_{6,0}$ and $C_{6,6}$, a very strong preference for certain perianth-patterns is noticed.

However, proceeding further according to the left, right and neutral classifications of structure as shown in 3.2.2, the observed numbers of patterns are respectively 144, 142 and 30 and the expected frequencies are 138.25, 138.25 and 19.75 correspondingly.

The computed χ^2 value is 5.79 and the significant tabulated value for χ^2_2 being 5.99 at 5% we can reject the hypothesis that the occurrence of structures is in accordance with the above left, right and neutral classifications.

5. Some Results

Collection and analysis of data of even what appears to be very ordinary phenomena such as bilateral symmetry in plants are not without desirable results. Numerical methods, according to Sokal and Sneath (1963), may open up a wide field in the exact measurement of evolutionary rates and may provide a more critical approach to phylogenetic problems. Encouragingly, a great awareness for evolving numerical methods even in taxonomy is fast developing.

5.1. When we study the relationship of the foliar arrangement of different organs, we find considerable variation between species even very closely related to each other. Thus, the foliar spirals of the trunk and first-order off-shoots in *Prunus cerasus* are positively associated, and in *P. avium* they are negatively associated. But in *Prunus domestica*, no significant dependence was observed (Davis, 1969a). Evolutionary trait may also be attributable to certain situations concerning the aestivation of floral whorls, especially the petals and sepals. While in families like Malvaceae and Bombacaceae, the left- and right-handed flowers (according to aestivation

of petals) are randomly distributed, in some species of *Arenga* and *Caryota* where the flowers are arranged in clusters of three (a female flower is surrounded by two males on opposite sides), a clear pattern is present. The two male flowers in a cluster have their sepals arranged in mirror image forms. The same is the situation with the males of all clusters. The female flower may either be a left-hander or a right-hander, but in a left-spiralled spike, majority of the female flowers are right-spiralled, and vice versa in a right-spiralled spike as evidenced from data given in Table 22 relating to *Caryota mitis* (Mitra, 1968).

TABLE 22. *CARYOTA MITIS* : AESTIVATION OF SEPALS OF FLOWER-CLUSTERS

spirality of spike	aestivation of flowers			total
	male	female	male	
	RLL		RRL	
left	6		50	56
,,	17		39	56
,,	13		42	55
	36		131	167
right	44		17	61
,,	33		8	41
,,	46		10	56
	123		35	158
Total	159		166	325

5.2. While plants with a particular type of morphological structures are favoured with greater productive capacity than those having different structures has been demonstrated with the coconut where the leaves are arranged in five spirals running either clockwise or counter-clockwise in a palm. The left-spiralled palms in certain plantations in India, the Pacific Is. and Tanzania produce more fruits than the right-spiralled ones (Davis, 1962b, 1963, 1964c) even though the foliar asymmetry is not genetically determined. With *Vigna sinensis* which always moves counter-clockwise, the reversed vines produced more fruits than the normal ones (Reber, 1960, 1964; Davis and Mitra, 1968).

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