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ENANTIOMORPHIC STRUCTURES IN THE ORNAMENTAL PALM *PTYCHOSPERMA MACARTHURII* (H. WENDLAND) NICHOLSON (ARECACEAE)

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ABSTRACT

The phyllotaxis in *Ptychosperma macarthurii*, as typical of palms, is alternate which leads to clockwise or counter-clockwise arrangement of leaves in its crown. Being a clustering palm, shoots with clockwise and counter-clockwise crowns are distributed randomly within any large clump of *P. macarthurii*. Because of the spiral phyllotaxis, the leaf becomes asymmetric, and on an average, a leaf from clockwise palm bears 8·81% more leaflets on its left half as compared to those on the right half. Similarly, a palm with counter-clockwise foliar spiral has on the right half of leaf, 8·28% leaflets in excess of that on the left half.

Clockwise and counter-clockwise spadices and spikes can also be distinguished. There is a positive association between the spirality of the spike and that of the spadix. Flowers are distributed on the spikes as triads, one female between two males. The three flowers stand in a line at right angles to the spike. Perianth can be easily distinguished into sepals and petals. The sepals of the male flower on the left of a cluster has always counter-clockwise aestivation and those of the male on the right has clockwise aestivation. But the arrangement of sepals of the female flowers positively associates with the spirality of the spike on which they are borne. Calyx and corolla in the female flowers imbricate oppositely in over 95% of the cases.

INTRODUCTION

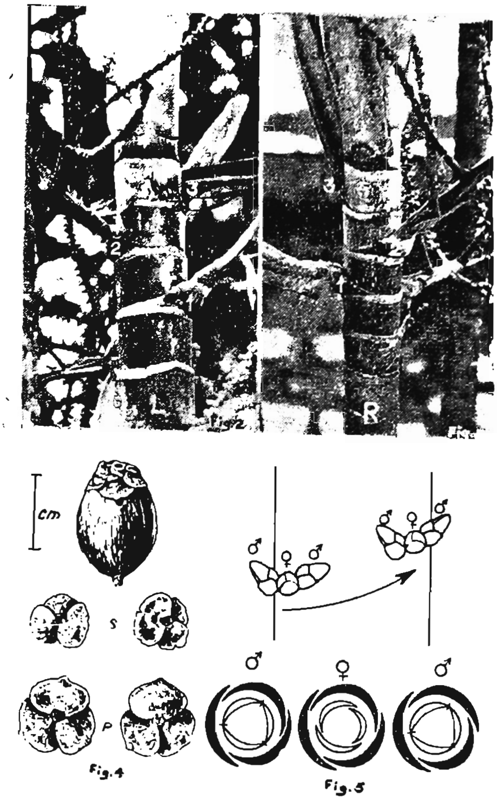
Ptychosperma macarthurii (H. Wendland) Nicholson is an elegant clustering palm (Fig. 1) of Malayan region. The biology of this ornamental and tub-plant has not been investigated adequately even though some less important species have been studied in detail (Bailey, 1939; Beccari, 1918; Murty and Bavappa, 1960; Nambiar, 1954; Tomlinson, 1971; Tomlinson and Moore, 1968; Uhl, 1966; Uhl and Moore, 1973). A critical study of the morphology of *P. macarthurii* has shown the existence of mirror-image patterns in some of its organs. As for example, the male and female flowers are distributed on the flowering spikes in triads, each comprising two males bordering a female. The flowers in a cluster lie in a line at right angles to the spike. One of these males has clockwise aestivation (imbrication) of calyx and the other has counter-clockwise imbrication. Such an enantiomorphic situation is noticed uniformly in all triads of all spikes of every shoot examined. Similar bilateral symmetry has been discovered in the foliar arrangement, in the forms of lamina, spadix, spikes, and in the arrangement of flower-triads. The data are summarised below.

MATERIALS AND METHODS

Phyllotaxis of palms is alternate (Blatter, 1926; Corner, 1966; Hartley, 1967; Menon and Pandalai, 1958; Moore, 1961; Patel, 1938; Tomlinson, 1961, a, b), and any two successive leaves in a crown are produced at a deflection approximating to the Fibonacci angle (Davis, 1971 a). This leads to the formation of foliar spirals. If the younger of any two consecutive leaves stands nearer to the older one by the left side, the foliar spirality of such a crown is regarded as clockwise, and if the younger leaf is nearer by the right side, the crown is counter-clockwise (Davis, 1971 b). Since the spadices indicate the former positions of shed leaves, the two kinds of crowns can be also made out from the positions of spadices (Figs. 2 and 3).

The various shoots in a clump of *P. macarthurii* do not show the same type of foliar spiral, and so the clockwise and counter-clockwise shoots of a few clumps were recorded. As a consequence to the spiral arrangement of leaves, each lamina has

FIG. 1. Clump of *Ptychosperma macarthurii* bearing several suckers of various heights, × ·04.



FIGS. 2–5. Clockwise and counter-clockwise shoots of *P. macarthurii*, × 2, and aestivation of perianth.

FIG 2. Consecutive spadices stand closer to each other by the clockwise direction. Four consecutive spadices are numbered.

FIG. 3. Four consecutive spadices (numbered) remain close to one another counter-clockwisely.

FIG. 4. Mature fruit, calyx of three imbricating sepals (s) and corolla of three imbricating petals (p).

FIG. 5. Semi-diagrammatic view of portion of right-twisting spike showing two triads and partial diagrams of female and male flowers.

turned asymmetric bilaterally, and the number of leaflets on one half differs from that on the other half (Davis *et al.*, 1971). One clockwise and one counter-clockwise shoots each from six clumps were marked, and 6–8 leaves from each shoot lopped. Leaflets on each half of leaves were recorded separately. From the spiral arrangement of spikes on the peduncle, two types of spadices can be recognised. Similarly, from the spiral arrangement of flower-clusters on spikes, two kinds of spikes become distinguishable. Several spadices were examined for recording these peculiarities. The six perianth members are easily distinguishable into calyx and corolla (Fig. 4). In female flowers, both the whorls imbricate, and in male flowers, the calyx imbricates while the corolla remains valvate. Where the calyx/corolla imbricates, the outermost sepal/petal remains fully exposed and the innermost one is overlapped on either side by the other two members. The middle member has one half exposed while the other half is overlapped by the outermost member. The direction of imbrication of the flower is determined according to the overlapping of the exposed half of the middle sepal/petal (Davis and Basu, 1971). The illustrations in Fig. 5 explain this further. Although the aestivation of calyx of male flowers is pre-set according to its position in the cluster, that of female flowers shows a different picture. The perianth arrangement of male as well as female flowers of several spadices of many palms was observed.

Results

In young clumps of *P. macarthurii,* it is easy to make out the mother shoot from suckers. Accordingly, nine clockwise and four counter-clockwise mother plants, each producing 3–8 suckers were examined for the numbers of the two types of shoots. Out of a total 63 suckers, 29 (or 46·03%) were clockwise. The difference between the two types is not statistically significant. However, the data are not sufficiently large to give importance to the results.

Asymmetry of Leaf :

On one half of the lamina, the leaflets start emanating from a lower position than on the other half (Fig. 6), hence the number of leaflets on the halves usually differ. Data on the numbers of leaflets on halves of leaves of the two types of palms are given in Table I.

Table I

P. macarthurii : *Numbers of leaflets on halves of leaves*

No. of shoots and spirality	No. of leaves	Leaflets on halves Left	Right	Total	Variance
6 clockwise	42	1111	1021	2132	1·99
6 counter-clockwise	46	1123	1216	2332	2·19
Mean per leaf		24·41	26·44	50·85	

Of the 42 leaves examined from clockwise crowns, 3 had equal numbers of leaflets on both the halves, in one the right half had two excess leaflets and in the remaining, the excess leaflets on the left half ranged from 1–5. On the aggregate, a leaf of this type of crown bore 8·81% more leaflets on the left half. Of the leaves sampled from the counter-clockwise crowns, 5 leaves bore equal numbers of leaflets on halves, in two others, the left half had an excess leaflet each and in the rest, the leaflets on right half were greater than those on the left by 1–5 leaflets. On the whole, a leaf of counter-clockwise crown bore 8·28% more leaflets on the right half. This situation is exactly the mirror-image of that prevalent in clockwise crowns. A leaf of a bearing crown of *P. macarthurii* bears 50–80 leaflets.

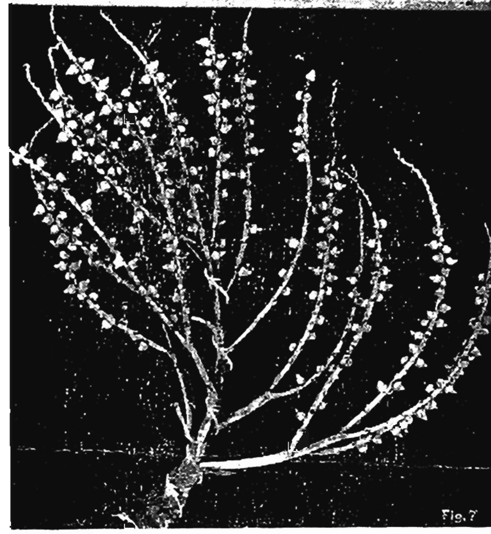


Fig. 6. Lower portions of leaves from clockwise and counter-clockwise crowns, × 1.

Fig. 7. Spadix showing counter-clockwise arrangement of spikes, × 2.

Bilateral Symmetry in Spadices and Spikes :

From the axil of each half of a mature shoot, a spadix is produced although some of them are under-developed or even sterile. The peduncle of the spadix gives rise to several lateral spikes which are arranged spirally (Fig. 7). Some spadices are clockwise and others counter-clockwise. There is a positive association between the spirality of the crown and that of its spadices as evidenced by the data given in Table II.

TABLE II

P. macarthurii : *Association of crown with spadices*

Type and number of crowns examined		Spadices: Clockwise	Spadices: Counter-clockwise	Total
Clockwise	16	51	33	84
Counter-clockwise	9	10	35	45
Total	25	61	68	129

During one season, a shoot produces about five spadices under our conditions.

From the cyclic arrangement of flower clusters, clockwise and counter-clockwise spikes can be distinguished. Here again, a positive association was found to exist between the spirality of spikes and that of spadices as per data in Table III.

TABLE III

P. macarthurii : *Association between spikes and spadices*

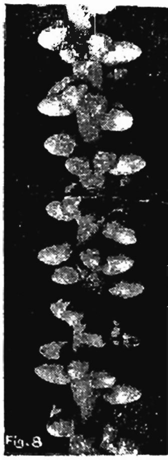
Type and number of spadices		Spikes: Clockwise	Spikes: Counter-clockwise	Total
Clockwise	51	729	345	1074
Counter-clockwise	33	225	417	642
Total	84	954	762	1716

A spadix bears 20·43 flowering spikes although there is great variation between spadices of the same tree and between trees. Those produced at the end of flowering season are much smaller or become sterile. A few of the lowermost spikes of large spadices may produce a few secondary spikes as well (Fig. 7).

In a clockwise crown, the clockwise spadices produce 67·88% clockwise spikes, and the counter-clockwise spadices produce 64·95% counter-clockwise spikes. Corresponding percentages for a counter-clockwise crown are 63·11 and 63·88. Thus, the crown does not seem to have any immediate influence on the spirality of the spikes.

Spirality of Spike and Aestivation of Female Flowers :

The three flowers of a cluster are placed almost in a line at right angles to the spike of their origin (Fig. 8). When the tip of the spike is held upwards, the male flower located to the left of the female flower has its sepals imbricated counter-clockwise. The male on the right has clockwisely imbricating sepals. The kinds of imbrication of sepals of the males remain unchanged whether the spikes are clockwise or counter-clockwise. Out of 4,579 flower-clusters examined, only a negligible 8 clusters deviated from the above condition. However, the aestivation of the female flower is associated with the spirality of its spike (Fig. 9). The sepals in a significantly greater number of flowers from a clockwise spike imbricate clockwisely, and *vice versa*, in a counter-clockwise spike (Table IV).



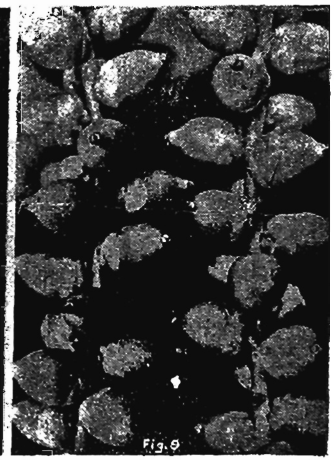


FIG. 8. Portion of spike with numerous flower clusters, arranged clockwisely, × 2.

FIG. 9. Portions of clockwise and counter-clockwise spikes bearing numerous fruits, × 1.

TABLE IV

P. macarthurii : *Spirality of spike and aestivation of female flowers*

Spirality and number of spike		Sepal imbrication: Clockwise	Sepal imbrication: Counter-clockwise	Total
Clockwise	30	403	283	686
Counter-clockwise	33	301	456	753
Total	66	704	739	1443

Calyx-Corolla Association :

Another important association noticed in this palm is that the calyx and corolla within a flower show opposing imbrication in about 97% of the flowers examined (Table V).

TABLE V

P. macarthurii : *Sepal-petal relationship*

Calyx	Corolla aestivation		Total
	Clockwise	Counter-clockwise	
Clockwise	39	1004	1043
Counter-clockwise	1022	25	1047
Total	1061	1029	2090

None of the flowers had contorting corolla although many other species of palms have varying numbers of flowers having contorting corolla in addition to others showing imbricating corolla.

DISCUSSION

The kind of aestivation of the male flowers depending on the position of their origin, in relation to the female flower in a triad, is by far the most important piece of information brought out by the present investigation on *Ptychosperma macarthurii.* Aestivation of corolla, manifesting clockwise and counter-clockwise rotations, was reported in Malvaceae (Davis, 1964 ; Davis and Selvaraj, 1964), Bombacaceae (Davis, 1966, 1967 ; Davis and Kundu, 1966) and a few other families. But in none of the species investigated, was an association found between the kind of aestivation of a flower and the place of its origin or the spirality of the shoot. Even where continuous observations on flowers distributed regularly on many shoots were possible, the clockwise and counter-clockwise rotating flowers were found distributed randomly.

Similar distribution of flowers in triads (or twins) as in *P. macarthurii* has been observed in some other Arecoid, Caryotoid, and Cocoid palms. Several spadices from one or a few species of *Areca, Arenga, Caryota, Chrysalidocarpus,* and *Cocos* were examined for similar morphological peculiarities. In *Areca,* the male flowers are distributed in two opposite rows on each spike, a single female flower occupying the base of the spike. In *Cocos,* the male flowers appear mostly as twins which are compactly distributed throughout the surface of the spike. At the tip, however, several solitary male flowers are seen, and the female flowers occupy the base of the spike. *Arenga, Caryota, Chrysalidocarpus,* and *Prychosperma* have almost similar kind of flower clusters, *i.e.,* triads, distributed throughout the length of the spike, although in *Arenga,* and less prominently in *Caryota,* female expression in the triads varies with spadix. That is, in the first-formed 2–3 spadices, the female flowers are very well developed, but in successive spadices, they become smaller and less pronounced, so much so, that in the last set of spadices, the clusters comprise only of two males. *Arenga* differs from *Ptychosperma, Caryota* or *Chrysalidocarpus* in another important aspect. While in *Ptychosperma,* the left male in a cluster has counter-clockwise imbrication of calyx (as reported), in *Arenga,* the male on the left has clockwise imbrication and that on the right has counter-clockwise aestivation (Table VI).

TABLE VI

*Aestivation of sepals of male flowers in three species**

Species	Clusters examined	Aestivation of males to the left and right of female		
		Clockwise and counter-clockwise combination	Clockwise and clockwise combination	Other 2 combinations
Arenga pinnata	2239	2136	8	95
Ptychosperma macarthurii	4579	4	4571	4
Caryota mitis	938	..	938	..

* The flower clusters include those from clockwise and counter-clockwise spikes. The spirality of spike has no influence on the kind of aestivation of male flowers.

The data in Table VI reveal the existence of double enantiomorphism in the aestivation of male flowers between genera *Ptychosperma* and *Caryota* on one hand, and *Arenga* on the other.

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