

CENTRIFUGAL STAMENS

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With seven text-figures

AN UNEXPECTED difference among the families of dicotyledons arises from the direction in which the stamens develop. In 1857, Payer showed that, in contrast to the usual centripetal or acropetal order, there were a few families in which it was centrifugal — “l'éruption staminale est donc centrifuge,” (4, p. 4). In modern works this remarkable contrast seems to have been almost entirely forgotten, yet clearly we cannot hope to understand the variations of the androecium in ignorance of it. So far as I have discovered in general reading, the following thirteen families have stamens developed centrifugally (I have placed the name of the authority in brackets):—

Actinidiaceae (Brown), Aizoaceae (Payer), Bixaceae (Corner), Cactaceae (Payer), Capparidaceae (Payer), Dilleniaceae (Payer), Hypericaceae (Payer), Loasaceae (Payer), Lecythidaceae (Mclean Thompson), Malvaceae (Payer), Paeoniaceae (Schöffel), Theaceae (Payer, Warming), Tiliaceae (Payer).

In contrast, the chief families with many centripetal stamens are:—

Annonaceae, Lauraceae, Leguminosae, Lythraceae, Magnoliaceae, Myrtaceae, Nymphaeaceae, Papaveraceae, Punicaceae, Ranunculaceae, Rosaceae.

In these, the androecium follows the perianth in normal sequence, whether spirally or by alternating whorls. In the centrifugal families, there is a break between the perianth and the androecium which is caused by the intercalation of the new stamens. Accordingly, they are not packed in parastichies but as closely as possible in centrifugal order to give the short, irregular, non-seriate rows which one finds also in the arrangement of the pores of the Polyporaceae and the spines of the Hydnaceae. We have, in fact, a new construction in which stamens arise, not in the logarithmic spirals of acropetal phyllotaxis, but on a peripherally expanding disc. In the more regular flowers of this kind, as will be mentioned, the stamens may be arranged in centrifugal whorls with a regular doubling of the number of stamens in each.

I propose to describe briefly the typical centrifugal androecium in the relatively massive flowers of *Wormia*, *Tetracera*, and *Bixa* — massive in the sense of having a large bud and wide receptacle. I will then indicate what seem to be derivative states caused by diminution in the size of the

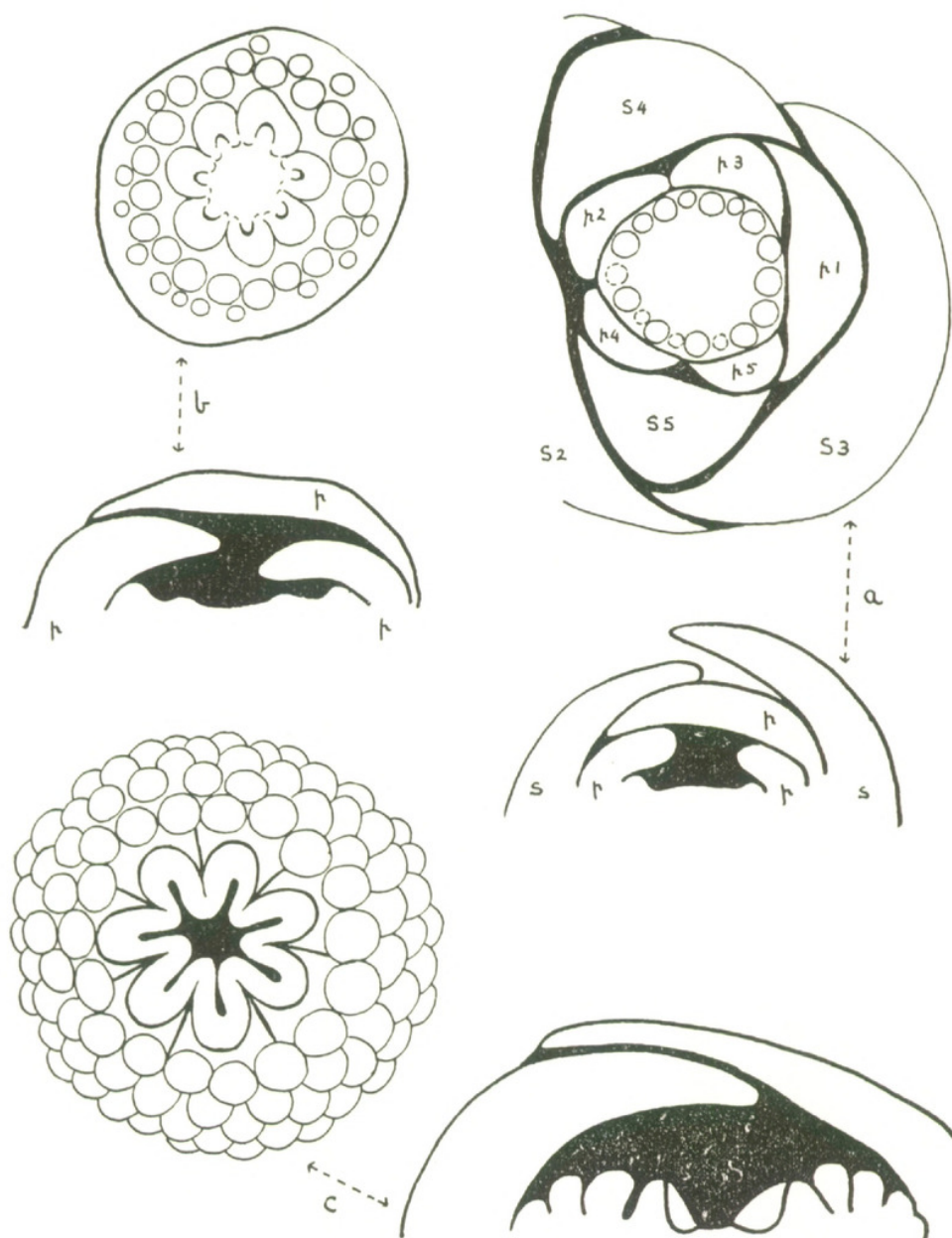


FIG. 1. *Wormia sufruticosa*: three stages in the development of the androecium, in surface-view (with the perianth cut off) and in section; *a* corresponds with *c* in Fig. 2, *b* with *d*, and *c* with *e*; *s* = sepals, *p* = petals; \times ca. 45.

flower; and, finally, I will discuss the systematic or phyletic value of the feature and how a more precise notation for the androecium must be introduced into the floral formula. Needless to say, much more research must be done on multistaminate tropical genera before we can hope for satisfactory understanding. A mathematical theory and geometrical construction must also be worked out for centrifugal development from detailed measures of series of enlarging flower-buds: for the order of development is the opposite of that of the classical Composite-inflorescence.

THE MASSIVE CENTRIFUGAL ANDROECIUM

The massive flowers of *Dillenia*, *Wormia*, *Bixa*, *Gordonia*, *Thea*, *Opuntia*, *Saurauja*, and, probably, the Lecythidaceae show the typical features of the centrifugal, multistaminate andrœcium, thus: —

1. After the initiation of the corolla, or even before it is complete, the floral apex becomes a wide, low disc with vague angles, and its apical growth gives place abruptly to radial growth.

2. The first stamens arise in a ring of 15–21, commonly 17–18, primordia, without obvious relation to the perianth, and practically simultaneously. They may precede the carpels (*Dillenia*, *Wormia*) or develop just after the carpels (*Tetracera*, *Bixa*), in which case the first stamens alternate, more or less, with the carpels and the gynœcium and andrœcium form one centrifugal system.

3. The floral disc expands basipetally, or peripherally, between the initial staminal ring and the corolla and, on this andrœcial annulus, the other stamens (numbering 50 to several hundred) develop centrifugally in closest apposition to the preceding stamens. A tendency to develop in alternating whorls of increasing members is generally obscured by asymmetry of the floral disc.

4. The mature flower is usually perigynous with the stamens united, more or less, in a short tube developed from the basipetal enlargement of the andrœcial annulus. (In *Tetracera* the flower is secondarily hypogynous.)

Figures 1–7 will illustrate the manner of development in *Wormia*, *Tetracera*, and *Bixa*. The later stages, in surface-view and longitudinal section, supplement Payer's solid views of *Opuntia*, *Thea*, and *Gordonia*.

In *Wormia suffruticosa* there are 16–20 initial stamens around the floral apex, and the outermost, or youngest, stamens are sterile and form short ligulate staminodes (homologous with the petals of *Mesembryanthemum*); the staminodes have neither the space, nor the time, nor the food-supply (probably) to become fertile and, though there are all transitions to fertile stamens, there are no transitions to the petals as there are in the centripetally developed flowers of the Nymphaeaceae. It must be noted that the variations of the dilleniaceous andrœcium, particularly in *Hibbertia*, can be understood only by reference to its centrifugal development and the sterilization of the later stamens; it is, thus, fundamentally different from the ranalian andrœcium.

Tetracera Assa (Dilleniaceae) differs from *Wormia* in the precocity and incipient oligomery of the gynœcium. The carpels are initiated before the stamens and follow the tetramery of the perianth so that there are 7 or 8 stamens developed slightly before the others in the initial ring; the gynœcium thus induces a slight centrifugal alternation of whorls in the andrœcium, but it is soon lost as more members are inserted. The outer stamens are fertile and identical in length and appearance with the inner-

most in the open flower. The receptacle elongates shortly during the expansion of the bud and renders the flower secondarily, or indirectly, hypogynous.

In *Bixa* the gynœcium is even more precocious and appears before the

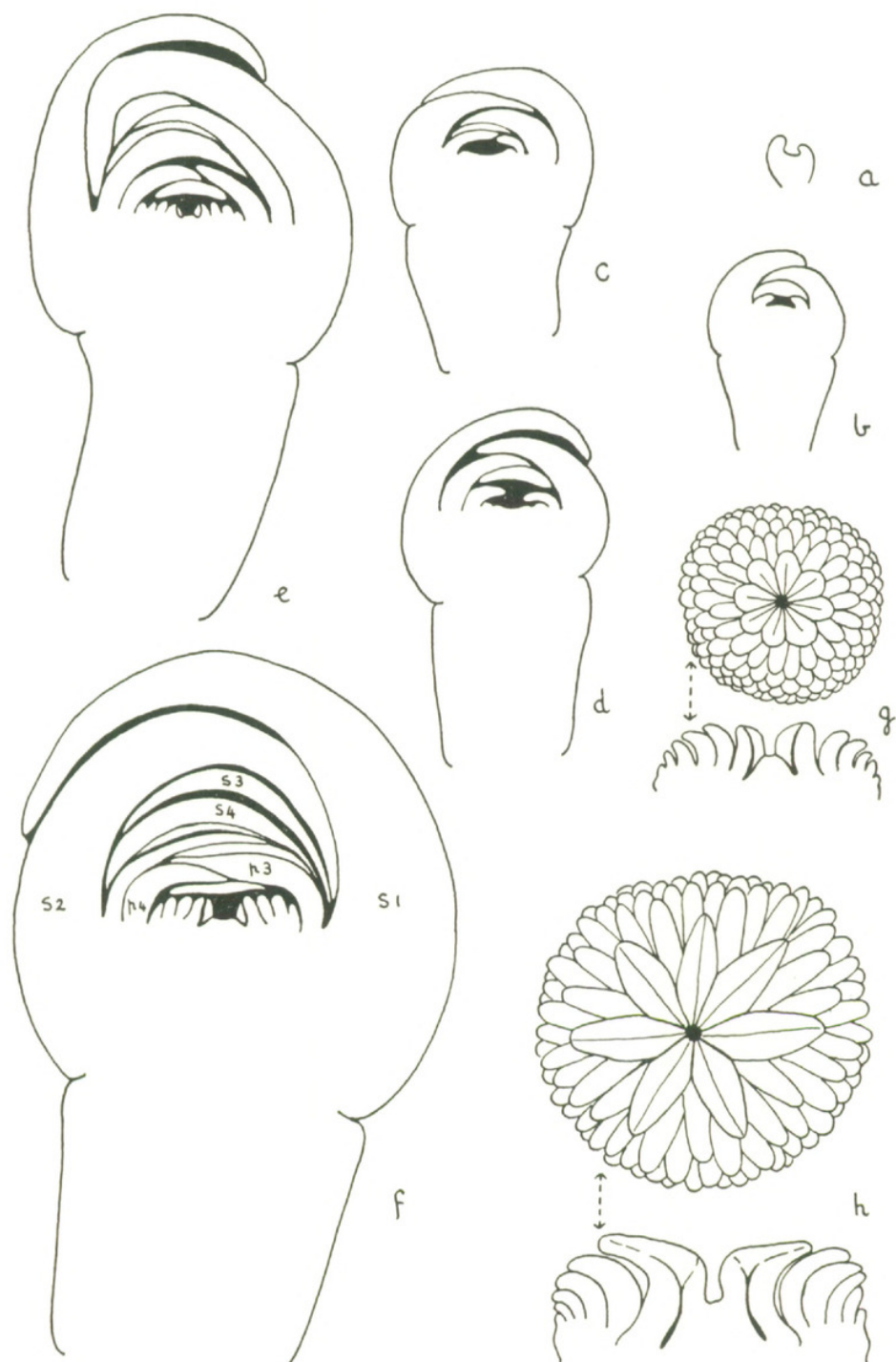


FIG. 2. *Wormia suffruticosa*: six stages (a — f) in the development of the massive flower-bud; two later stages (g — h) in the development of the androecium and gynœcium; f corresponds with a in Fig. 3; s = sepals, p = petals; \times ca. 15.

4th and 5th petals. The floral apex is very massive when the initial ring of 17 or 18 stamens arises practically at once round the subcircular gynœcium; the ring bears no obvious geometrical relation to the perianth. In this respect, *Bixa* has the most independent andrœcium governed, apparently, merely by the spacing-relations (or bulk-ratio) between the staminal primordia and the area of the "andrœcial disc" and by the centrifugal order. All the stamens are fertile and equally long in the open flower and the only indication of its unusual development is the slight perigynous disc on the outer slope of which the stamens are inserted.

In *Saurauja subspinos*a (Actinidiaceae, 2) the andrœcium of about 50 stamens starts from a ring of 15–21. When there are only 15, five are opposite the sepals and five pairs oppose the petals, but they arise practically simultaneously. This precision in number and position, conforming with the perianth, coincides with reduction in size of the floral apex and leads to the derivative and specialised conditions in the smaller flowers which will be considered next.

The obvious interpretation of the massive centrifugal andrœcium is that the order of development has been reversed through the abrupt cessation of the apical growth of the floral bud while its radial growth continues between the gynœcium and the perianth. The generating field of the andrœcium is transformed from an acropetal cone to a centrifugal disc on which the primordia develop as enations packed as closely as their minimal initial areas admit without interference. The state is clearly derived from the massive multistaminate flower with normal acropetal sequence of stamens of modern form, for in acropetal flowers radial growth of the floral apex is regularly co-ordinated with apical growth, and both decline together; in the centrifugal flower the two are, as it were, dissociated in a curious way which should help us to analyse more clearly the growth of the stem-apex.

DERIVED CENTRIFUGAL ANDROECIA

The following four constructions seem to show how diminution in the growth of the floral bud, recognizable from the sharper angles of the floral disc after initiation of the perianth, introduces greater precision in the number and position of the stamens. For illustration, I must refer to Payer's figures.

1. *Initial whorls.* *Saurauja subspinos*a, just mentioned, is an instance. The floral disc, after the initiation of the perianth, becomes more or less sharply angled because it does not undergo such rapid radial expansion. On the points, or shoulders, of the disc arise five antisepalous stamens, alternating with the petals, and then ten antipetalous stamens in five pairs, slightly external to the antisepalous; after this other stamens develop as in the more massive flowers. In *Cistus* and *Helianthus* it seems that only five antipetalous stamens develop, giving an initial, regular phase of $A5 + 5$. In the tetramerous *Capparis spinosa* the andrœcium appears to be wholly

whorled in the centrifugal order $4 + 4 + 8 + 16 + 32$ (? + 64. . . .) so that the stamens in the mature flower appear to be arranged according to the normal centripetal, but falling, whorled phyllotaxis of the Papaveraceae.

2. *Centrifugal fascicles*. In the dilleniaceous genera *Candollea* and *Hibbertia*, after the initiation of the five petals, the pentagonal floral disc forms five antisepalous humps on each of which the stamens develop cen-

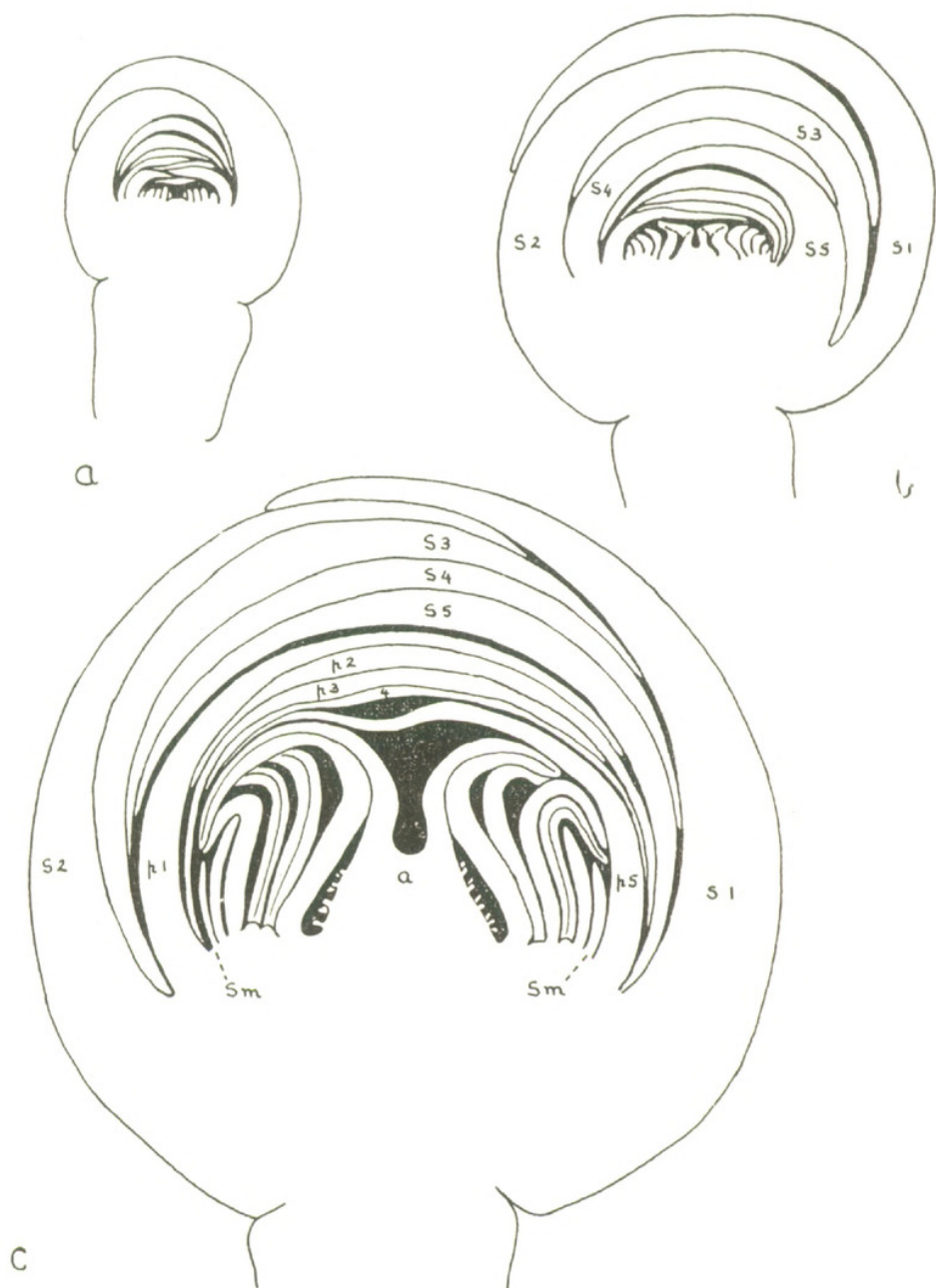


FIG. 3. *Wormia suffruticosa*: three stages in the later development of the flower, *a* corresponding with *f* in Fig. 2, *c* about half-grown; *s* = sepals, *p* = petals, *sm* = staminodes; \times ca. 7.

trifugally. If the stamens are very numerous, the five groups coalesce centrifugally, but if they are relatively few (? in smaller flowers), they remain in five antisepalous clusters in the open flower. In the Hypericaceae, *Bathys prolifica* has five slight *antipetalous* humps on which the stamens develop centrifugally, but they coalesce to give a homogeneous andrœcium; in *Hypericum* the humps are more pronounced and give five bundles of stamens (or three in the case of smaller flowers with rapidly falling phyllotaxis). In the Tiliaceae and Malvaceae the stamens also tend to be in *antipetalous* fascicles developed centrifugally on antipetalous humps of the young floral disc; in *Sparmannia* (Tiliaceae), however, they are antisepalous.

Fasciculation of this kind, resulting from prominent humping, or radial lobing, of the floral disc in its early stages seems very clearly to be connected with the diminution in size of the floral bud, and the humping, itself, seems to be caused both by the pressure of the perianth segments on the floral disc as they develop, and by their very close proximity with the incipient andrœcium. More detailed studies of floral development, by section and dissection, will doubtless explain the peculiar ridging of the young andrœcium. The basipetal elongation of the receptacular tissue of the humps, corresponding with the basipetal (or centrifugal) growth of the andrœcium, elevates each bundle of stamens on a common stalk, exactly as in the development of floral tubes.

Payer and many botanists after him have regarded fasciculate stamens as branched systems, or compound microsporophylls, derived from the repeated branching of the initial hump, as pinnae are produced on the compound leaf. When there is no visible stalk or axis to the hump, the staminal primordia which appear on it are supposed to have arisen by "congenital" branching in the solid mass of tissue. This is clearly a *reductio ad absurdum*. There are all transitions from the massive centrifugal andrœcium to the fasciculate state, e. g. Dilleniaceae, and one cannot conceive the evenly centrifugal and ring-like andrœcium of *Wormia* or *Bixa* either as compounded of congenital initials or as representing one amplexicaul sporophyll, not even from the point of view of the vascular bundles, as recently maintained (2, 9).¹ The centrifugal andrœcium is merely a reversal of the normal state, for the explanation of which we must consider what disturbance of the growth-processes can produce a reversal; fasciculation is an added complication which does not involve abstract morphology. That bilobed staminal primordia sometimes form on the floral disc does not indicate branching of a compound sporophyll but the manner of interference of unit-primordia on origin, exactly as bilobed and trilobed pores in Polyporaceae or spines in Hydnaceae indicate con-

¹ In the centrifugal flowers the initial androecial vascular bundles develop in spiral sequence after those of the perianth, thus indicating the normal acropetal organization of the interior of the floral apex; they then break up into a plexus immediately below the surface of the androecial disc, to supply its new departures.

genital fusion, from uneven spacing, of normally discrete primordia. Centrifugal enation in an asymmetric or confined space is far more likely to produce irregularities than the normal acropetal and centripetal process.

3. *Zonation*. In the Theaceae, the reduced andrœcium of *Visnea* develops five, initial, antisepalous stamens, then two more stamens beside

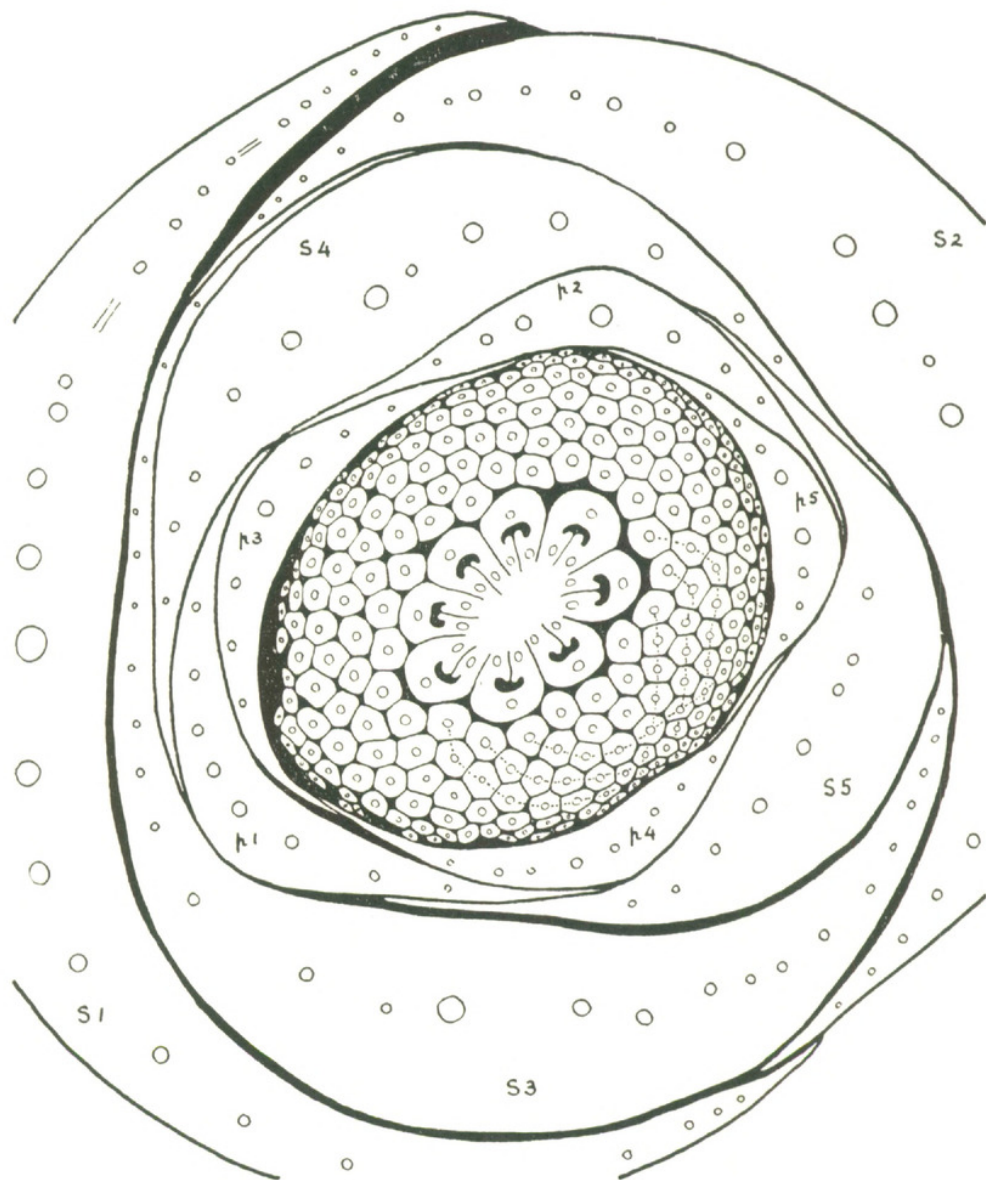


FIG. 4. *Wormia suffruticosa*: transverse section of a flower-bud about one-third grown (between stages *b* and *c* in Fig. 3), the stamens irregularly centrifugally whorled ($20 + 20$), the v. b. shown; \times ca. 15.

each, first one on one side and then one on the other of each of the original five. Thus a single ring of 15 stamens is produced and it appears as the natural reduction of the massive, centrifugal andrœcium of *Thea* and *Gordonia* to the initial ring of 15; centrifugal growth of the andrœcial disc is so limited that only 10 slightly external stamens arise after the

first five and all appear inserted at the same level in the open flower. The andrœcia of *Portulaca*, *Philadelphus*, and *Citrus* seem to develop in the same way, but in *Citrus* there is prolonged tangential enlargement of the andrœcial disc which allows many more stamens to be intercalated in the same zone.

4. *Centrifugal obdiplostemony*. The andrœcium of *Visnea* is obdiplostemonous with an outer, though later, whorl of five pairs of antipetalous stamens. If one imagines the centrifugal growth of the andrœcium so

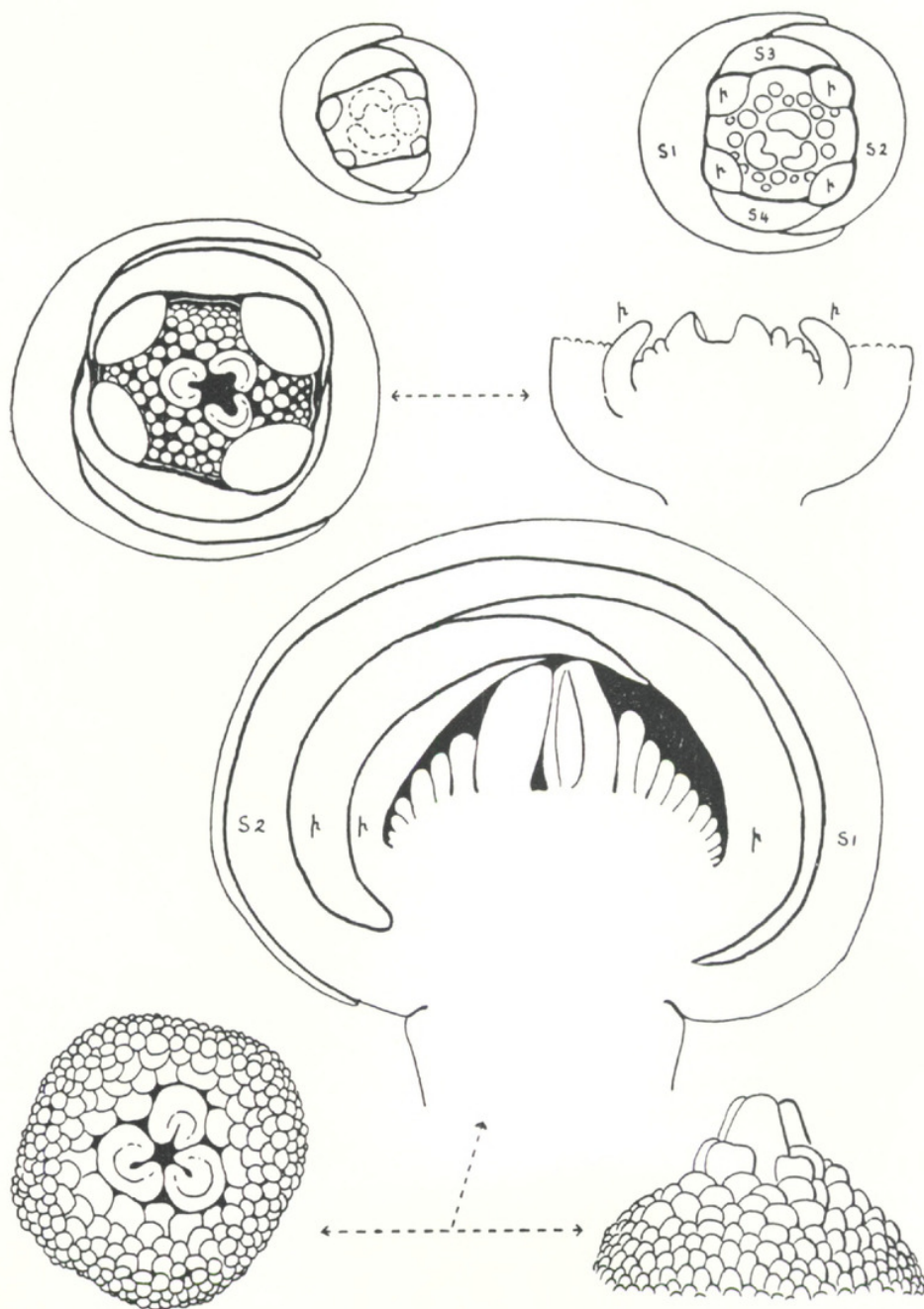


FIG. 5. *Tetracera Assa*: early stages in the development of the flower-bud (these buds with only 3 carpels); s = sepals (4), p = petals (4); \times ca. 27.

limited that only one stamen can be inserted in each of the gaps between the initial five, then the $5 + 5$ obdiplostemonous andrœcium will be formed, c. f. *Cistus* and *Helianthemum*. Such appears to have been the case in the Geraniaceae, for *Monsunia* has 15 stamens in two whorls, the outer (and later in development) consisting of five antipetalous pairs, while *Geranium* has only five stamens in the outer, and later, whorl. Similarly in the Zygophyllaceae, *Peganum* and *Nitraria* have 15 stamens as in *Monsunia*. Indeed, both families agree with the Rutaceae in showing traces of descent from the massive centrifugal andrœcium. The obdiplostemony of the Caryophyllaceae, Ericaceae, and Epacridaceae seems explicable in the same manner.

In the Capparidaceae, the reduction of the multistaminate state in *Capparis* has produced the 6-staminate condition of *Cleome*, in the slender little flowers of which the stamens develop centrifugally in 2 whorls, $2 + 4$, to give the same tetradynamous arrangement as in the Cruciferae. Thus the cruciferous andrœcium appears to be another limiting state of the centrifugal gynœcium in the tetramerous flower.

According to Eichler, this was the interpretation of obdiplostemony given by Chatin, Pax, and Hofmeister; he affirms that in obdiplostemonous flowers the antipetalous stamens develop after the antisepalous (3, p. 336). It is noteworthy, as corroborative, that in monocotyledons staminal development is always centripetal and obdiplostemony seems not to occur (5, p. 297). In centrifugal obdiplostemony there is no interruption in the alternating whorls of the flower but a reversal in the direction of development of new stamens after the first whorl, and this reversal, in the limiting case of two whorls of $n + n$ or $n + 2n$ members, gives a false appearance in the mature flower. Nevertheless, in the Tiliaceae, Malvaceae, and Hypericaceae there is a form of obdiplostemony which does interrupt the sequence of alternating floral whorls, for the initial andrœcial humps in the floral bud are *antipetalous* and the reduction of their centrifugal andrœcia to two whorls would give apparent *diplostemony*. It is clear that our macroscopic interpretations of andrœcia will remain confused or uncertain until there is much more precise knowledge of the developmental sequence of the stamens and of the spacing factors in the floral bud.

PHYLETIC VALUE

The systematic importance of the centrifugal andrœcium is shown by the two instances of *Paeonia* and *Saurauja*.

Paeonia is usually placed in the Ranunculaceae, where its persistent sepals and distinct, if rudimentary, aril are anomalous. In 1908, Worsdell wrote (10):—

“From a consideration of the character of the vascular anatomy alone I am sure that no one would ever dream of classing *Paeonia* with the *Ranunculaceae*; on the other hand, a very fair case could be made out for classing the genus with the *Magnoliaceae*.”

Worsdell proposed the family Paeoniaceae as a link between the Ranunculaceae, Magnoliaceae, and Calycanthaceae. Yet, the two anomalies of persistent sepals and aril still remain, and the comparison with the Magnoliaceae introduces three or more anomalies in the pinnate leaves, the acyclic calyx and corolla, and the flat receptacle of *Paeonia*.

In 1932, Schöffel discovered that the andrœcium of *Paeonia*, consisting of 200 or more stamens, developed centrifugally on a slightly raised staminal disc (evidently as in *Wormia*), and that this feature was unique among the Ranunculaceae (6).

If, now, we follow this clue and compare *Paeonia* with the Dilleniaceae,

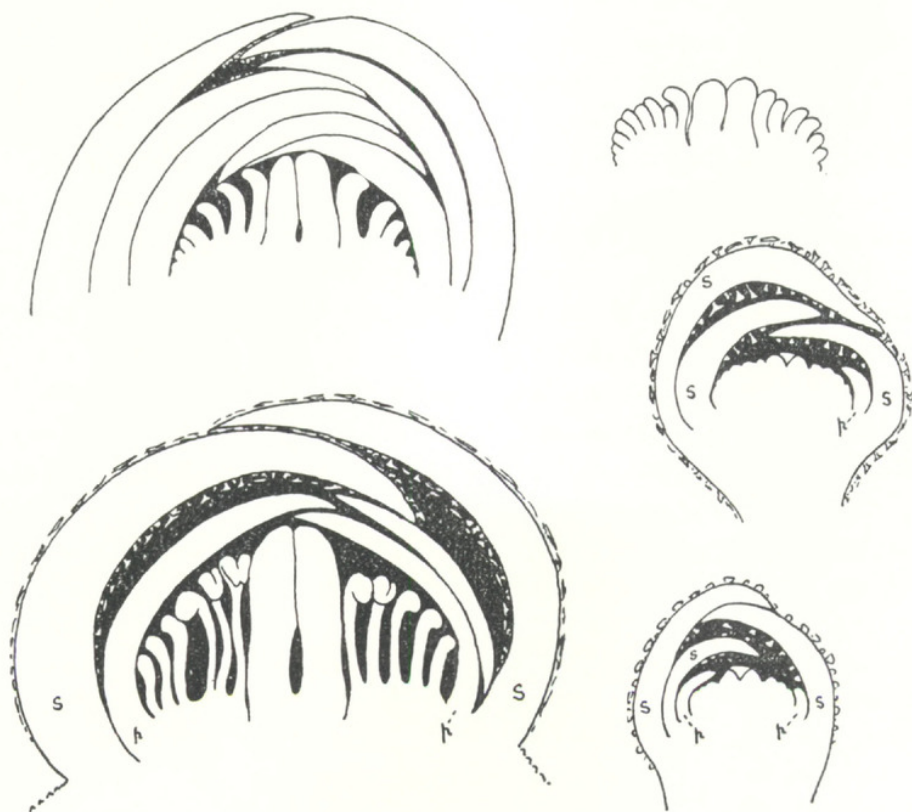


FIG. 6. *Bixa Orellana*: early stages in the development of the flower-bud; s = sepals, p = petals; \times ca. 27.

we find that the vascular character emphasized by Worsdell, the persistent sepals, the aril, the hard testa, the woody tendency and, even, the pinnate, exstipulate leaves are as much dilleniaceous as the centrifugal andrœcium. Dilleniaceous leaves are typically simple, but the large, acropetally developing, toothed leaves of *Dillenia* give every appearance of a webbed pinnate leaf, and in the dwarf shrubs, or woody herbs, of *Acrotrema* there are species with doubly or simply pinnatifid leaves and simple leaves. Indeed, there are no obvious features to separate the Paeoniaceae from the Dilleniaceae, particularly if *Actinidia* is included among them. *Paeonia*, thus, appears naturally as a temperate derivative of the Indo-Malaysian

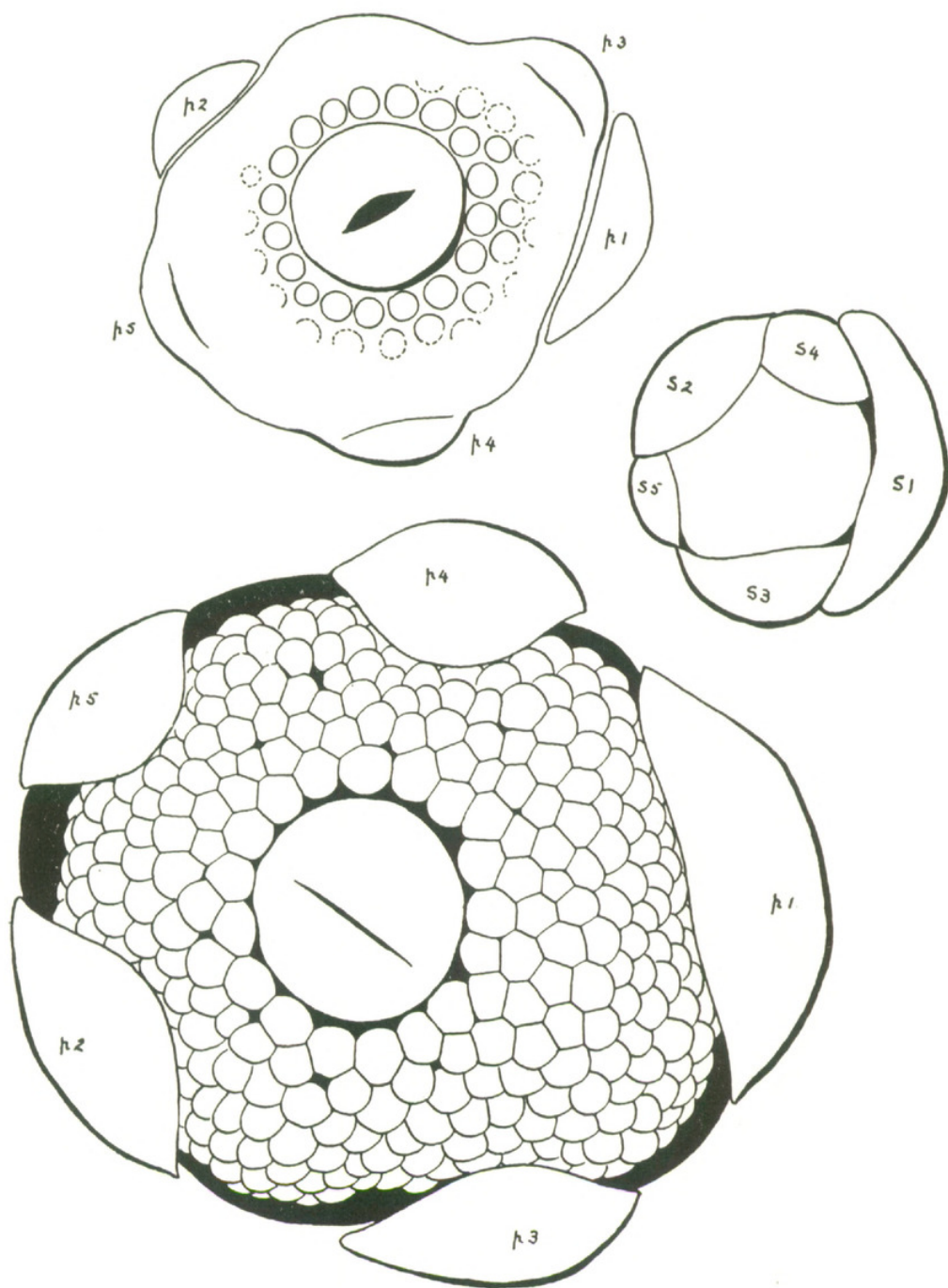


FIG. 7. *Bixa Orellana*: early stages in the development of the flower-bud in surface-view, \times ca. 45.

Dilleniaceae closely comparable with *Actinidia*. It is not at all odd that they should be typically oriental, for the great land-mass of southern China has been the only part of the world where the tropical flora has been able for ages to invade over a vast front the north temperate region. It is worth noting, too, that another anomalous genus, *Crossosoma*, which has

been put in the Dilleniaceae, was classed by Baillon with *Paeonia* (1, p. 66).

Saurauja is another problematic genus which has been placed in the Dilleniaceae, the Theaceae, and, with *Actinidia*, in the Actinidiaceae. Brown has shown that its andræcium is centrifugal, exactly as in the Dilleniaceae and Theaceae. This agreement clinches the close affinity between the two families; and, again, the Theaceae appear naturally as an oriental and temperate off-shoot of the older, Indo-Malaysian Dilleniaceae.

A third instance, far less certain, through lack of knowledge, may be found in the Parietales as a whole. The series appears to be a very vague group of diverse families without any character in common, not even the placentation. It is a natural group by "concatenation." Yet, so far as known, the andræcium is centrifugal in six families—Hypericaceae, Cistaceae, Dilleniaceae, Theaceae, Bixaceae, and Loasaceae; it may well be centrifugal also in the Ochnaceae, Caryocaraceae, Guttiferae, and Flacourtiaceae. It is centrifugal in the allied Opuntiales.

From these considerations I am compelled to regard the centrifugal andræcium as a most important systematic character which defines, as a natural phylum, a large number of dicotyledonous families at present confused with other series of families possessing the centripetal andræcium. On the one hand there are the primary ranalian, rosalian, myrtalian series and, on the other hand, there is the centrifugal series derivative from one or other of the primary series, or their ancestors. It is likely that, beside the Parietales and Opuntiales, most of the Geraniales, Malvales, Centrospermae, and Ericales belong to the centrifugal series.

Dogmatic and biased as this may seem at first sight, yet a clear standpoint is to be preferred when a new idea emerges. Morphologically I would expect so profound a disturbance in floral development as the reversal of the andræcium to be highly peculiar and, therefore, phyletic. On the other hand, particularly in flowering plants, we know that homoplasy is general, that such floral features as sympetaly, synandry, syncarpy, epigyny, and so on, have arisen independently in many different series, for which reason we might consider the centrifugal andræcium as merely another instance of this confusing phenomenon. Yet, one must remark that, whereas all such homoplastic features occur in many different dicotyledonous *and* monocotyledonous series, the centrifugal andræcium does not occur among the monocotyledons, and among the dicotyledons it is centered around the Parietales. Therefore, I think one must regard as anomalous the association of the centrifugal Capparidaceae *cum* Cruciferae with the centripetal Papaveraceae in the Rhoeadales and that of the centrifugal Lecythidaceae with the centripetal Myrtaceae and Lythraceae in the Myrtales. One must ask whether they have not been as mistakenly classified as *Paeonia* with the Ranunculaceae. And the position of all obdiplostemonous families must come under review.

NOTATION

The symbols $A \overset{\rightarrow}{\infty}$ and $A n + n \dots$ must be resolved into

$A \overset{\rightarrow}{\infty}$ and $A \overset{\leftarrow}{\infty}$ for centripetal and centrifugal stamens, respectively; and

$A \vec{n} + n \dots$ and $A \dots n + \overset{\leftarrow}{n}$.

Thus, a major difference between the Ranunculaceae and the Dilleniaceae can now be shown in their floral formulae.

For the Lauraceae, we may write $A \overset{\rightarrow}{3} + 3 + 3 + 3$, but for *Capparis* $A \dots 32 + 16 + 8 + 4 + 4$.

Monsonia becomes $A 10 + \overset{\leftarrow}{5}$, and *Geranium* $A 5 + \overset{\leftarrow}{5}$, while *Brownea* may be $A \overset{\rightarrow}{5} + 5 + 5$ and *Caesalpinia* $A \overset{\rightarrow}{5} + 5$.

In the case of the fasciculate stamens, we may write $A n(\overset{\leftarrow}{\infty})$, as in *Hypericum* $A 5(\overset{\rightarrow}{\infty})$.

For zonate stamens, the notation is more difficult, but it may suffice to write $A \overset{\leftrightarrow}{n}$ or $A \overset{\leftrightarrow}{n} + \overset{\leftrightarrow}{m}$, where n is the number of initials and m the number of stamens intercalated between them. The symbol $A \overset{\leftrightarrow}{\infty}$ would imply amphipetal development of the androecium, which is not known.

Obdiplostemony appears to be represented better by

$K n C n A \overset{\leftarrow}{n} + \overset{\leftarrow}{n} G n$
than by the usual formula

$K n C n A \vec{n} + n G n$.

SUMMARY

1. A list of 13 families of dicotyledons is given in which the stamens develop centrifugally. The mechanism is explained in detail for *Wormia*, *Tetracera*, and *Bixa*.

2. The centrifugal androecium appears to be a feature of considerable systematic importance which indicates a common origin for the families in which it occurs. Thus the Paeoniaceae, with centrifugal androecium, are referred to the Dilleniaceae rather than to the Ranales.

3. The primitively massive, centrifugal androecium must have been derived from the usual centripetal state. Reduction-specialization, leading to fasciculate, zonate, and diplostemonous androecia, seems to have occurred in both kinds of flower, resulting in a confusion in classification which takes no account of manner of development. Particularly is this so in obdiplostemonous families, e. g. Geraniales, Centrospermae, and Cruciferae, which seem referable to the centrifugal series.

4. There is no evidence that centrifugal fasciculate stamens (Hypericaceae, Tiliaceae, Malvaceae, Dilleniaceae) are branched sporophylls.

5. More critical notation for the andrœcium in the floral formula is suggested.

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