

On the Floral Organogeny and Anatomy of *Brownea* and *Saraca*.

BY

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With Woodcuts 14, 15, and 16.
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THE *Caesalpinieae* have been scarcely investigated from any but a purely systematic point of view; a study of the floral ontogeny of *Cassia* by Rohrbach¹ and of *Amherstia* by Griffith² are the only two extant. The free flowering of several specimens of *Brownea coccinea*, *B. grandiceps*, and *Saraca indica*, L. (*Fonesia Asoca*, Roxb.) in the plant-houses of Queen's College, Cork, has led me to investigate these two closely allied genera with a view to fill up a gap in our knowledge. Both genera belong to the group *Amherstieae*, characterised by the excentric position of the gynaeceum on the posterior lip of the calyx-tube next the vexillary petal, and with the dorsal suture towards the tube.

Brownea coccinea (from which *B. grandiceps* differs in no essential point) has shortly stalked flowers in short capitate racemes, often from defoliated axils and on the old wood. The lower bracts are distichous and equitant when young, empty or with their axillary flowers developing late; the upper are narrower, spathulate, arranged in a $\frac{3}{8}$ spiral, and all axillant to flowers. Each pedicel bears two closely connate bractlets forming an obconical sac, opening by an apical slit (antero-posterior). The flower shows only four sepals, owing to the connation of the posterior pair; allowing for this they

¹ Bot. Zeit. 1879.

² Notulae.

imbricate quincuncially (sep. 1 antr.). The four sepals become free at the rim of the long floral tube, on which are also inserted the five (variably) imbricate petals, not markedly heteromorphic or unequal, and nine or eleven¹ stamens monadelphous, the long erect tube split to the base on the posterior (vexillary) side. The solitary carpel has the normal orientation of the Leguminosae, its dorsal suture being anterior, its placenta posterior; its stipe is adnate as a ridge to the posterior edge of the floral tube, and becomes free at the posterior edge just within the vexillary petal.

Saraca has the calyx, gynaeceum, and floral tube of *Brownea*; but it is free, only slightly equitant. The flower is always apetalous, and has only the seven anterior stamens, which are free to their base; an eighth sometimes occurs, it is then posterior. The inflorescence is a stiff panicle twice or thrice branched, from the old wood. The bracts of the base of the main peduncle are distichous, but higher up they are spiral with the divergence $\frac{3}{8}$ as they are (with antidromy) on the secondary and tertiary axes. The upper bracts of the primary and secondary branches and all the tertiary are axillant to flowers.

I. THE FLORAL DEVELOPMENT OF BROWNEA AND SARACA.

The young inflorescences of *Brownea*, like so many closely-packed racemes, contain flowers nearly of the same age. These appear first in the axils of the lowest of the spiral bracts, and follow in rapid basifugal succession, the main axis often bearing finally a terminal flower. The lower floral bracts occasionally bear flowers, which, however, take origin much later than those in the axils of the spiral bracts. The bractlets appear right and left in quick succession, one a little before the other. They soon become connate, i. e. their bases are confluent and rise up so as to form a bag of truncated

¹ Ten is a very rare number to find; eleven is commoner in *B. coccinea*, nine in *B. grandiceps*.

conical form, with only a median slit at the apex, the margin of the older (Fig. 14, α) bractlet overlapping the other (Fig. 14, β). Within this sac the receptacle has widened and become obconical, somewhat tilted outward, so that the rounded upper surface, covered by the slit of the bracteolar sac, looks towards the hollow of the bract; hence in *Brownea* we have not the same marked difference of pressure between the anterior and posterior sides of the flower that usually prevails at this stage in closely-packed inflorescences. The sepals appear in quincuncial order; sepal 1 is anterior (see Fig. 14), 2 postero-lateral on the side of bractlet α , 3 antero-lateral on the β bractlet side, 4 antero-lateral on the α side, 5 postero-lateral on the β side again; 2 and 5 early become confluent at the base; but the resulting posterior member is long, unequally divided by a notch into a larger portion corresponding to 2, and a smaller to 5.

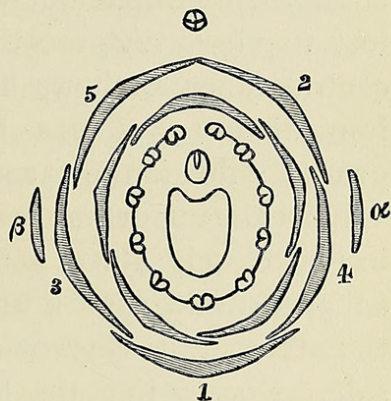


Fig. 14. Floral diagram of *Brownea coccinea*. *Saraca* has the same diagram with the omission of the petals and the four posterior stamens.

The petals arise as a simultaneous whorl, and so do the alternipetalous outer stamens. At this stage the swollen centre of the floral receptacle has become excentric to the flower, coming close up to the base of the vexillary petal behind. Hence we usually find in *B. grandiceps* only four antipetalous inner stamens, there being no room left for a posterior stamen before the vexillum; in *B. coccinea*, however, two are formed here; we may regard this as a true case of chorisis due to the pressure of the gynaecial tubercle. This now rises up as a horseshoe with its limbs closely approximated behind. The staminal sheath forms late, and so do the receptacular tube and gynophore.

In *Saraca* the bractlets soon overlap above the young receptacle, on the side of the bract, but leave a small gap at the posterior side of the flower until the appearance of the sepals; they never become connate, though α overlaps β on

the posterior as well as anterior side of the flower. The receptacle is nearly erect, not tilted outwards. The calyx develops as in *Brownea*, but the confluence of the sepals, 2 and 5, is earlier and more complete. I have failed to see any sign of petaline tubercles. The stamens appear in ascending order in an antero-posterior direction in rapid succession. First, an anterior stamen, then the pair next to it, then another pair, and then another; between these, on the posterior side of the flower, is seen a narrow ridge which soon shows three minute tubercles; the middle one may enlarge somewhat, but their identity and presence are soon lost to view. At the time that there are five stamens, the central tubercle shows a slight annular margin which almost immediately becomes horseshoe-shaped owing to uneven growth; this is the carpel.

Now the important point in the above developments is, that in two closely allied genera the flower of the one develops as one would say 'normally,' by successive whorls, and in the other genus there is a marked acceleration of the anterior side. Considering the flowers of these two genera alone, it might be thought that *Saraca*, the more modified form of the two, with its apetalous flowers and reduced androecium, owed to these points a distorted ontogeny. This conclusion, however, is unsustainable. In all Leguminosae hitherto studied, including the actinomorphic Mimoseae, the flower is known to develop from below upwards, with the appearance of the parts next the bract accelerated, those next the inflorescence-axis retarded. In this order then *Saraca* is normal, *Brownea* is exceptional; and it is the eucyclic development of *Brownea* which calls for explanation. We must, therefore, regard this eucyclic development as secondary, and hold that a reversion has taken place here, conditioned by the nearly actinomorphic relations of the adult flower. With this is correlated the peculiar position of the flower-axis (at right angles to the inflorescence-axis) at the stage when the flower-leaves make their first appearance.

It is obvious that the flowers of most Leguminosae must

rank as dorsiventral structures, while in *Brownea* they are, by adaptation or reversion, radial structures. Suppose now that the flower-leaves themselves were caulomes, not phyllomes; then, taking for our guide the aphorism that development, i.e. ontogeny, can alone elucidate the true nature of a structure, we should be constrained to refer the development of the flower in the two species to different types of branching. Now I do not see how the substitution of phyllome for caulome can modify the validity of the precept. If we regard the scorpioid inflorescence of a *Cordia* as morphologically different from that of a *Borago*, that of one species of *Urtica* as different from that of another, we must admit that the flower of *Brownea* is morphologically different from that of *Saraca*, *Cassia*, *Mimosa*, and every leguminous flower that has been studied; and herein we have a *reductio ad absurdum* of the above aphorism.

II. THE DISTRIBUTION OF THE FLORAL LEAF-TRACES IN BROWNEA AND SARACA.

This was the next problem to attack in order to see if it would shed any light on the morphology of the floral tube; but I soon discovered that the anomalies presented needed themselves to be explained before they could be utilised to explain other difficulties.

1. *The bractlets.* The arrangement in *Saraca* presents no difficulties. The fibro-vascular cylinder of the pedicel below the bractlets consists of six little arcs, two anterior, two posterior, and one on either side. The lateral arcs detach themselves at the node to go one to either bractlet, the one to the lower bractlet at a slightly lower level; in other words, each bractlet sends down a single leaf-trace which enters the cylinder at the extremity of the lateral axis.

In *Brownea* the bractlets send down numerous traces which are inserted uniformly at equal distances all round the pedicel. We must regard this distribution as a mere matter of convenience as it were; for, considering the development of the bracteolar sheath, the general occurrence of paired bractlets

in other orders, the close kinship with *Saraca*, we are constrained to admit that the uniformity of size and distribution and the number of the bracteolar leaf-traces in *Brownea* still do not justify us in regarding the sheath as composed of more than two connate bractlets.

2. *The flower proper.*—The easiest way to describe the distribution of the floral leaf-traces is perhaps to follow them from below upwards. In *Saraca* the vascular ring above the bractlets assumes a very irregular shape, with nine angular prominences, and as many bays, the posterior bay being the largest. The apex of each of the angles becomes detached

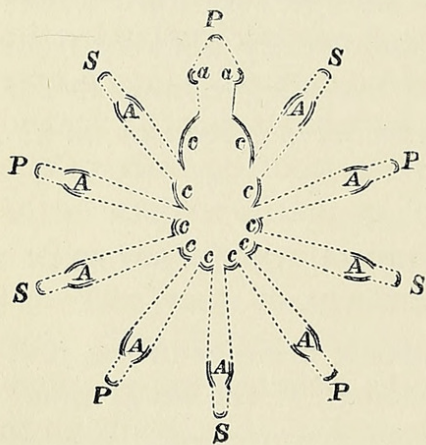


Fig. 15. Diagram to show the arrangement of the leaf-traces in the flower of *Brownea coccinea*. The dotted lines show how they unite edge to edge in their descent. S, sepal; P, petal; A, stamen (of the 9 anterior); a, stamen derived from the chorisis of the one in front of the vexillum; c, traces of the carpellary stipe.

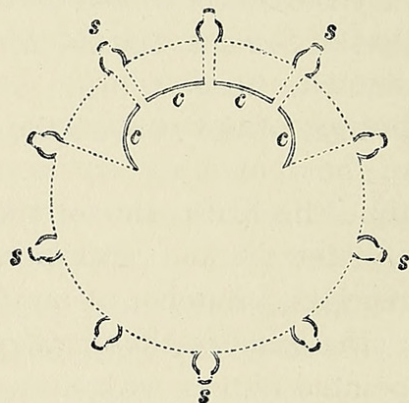


Fig. 16. A similar diagram of *Saraca indica*; the traces of the missing petals are present, but the small anterior traces of the carpellary stipe are absent; and so are those of the anterior stamens.

as the trace of a flower-leaf, sepal or (suppressed) petal, excluding the vexillum. The flanks of each of the seven anterior prominences separate from their neighbours and converge first on the outer and then on the inner side to form crescentic or concentric bundles for the stamens. The outer flank bundles of the two posterior angles now move inwards with a rotation on themselves, and soon, with the posterior bay, constitute a new (broken) vascular ring wholly posterior to the cavity

of the tube, which is now visible. A little higher up the ring at the posterior side of the flower gives off three bundles: one posterior for the (absent) vexillum, two lateral to the two posterior staminal rudiments (mostly undeveloped) in the adult flower; the two latter are inconstant. The lateral gaps soon close up, but the posterior is continued upwards as the gap of the ventral suture of the carpel. To state the case in other words:—the leaf-trace of the carpel forms a horseshoe with the opening posterior. The trace of the (absent) vexillum closes this gap, and the two posterior staminal traces enter the sides of the cylinder thus formed. Lower down the cylinder opens out on its anterior side; and the posterior arc so formed receives in its flanks the insertion of the traces from the posterior sepals (2 and 5). The traces of the remaining nine stamens are concentric above; below each opens into two, and between the two of each stamen is inserted the trace of one of the remaining sepals or petals. In the upper part of the tube the leaf-traces of the sepals and (absent) petals branch collaterally and approximate irregularly, so that each leaf receives a number of bundles.

In *Brownea* the arrangement of the bundles is also a nine-pointed festoon with the odd bay posterior. The points go to the nine anterior flower-leaves, i. e. to the sepals and the four anterior petals. The flanks of each of the seven anterior cusps bend inwards, and converge in pairs to the seven anterior stamens. The remaining small bundles, one from each of the six anterior bays, cross obliquely towards the back of the flower, and form a crescent open behind for the posterior part of the gynophore; the flanks of the two anterior cusps also converge to form each a posterior staminal trace, smaller than the seven anterior. The posterior bay now becomes convex behind, and with the large bundles from the two adjacent bays and the crescent formed of the six small bundles from the lateral and anterior bays, forms a circle at the posterior side of the flower, separated from the excentric arc of the seven more anterior staminal traces by the opening of the tube. Higher up the vexillary trace (flanked by two small crescents for the tenth

and eleventh stamens in *B. coccinea*) separates from the rest of the circle which is continued in the gynophore. In other words, each staminal trace splits into two 'half-traces,' which are inserted on either side of the corresponding sepaline or petaline trace; with the exception that when eleven stamens are present, the traces of the posterior pair go without splitting to either side of the vexillary trace. The traces from the gynophore are inserted between the 'half-traces' of adjacent stamens, from this point of view the two posterior of eleven stamens behave as 'half-traces'; the anterior traces from the gynophore are smallest.

Further, we must note that irregularities often occur; especially that the small traces of the gynophore from the seven anterior stamens may be much reduced, and I think in some cases absent.

Let us see what morphological light we can get from this study. First of all, *Saraca*, though apetalous, is equipped with a full set of alternisepalous traces obviously equivalent to the petaline traces of *Brownea*. Here we have evidence of the phylogenetic abortion of the petals, such as could not have been gleaned from the ontogeny. Again the double nature of the posterior sepal in both genera is confirmed. Then the congenital chorisis of the two posterior stamens (completing eleven) in *Brownea coccinea*, inferred from comparison with other Leguminosae, is confirmed by the fact that either sends down a single trace to be inserted on one flank of the vexillary trace; the others send down a trace which divides into two 'half-traces,' going to either flank of a floral leaf-trace.

All this is plain sailing; but it is otherwise when we look at the gynophoral traces of *Saraca*, taken by itself.

Here the stipe of the pistil receives its traces only from the posterior side of the vascular cylinder of the pedicel; in other words, they enter between those of the other floral organs of the posterior side only. If we consider the stipe as an internode between the stamens and pistil, it is obvious that its components should be inserted symmetrically between those of the lower verticels. If, on the contrary, with Karl

Schumann, we regard it as the petiolar base of the carpellary leaf, since the carpel is certainly anterior, its bundles should join those of the anterior organs. Taken alone, the distribution of the leaf-trace bundles of *Saraca*, instead of shedding light on the morphology of the gynophore, presents an enigma for solution.

In *Brownea* and the Proteaceae we find an explanation of the enigmatical conditions of *Saraca*. The proteaceous flower has a four-leaved perianth with antiphyllous stamens; and a single stipitate carpel with its placenta posterior—consequently the carpel itself is anterior, as in *Saraca*, *Brownea*, and the other Amherstieae. In some species the flower is actinomorphic; in others the perianth is open to the base in front, gamophyllous and gibbous towards the back, so as to form a short tube on the side next the ventral suture of the carpel, not the dorsal as in Amherstieae. In the actinomorphic species I have examined the leaf-traces of the gynophore are inserted symmetrically; in the zygomorphic we may distinguish two cases. In some (*Grevillea* spp.) the leaf-traces from the posterior side of the flower are present, but weaker; in the other case (*Stenocarpus salignus*) they are absent, and the bundles are exclusively derived from the anterior side of the flower. A judgment founded exclusively on the flower-anatomy of such a flower would say that the carpel being anterior received its bundles from the anterior side of the flower; but the case of *Saraca*, where the stipe of the anterior carpel receives all its traces from the posterior side, prevents this easy solution.

But the true conditions are obvious; the excentric position of the stipe, owing to the formation of the flower-tube, has influenced the internal anatomy. With the tube posterior, the posterior bundles are reduced or absent, as in Proteaceae¹; with the tube anterior, the anterior leaf-traces are reduced (*Brownea*) or absent (*Saraca*).

¹ From examination of some specimens of a *Bauhinia* kindly sent by Prof. Oliver, I believe the conditions are the same as in *Stenocarpus salignus*, the tube being anterior to the adnate stipe; but I failed to obtain satisfactory preparations from the dry material.

The presence of a complete or only partially reduced cycle of traces in the stipe of Proteaceae and *Brownea* would seem to favour the view that this is really the prolongation of the floral axis, and not a petiolar organ.

All the evidence is consistent with the view that the flower-tube is a hypertrophy of the cortical zone of the axis through which the leaf-traces bend outwards to their leaves.

In conclusion, we may note that this research, limited as its field has been, has shown the inadequacy of any single method or criterion of morphological research. I have striven to follow in the footsteps of our regretted master, Eichler, and to seek on every side evidence as to the modifications and filiation of structures which we are compelled to regard as having a common origin, and to reject all conclusions that ignore this necessary filiation.

One word as to technique. For development I have worked mostly with the simple microscope and spear-headed needles, using sections of developing buds, and the compound microscope only to elucidate one or two difficulties, and especially to verify the exact phyllotaxis of the floral bracts. I have found a most useful adjunct to my outfit in Nobbe's germinator, a thick block of porous pottery with a central disc surrounded by a gutter for water, and provided with a cover. On the disc the buds keep fresh for many days in a cool room; and a bud half dissected at night has remained in good condition till next morning. The only necessary precaution is that the disc should not be wet, only damp, as wet accelerates the browning and softening of the flowers in their meristem state.

The distribution of the vascular bundles has been chiefly worked out by moderately thick transverse sections treated with ammonia and glycerine, and sketched under the camera. For this purpose I have found the adjustable objective a* Zeiss invaluable.

ERRATA.

In Prof. Hartog's paper on the Floral organogeny and anatomy of *Brownea*
and *Saraca*.

P. 311, line 17, *omit* comma *after* long.

P. 314, Fig. xvi, the semicircular traces for the unpaired posterior stamen should
be omitted.

P. 315, line 9, from foot, *read* posterior *for* anterior.



Hartog, Marcus. 1888. "On the floral organogeny and anatomy of Brownea and Saraca." *Annals of botany* 2, 309–318.

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