FLORAL ANATOMY OF *RIVINA HUMILIS* L., AND THE THEORY OF CARPEL POLYMORPHISM

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(With 6 figures in the text)

Some time ago, in the pages of this journal, Miss Saunders described the anatomy of flowers of some members of the family Phytolaccaceae (1) and from that derived various conclusions, one of which was that in the genus *Rivina*, the gynaecium is composed not of a single carpel, as had been believed so far, but of two carpels, one anterior, valve, sterile and possessing a style and another posterior, solid, fertile and without a style. Going over her description of the plant and figures, we found that the anatomy of the gynaecium in *Rivina* is very similar to that found in the family Nyctaginaceae on which we had been working for some time and in which we had evidence for believing that there is only a single carpel. It was unfortunately not possible to obtain proper material of more than one species, namely, *Rivina humilis* L. The study of this alone, however, confirmed our first suspicions as to the validity of Miss Saunders' conclusions and revealed also some differences from her observations.

The material of *Rivina humilis* was taken from the botanic garden of the Benares Hindu University and was fixed in a mixture of formalin, acetic acid and 60 per cent. alcohol. The observations are based on serial microstome sections of flowers just before opening. The accompanying figures are all camera lucida drawings.

Observations

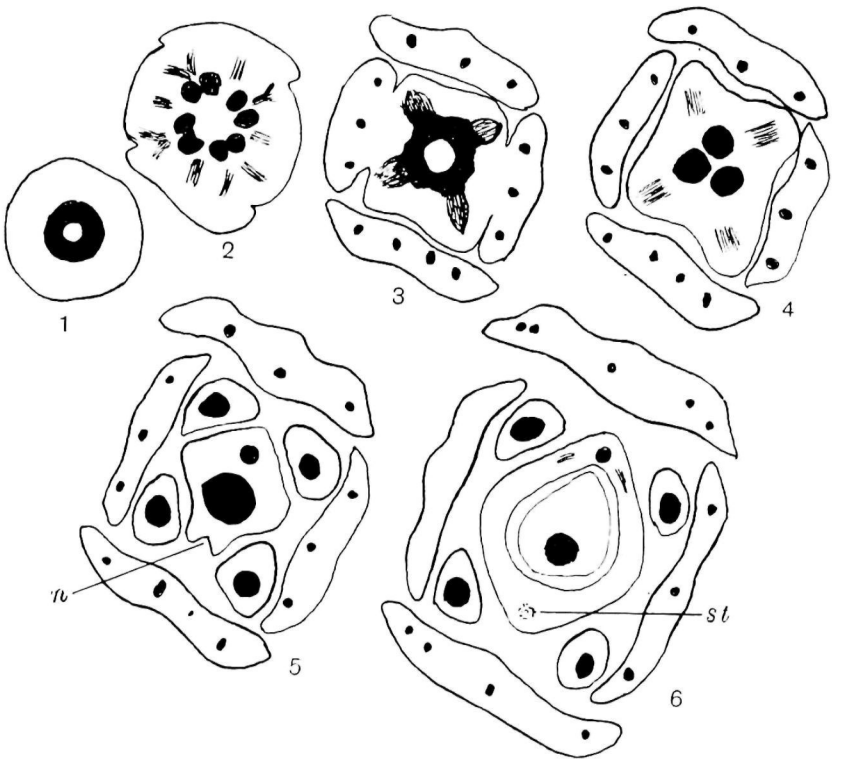
The pedicel just below the receptacle shows a complete ring of vascular tissue (Fig. 1) having xylem on the inside and phloem on the outside. This ring enlarges slightly as it reaches the receptacle and here it becomes also somewhat rectangular, conforming more or less to the shape of the receptacle itself. Both these features are due to the presence of four perianth leaves in a flower. The perianth traces are, to begin with, only eight in number (Fig. 2). Four are given off

from the sides of the rectangular stele of the thalamus and these pass out undivided to the respective perianth leaves on the four sides and form their midribs. The other four traces are given off from the four corners of the central cylinder. Each of these divides at its very base into two equal branches which pass to adjacent perianth leaves and form their laterals. In this manner every perianth leaf gets three main vascular strands which may divide a few times (especially the laterals), or may not (generally the midrib bundles), but ultimately all reach the apex and there they fade away. Both the midrib traces and lateral traces of the perianth leaves cause gaps in the stele of the thalamus on their departure, but the gaps caused by the midrib traces are more prominent and close at a higher level than those caused by the lateral traces, which are very narrow and soon close up. Miss Saunders does not describe the origin of the perianth traces. The four perianth leaves do not arise at the same level. The antero-posterior pair is the first to detach itself from the floral axis and the lateral pair of perianth leaves is detached at a slightly higher level than the former (Fig. 3).

After the departure of the perianth traces, the vascular tissue of the floral axis again forms a complete ring and now there are given off four traces for the stamens, one for each. These alternate in their position with the midrib traces and are situated just above the points of origin of the lateral traces of the perianth leaves (Fig. 3). The origin of the staminal traces causes no gaps in the stele of the floral axis. It may happen that sometimes the gaps caused by the departure of the median perianth traces may not have closed at the level of origin of the staminal traces, but absolutely no gap is seen in the stele at the points of origin of the latter, and the vascular tissue of the floral axis continues to form a more or less closed ring. Miss Saunders on the other hand figures the staminal traces as causing definite gaps in the stele and leaving behind four separate strands which she describes as the traces of the gynaecium. Even after an examination of serial sections of a number of flowers we have not been able to see such a condition. The four stamens are detached from the floral axis almost simultaneously.

Immediately after the departure of the staminal traces, and just as these reach the base of their respective stamens, the stele of the floral axis breaks up into three strands, which to begin with are nearly of an equal size (Fig. 4). Higher up one of these becomes somewhat smaller, while the other two unite to form one large bundle. In this manner a cross-section of the base of the ovary shows one large

and one small bundle (Fig. 5). The large bundle goes directly to supply the single basal ovule, while the smaller bundle passes into the ovary wall on the anterior side (Fig. 6). It gives a few branches during its course towards the style. A stylar canal (marked *st.* in Fig. 6)



Figs. 1–6. *Rivina humilis*. Figs. 1–6 are cross-sections of a flower at various levels from below upwards. Fig. 1 shows the structure of the pedicel; Fig. 2, the origin of the perianth traces; Fig. 3, the separation of the perianth leaves and the origin of the staminal traces; Fig. 4, the three traces of the gynaecium; Fig. 5 the lateral notch (*n*) in the gynaecium; Fig. 6 shows the passing of the dorsal bundle into the ovary wall and of the ventral bundle into the ovule, and a stylar canal (*st*) on the ventral side in the ovary wall. Vascular tissue in Figs. 1–6 is represented in black when cut transversely, by lines when cut lengthwise. Magnification, × 48.

makes its appearance in the ovary wall on the side opposite the vascular strand, at some distance from the base, and both this and the vascular bundle ultimately pass into the style and end in the stigma. Miss Saunders in her account says that there are four traces for the gynaecium, but we have always found only three. This is of importance as it goes against her conclusions.

Another point which she does not mention but which appears to be of great importance to us is that on the posterior side of the ovary, i.e. on the side opposite to the one which receives the small bundle, there is a marked notch at the base. This is shown in Fig. 5. This notch is found just at the base of the ovary, at about the level at which the loculus of the ovary makes its appearance. It is not so long as it is in some other plants, but even so its presence is quite clear and no doubt is left about its significance when comparison is made with the related family Nyctaginaceae. In that family we have found that in species of *Boerhaavia* the carpel remains open along this line throughout its life even in the fruit; in *Mirabilis* there is a clear line at this place showing the fusion of the margins of the original carpellary leaf, while in *Bougainvillea* there is a notch at the same place. From this series it is clear that the notch also represents the line of fusion of the margins of an originally open carpel.

DISCUSSION

The structure of the gynaecium then in *Rivina* is this. There are three traces, and this is generally believed to be the primary number in the floral leaves of flowering plants. One of these passes into the wall of the ovary, while the other two jointly supply the basal ovule. Secondly, there is a distinct notch in the ovary at its base on the posterior side, which from comparison with the family Nyctaginaceae is seen to represent the line along which the fusion of the margins of the originally open carpel has occurred. The bundle traversing the wall of the ovary is situated opposite to this notch. The simple conclusion from this evidence is that there is only a single carpel in the gynaecium of *Rivina*. The bundle supplying the ovary wall has to be interpreted as the midrib bundle of the carpel or the so-called dorsal bundle, and the two bundles supplying the ovule are to be regarded as the marginal bundles of a three-traced carpel. The latter have united and do not extend into the ovary wall, as there is only a single basal ovule. The position of the notch on the side of the ovary opposite to that of the dorsal bundle fully supports such a view. If there had been four traces for the gynaecium as Miss Saunders describes then there would have been some support for concluding that there are two carpels in *Rivina*. The present investigation shows that there are only three traces and there is absolutely no ground for her view. Eames(2) has already pointed out the inconsistency in Miss Saunders' conclusions in regarding the carpels of *Phytolacca, Ercilla,*

etc., as monomorphic and those of *Rivina* as polymorphic when all have the same vascular anatomy. He would call them all monomorphic and the present observations support his conclusions.

The monocarpellary view of the gynaecium of *Rivina* is also supported by a study of its development. A study undertaken by one of us shows that the carpel at first develops only on one side of the terminal ovule—on the side away from the axis of the inflorescence—and only later on encloses the other side. Such a development of the gynaecium is quite similar to the development of a single carpel of *Ranunculus* (3) or that of *Alchemilla* (4).

Summary

The anatomy of flowers of *Rivina humilis* is described. Two important differences are found from the account given by Saunders. First, the staminal traces do not cause any gaps in the stele of the floral axis on their departure and secondly, there are only three traces for the gynaecium.

In addition to this it has been found that there is a distinct notch on the posterior side of the gynaecium in *Rivina* which from comparison with other plants is seen to represent the line of fusion of the margins of an originally open carpel.

From these observations it is concluded that there is only a single carpel in this genus.

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