

Morphology of the Stylar Canal in Angiosperms.

BY

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With twenty-seven Figures in the Text.

THE stylar canal¹ or the conducting tissue of the style has received little attention from botanists. It is known that in the case of the hollow styles, as in *Lilium*, *Butomus*, *Agave*, *Erythronium*, *Viola*, *Campanula*, *Sarcodes*, &c., the conducting tissue lines the canal as a glandular layer or in some cases, as in *Anagallis*, fills up a hollow style; but in most cases the style is solid, with the conducting tissue as an axial strand. Coulter and Chamberlain (1) have further suggested that the hollow stylar canal with its lining of conducting tissue represents a primitive angiospermous condition, and the larger development of this tissue has resulted in the prevailing solid style; but they admit the possibility that the reverse may be true, and the hollow stylar canal may be the result of breaking down or rupture from the solid type.

No serious attempt has hitherto been made to trace the relation of the stylar canal with the other parts of the carpel, especially with the vascular system. The purpose of the present paper is to follow this relationship in a few families, the floral anatomy of which the writer has been studying.

It will be useful, however, to indicate first the present position of the anatomy of the carpel. As Eames (2) has shown, the carpel has primarily three traces, a median and two laterals, all arising from separate gaps. The median trace runs along the midrib of the carpel on its dorsal side, and is hence called the dorsal trace or the dorsal bundle. The lateral traces run along the margins of the carpel—along its ventral side—and are hence called the marginal or the ventral traces or bundles. The ovule

¹ The words stylar canal are used here in a rather comprehensive sense. Some authors restrict their use to the hollow type of style. As used here they include both the hollow and the solid types and also the whole pollen-tube conducting tissue of the style and its extensions into the ovary wall which sometimes may reach the very base of the carpel.

traces are derived from the ventral bundles. Sometimes the midrib bundles give rise very near the base of the carpel to two branches, one on either side. These are then called the median laterals. A larger number of traces than three for a carpel has been derived by multiplication from the original three and a smaller number by union or reduction.

The material studied includes the following plants: (1) *Rivina humilis* Linn. (Phytolaccaceae). (2) *Boerhaavia diffusa* Linn., *B. repanda* Willd., *Mirabilis Jalapa* L., and *Bougainvillea spectabilis* Willd. (Nyctaginaceae). (3) *Stellera Chamaejasma* L. (Thymelaeaceae). (4) *Mollugo verticillata* Linn., *Gisekia pharnaceoides* Linn., *Trianthema monogyna* Linn., and *T. pentandra* Linn. (Aizoaceae).

PHYTOLACCACEAE.

In *R. humilis*,¹ at the base of the gynaeceum, there are three vascular bundles (Fig. 1). One of these passes into the midrib of the carpel and is the dorsal bundle. The other two ventral bundles unite to form one strand (Fig. 2) which supplies the single basal ovule (Fig. 3). There is no vascular bundle on the ventral side of the ovary, but here the stylar canal makes its appearance (Fig. 3). Both the dorsal bundle and the stylar canal continue up to the apex of the style (Fig. 4).

A glance at Figs. 1-4 leaves no doubt that the stylar canal occupies the place which ordinarily should be occupied by the ventral bundles of the carpel. If these had not been completely exhausted in supplying the ovule, they would have occupied the same place.

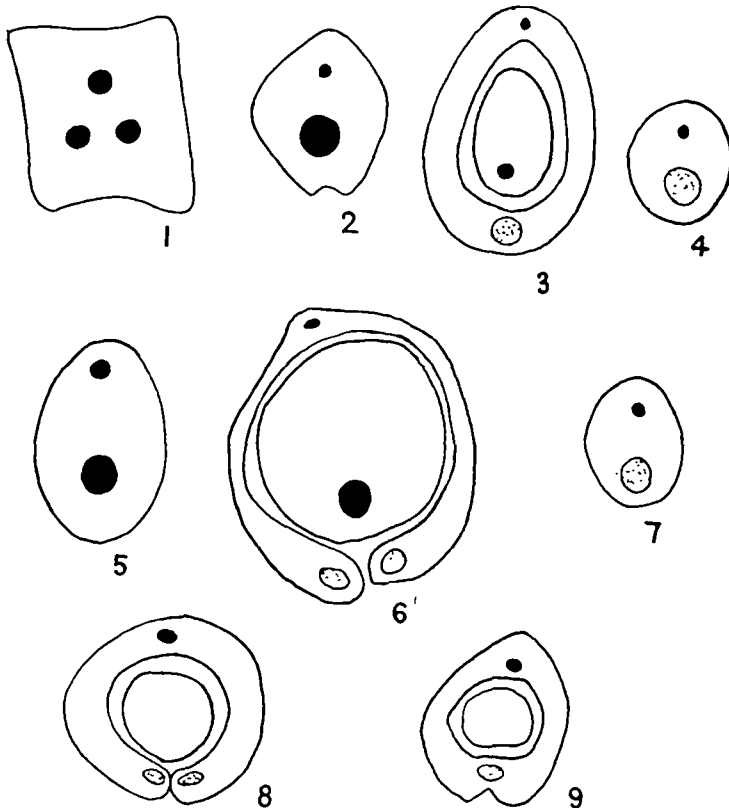
NYCTAGINACEAE.²

The vascular supply of the carpel and the relation of the stylar canal to the vascular system in the Nyctaginaceae is very similar to that of *Rivina*. Here there are, however, only two bundles at the base of the gynaeceum (Fig. 5), one large and one small. The smaller one is the dorsal bundle and passes on into the midrib of the carpel, the larger one represents the fused ventrals and passes on to supply the ovule. In species of *Boerhaavia* (*B. diffusa* and *B. repanda*) the margins of the carpel near its base never fuse with each other on the ventral side for a short distance, and it remains permanently open at this place. Correlated with this fact, two separate stylar canals make their appearance here (Fig. 6). They occupy exactly the position which is occupied ordinarily by the ventral traces of the carpel. Higher up the two stylar canals join and form one structure. This single stylar canal and the dorsal bundle of the carpel extend right up to the apex of the style, as in *Rivina* (Fig. 7).

¹ Saunders (6) regards the ovary of this plant as bicarpellary. The writer and Rao (4) have shown that it is really monocarpellary as has always been believed. Further details of floral anatomy of this plant are also given in the latter paper.

² Complete floral anatomy of some members of this family has been described elsewhere (5).

In *Mirabilis Jalapa* (Fig. 8), although the carpel is not an open structure at the base, there is a distinct line marking the union of its



FIGS. 1-9. *Rivina humilis*; transverse sections of the carpel at different levels from below upwards. 1. Just at the base, showing its three traces. 2. Slightly higher up showing the fusion of the two ventral traces to form one large bundle. 3. Passing of the larger bundle into the ovule and of the smaller into the dorsal wall of the carpel. Styelar canal has appeared at the ventral side. 4. Transverse section of the style,—the dorsal bundle and the styelar canal continue into this. 5-7. *Boerhaavia diffusa*; there are only two bundles at the base of the carpel (fig. 5). The margins of the carpel are open at the ventral side (fig. 6) and to begin with there are two styelar canals. 7. Transverse section of the style. It agrees with *Rivina* in its structure. 8. *Mirabilis Jalapa*, transverse section of the ovary. The carpel here is closed but the line of union of the two margins is quite clear. Styelar canals are similar to those of *Boerhaavia*. 9. *Bougainvillea spectabilis*, transverse section of the ovary. Carpel is closed and there is only a single styelar canal from the very base. The vascular tissue in all figures is shown in black and the styelar canals are dotted.

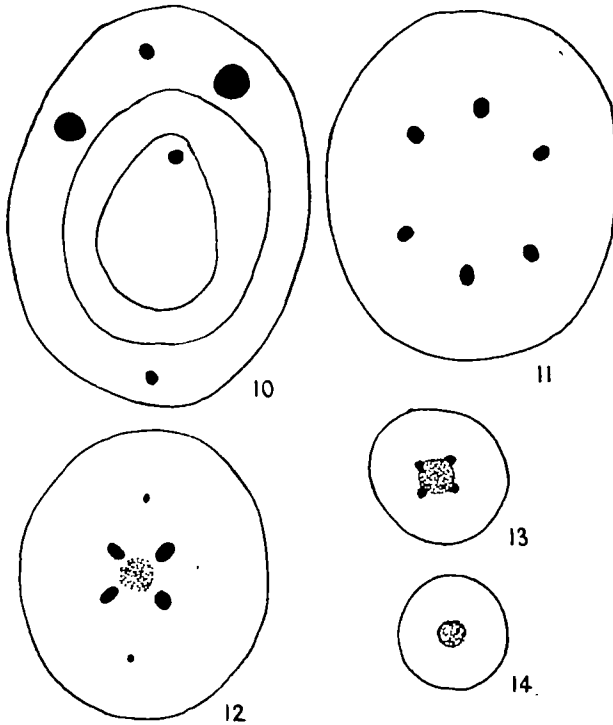
margins, and here also there are two separate styelar canals at the base which fuse higher up into one, just as in *Boerhaavia*.

In *B. spectabilis* the carpel is closed at its base, though there is a notch here marking the line of union of the carpel margins. There is a single styelar canal from the very beginning, just as in *Rivina* (Fig. 9).

It will be seen that, in every case in the family, the styelar canal occupies the place of the ventral traces of the carpel.

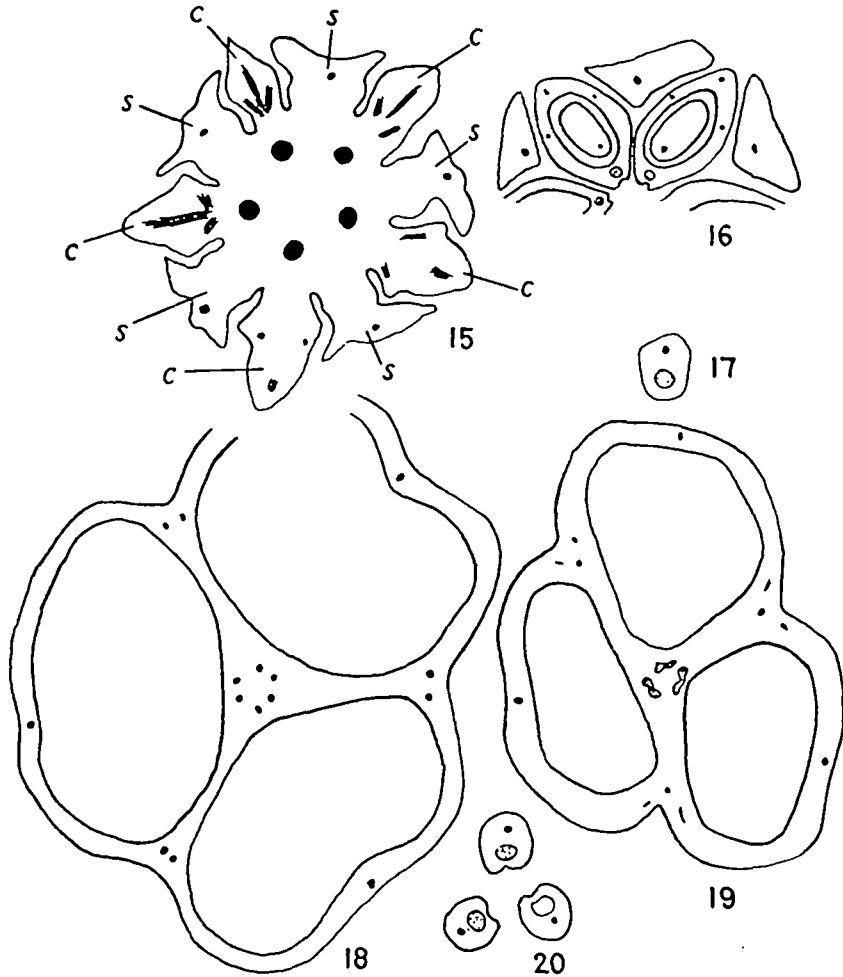
THYMELAEACEAE.

In *S. Chamaejasmae* the gynaecium is usually regarded as mono-carpellary, but the writer has shown at another place that it should be really considered bicarpellary (3). Through the greater length of its ovary



FIGS. 10-14. *Stellera Chamaejasmae*; transverse sections of the gynaecium from below upwards. 10. Ovary about its middle, showing four bundles in its wall. 11. Just below the style, showing six bundles. 12. Base of the style; four bundles pass inwards and two remain at the periphery; styler canal appears in the centre. 13-14. The style; two bundles disappear and the four others merge into the styler canal. In all figures vascular tissue is shown in black and the styler canal is dotted.

(Fig. 10) there are four vascular bundles, two of these are larger and supply the ovule and represent the ventral bundles. The other two are smaller and are the midrib bundles. After the vascular supply has been given off to the ovule, each of the larger bundles divides into two so that just below the commencement of the style or at its base there are six bundles, arranged in two groups of three each. In each group there is one dorsal bundle and two ventral or marginal bundles of the carpel (Fig. 11). The dorsal bundles simply disappear at this stage at the periphery of the style, while the four ventral bundles pass inwards (Fig. 12) and merge into the conducting tissue of the style (Figs. 13-14), which is thus seen to be continuous with the ventral traces of the carpels.

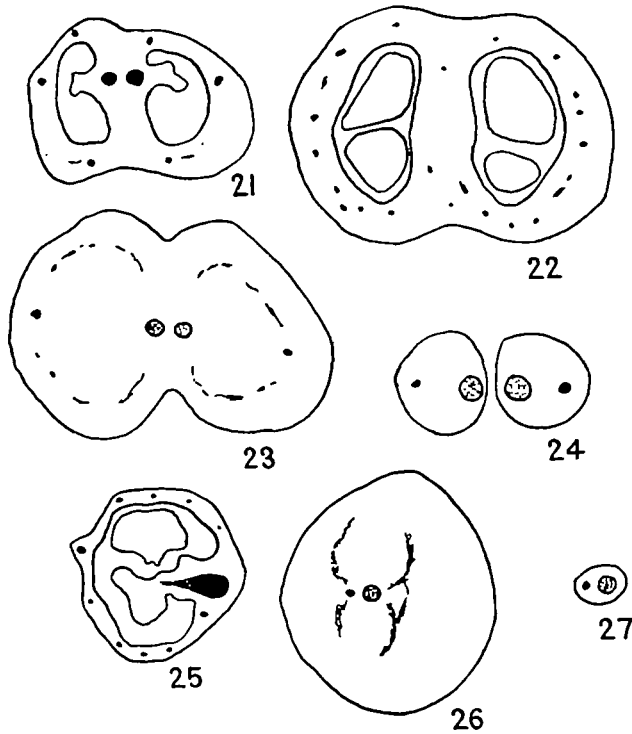


FIGS. 15-20. *Gisekia pharnaceoides*. 15. Transverse section of the thalamus after the perianth leaves have separated, showing the traces of the five carpels marked C. The stamens have not yet separated and are marked S. There are five large bundles in the centre representing the fused ventrals of the carpels. Besides these, in each carpel there is one dorsal bundle and two median laterals. 16. A part of the transverse section of the gynaeceum higher up, showing two carpels completely. The ventral bundles have passed into the ovules and the styler canals have appeared on the ventral side of the carpels. 17. Transverse section of one style, showing the presence of the dorsal bundle and styler canal. 18-20. *Mollugo verticillata*. 18. Transverse section of the ovary about the middle. There are three carpels, each with one dorsal midrib bundle, two median laterals opposite the septa and two ventrals in the centre. 19. Transverse section on the ovary just below the styles, showing the origin of the styler canals just at the place of the ventral traces of the carpels. 20. Transverse section of the styles. As before, the vascular tissue in all figures is represented in black and styler canals are dotted.

AIZOACEAE.

In *G. pharnaceoides* the gynaeceum consists of a whorl of five free carpels. Just at its base (Fig. 15) before the carpels have separated off, there are five large bundles in the centre, which represent the fused ventral

traces of the carpels, and opposite to these there are the dorsal bundles. Each of these gives rise on its sides to two median laterals. The dorsal bundles pass into the midribs of the carpels, the median laterals on to their



FIGS. 21-7. *Trianthema pentandra*. 21. Transverse section of the ovary. The structure of each carpel is similar to that of *Mollugo* except that the ventrals of each carpel are fused and form only one bundle. 22. The same higher up; the ventral bundles are found to exhaust themselves in supplying the ovules. 23. Shows the origin of the styler canals just in place of the ventral bundles. 24. Transverse section of the two styles. 25-7. *T. monogyna*, transverse sections of the carpel from below upwards. The carpel is many traced, but there is one distinct large ventral bundle and opposite to this a clear dorsal bundle (fig. 25). The styler canal appears at the place of the ventral bundle (fig. 26) and both this and the dorsal bundle continue into the style (fig. 27). As in the previous figures, the vascular tissue is represented in black and styler canals are dotted.

sides, and the fused ventrals into the solitary basal ovules of each carpel. Styler canals appear at this stage on the ventral sides of carpels, so that the condition of each carpel is very similar to that of *Rivina* (Fig. 16), and in the style also, besides the styler canal, the dorsal bundle continues right up to its apex (Fig. 17).

In *Mollugo verticillata* the gynaeceum is tricarpeillary syncarpous, with a trilocular ovary, axile placentation, and three distinct styles. A transverse section of the ovary about its middle (Fig. 18) shows six vascular strands, two opposite to each loculus. These are the ventral bundles of the carpels. Opposite to the ventral bundles, in the outer wall of the

ovary lie the midrib bundles and just opposite to the septa, the median laterals. Proceeding higher up, the ventral bundles are found to exhaust themselves in supplying the ovules and slightly higher up in their places appear the stylar canals. There is one for each carpel, and just at the base these are clearly bilobed in a transverse section, and thus show in their form that they are taking the place of the two ventral bundles (Fig. 19). The greater part of the vascular tissue disappears at the top of the ovary, but the midrib bundles continue as very weak strands along with the stylar canals into the three styles (Fig. 20).

In *T. pentandra* the gynaecium is bicarpellary-syncarpous, ovary is bilocular, with central axile placentation and bears at the top two separate styles. About the middle of the ovary (Fig. 21) there are found two large bundles in the axile placenta. These are equivalent to the fused ventrals of each carpel. Opposite to each of these are in the ovary wall, the dorsal or the midrib bundles, and at the sides of the ovary are four median laterals, two belonging to each carpel. The central axile bundles become exhausted higher up in supplying the ovules (Fig. 22). Still slightly higher up two stylar canals make their appearance exactly at the same situation (Fig. 23). Going higher up, the other vascular tissue is found to disappear, but the midrib bundles remain persistent, and one of these and one stylar canal pass into each style (Fig. 24).

T. monogyna has a half-inferior monocarpellary pistil with a single parietal placenta bearing many ovules. It receives a large number of traces from the floral axis, but one large one can be at once distinguished at the ventral side, as representing the fused ventrals (Fig. 25). It supplies the ovules. Opposite to it is the midrib bundle. This is also slightly bigger than the other bundles. Higher up the ventral bundle is absorbed in supplying the ovules. All the other traces disappear except the median dorsal. A stylar canal makes its appearance in place of the ventral bundle (Fig. 26), and this and the median dorsal bundle continue into the style (Fig. 27).

CONCLUSION AND SUMMARY.

From the description of the various plants given above, it will be seen that in every case the stylar canals are either continuous with the ventral traces of the carpel or make their appearance at, and occupy exactly the situation of, such traces. The conclusion is reached that the stylar canals have been derived from, and represent modified ventral bundles of, the carpels.

The above conclusion appears to be the obvious one. With the origin of the closed carpel with its distinct style and stigma from an open megasporophyll, nothing could be more simple than that the pollen tubes, in order to reach the ovules in the lower part of the carpel, should progress

through some of its vascular bundles. The ventral traces would be the obvious channels since the ovules are borne on the ventral side, and the earliest stylar canals must have originated by a mere cessation of the differentiation of the ventral traces of the carpel at the procambial stage. The solid type of stylar canal is therefore to be regarded as primitive. That this is the form found even at the present day in the majority of angiosperms supports such a conclusion. The hollow type of stylar canal with only a lining of conducting tissue is to be regarded as a derived and more recent condition.

The writer is indebted to Mr. R. A. Laubengayer of Cornell University, Ithaca, New York, for the material of *Mollugo verticillata*.

POSTSCRIPT.

The article by Thomas (7) appeared since this paper was in the press.

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