THE PISTIL OF BERTOLONIA MARMORATA NAUD.
(MELASTOMATACEAE)

by

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General

The flower of Bertolonia marmorata, a small herbaceous plant from South Brazil, is epigynous, pentamerous except for the trimerous gynaeicum, pentacyclic and diplostemonous. The ovary is fused to the perianth-tube basally, on cross-section it appears as an equilateral triangle, one corner of which is taken by a locule situated abaxially and epipetalous. The style is terminal, and the stigma simple, but around the style the walls of the ovary, especially their middle parts, extend freely upwards (Fig. 13).

The axillary placenta is an awl-formed structure, projecting into the locule rather perpendicular to the pistil axis.

Ontogeny

At a very early stage this pistil is a chimney-like primordium, triangular on cross-section, which later develops into the style (Fig. 1). This primordium presently becomes supported by a basal mass of meristematic tissue, and when the young pistil is about 0.15 mm high, this basal mass is differentiated into a hemispheric centre tightly enclosed by three ovary walls (Fig. 2). This centre ultimately delivers the axis and placentae of the ovary. Between this centre and the walls no septa develop until the primordium is at least 0.5 mm high. Consequently, the whole ovary comes into being as one structure, no fusion between any supposed units can be perceived. This is not so in the case of the style, for when the primordium is about 0.15 mm high, the septa, which hitherto were freely prominent, begin to touch each other in the base of the young style, and start to fuse jointlessly when the pistil is about 0.3 mm high, giving rise to the style canals (Fig. 3).

Vascular supply and further particulars

When the vascular supply was studied in some adult flowers, it was found that the pedicel contains a siphonostele with intraxylary phloem, as universally occurs within the family (Metcalf and Chalk). This stele separates into ten bundles expanding into the perianth-tube, leaving behind six arcs of vascular tissue, three outer ones and three alternating inner
ones (*Fig. 6*). The outer arched vascular strands each divide into the vascular bundles of one locule wall (*Fig. 7*). At the same time the median locule bundle already fades away a little above the base of the ovary, and a narrow cord of small-celled parenchyma takes its place. A curious fact is that in the ovary wall usually no fused bundles are formed in line with the septa, and that the bundles all end in the prolonged ends of the walls, not fusing with the stylar vascular system. The three inner arched vascular strands may often have a double origin, and in consequence the ring of vascular tissue which is formed by the three complexes when entering the central column of the ovary, often appears to be composed of six bundles. Higher up, however, the ring is completely homogeneous and provided with intraxylary phloem (*Fig. 7*).

From this ring arise three weakly developed bundles in line with the septa, which continue their course upwards, staying in the central column, and ending freely at about the level of placenta insertion (*Fig. 8*). At this level three parts of the ring branch off to the placenta, but immediately above, the ring becomes reformed by the three remaining episeptal parts, after which, however, the latter are more strongly developed than the reformed parts (*Fig. 9*).

Immediately above the placentae, the epidermic cells of the central column sectors, situated between two septa, take on a rounded cylindrical form, become densely protoplasmatic and are provided with a large nucleus. If, in successively higher cross-sections, the outline of such a central column sector is followed, a tangentially stretched style canal is seen to arise from the fusion of two lateral parts growing over a middle part (*Fig. 10*, heavy line). The inner lining of the style canal is thus formed by the epidermic tissue described above. It is noteworthy that the middle part just mentioned is two-lobed up to a short distance into the style canal, and that accordingly the vascular ring divides into two small bundles in line with each pair of lobes (*Fig. 10*). When the wall of the style canal becomes smooth again, the ring is once more reconstituted.

More upwards into the style, the vascular tissue loses its circular form and becomes triangular on cross-section, the episeptal stronger parts lying at the angles (*Fig. 11*). The triangle gradually contracts into a star-like figure at about the level where the style becomes free from the ovary. In the base of the free end of the style, the rays of the star are condensed into the vascular tissue of its points, the episeptal bundles, thus constituted, continue into the stigma. Alternating with the bundles run the style canals, which become radially elongated, and after a while fuse in the middle (*Fig. 14*).

In the adult state, as described here, the upwardly extended ovary is open, not only by means of the style canals, but also apically by three very narrow fissures between the walls (dotted in *Fig. 12*). These fissures are lined with compressed parenchyma, which is connected with the above mentioned small-celled parenchyma median dorsally to the locules, and with compressed tissue of the same appearance between the septa and the central column (*Fig. 10*, dotted line). Therefore it is evident that these phenomena anticipate the opening of the pistil as a loculicidal and septifragal fruit.
Discussion

If we want to know which parts of the gynaecium of *Bertolonia marmorata* should be called carpels, we may look for any tissue developing as margins. In doing so, we need not look at the pistil base, because it comes into being as one whole. In the style, however, the fusing septa may be considered carpellary margins, if not belonging to the placental system. For if we compare the trimerous pistil of *B. marmorata* with tetramerous or pentameric pistils (frequently present in the family, even in one species), it leads us to the idea of two different pistil sectors as possible composing units, one comprising the tissue around a locule, the other consisting of one ovary wall with the septum and part of the placental tissue perpendicular to it. This second possibility, which brings us to the conceptions of Saunders, does not offer the best explanation here, (1) because it is difficult to see how such a gynaecium could be compared with an apocarpous one, there being not any trace of a whorl of sterile carpels, (2) because the double origin of the vascular system to the supposed unit is not easily comprehensible, and (3) because of the phenomena accompanying the formation of the base of the adult style canals.

On the other hand, these objections may be ruled out if we interpret the locule wall as a carpel. It is then not necessary to accept the presence of a sterile carpel whorl, and the double origin of the vascular system uniting into a ring agrees with the supposition of fused lateral carpel parts. In this way, commissural lateral bundles are formed, which, together with the placental bundles, unite into the ring. The same bundles do not form a ring in *Centradenia floribunda* (Fig. 17) and in the genus *Mouriri* (Morley). Moreover, the epistetal stylar bundles, continuing the commissural lateral carpel bundles, split collaterally in the stigma of *C. floribunda* and *Clidemia hirta*.

To settle the question at issue, nothing can be deduced from the orientation of the vascular bundles, as they are all amphiphloic.

The three weakly developed bundles in the central column of the ovary of *B. marmorata* have to be conceived as commissural lateral carpel bundles. In *Centradenia floribunda*, *Clidemia hirta* and in the genus *Mouriri* (Morley) fused lateral carpel bundles occur in the ovary wall at the radii of the septa. In every species under consideration the septa seem to be devoid of any vascular tissue.

Concerning the structures at the base of the adult style, the two lobes described above (Fig. 10), according to this carpel conception, seem to represent the carpel margins which are involute a short distance into the

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Fig. 1—14. *Bertolonia marmorata*, magnification indicated by 0.5 cm = in reality x mm. 1, 3, 4. Longitudinal sections of pistil primordium resp. about 0.06, 0.3 and 0.4 mm high. Epidermis of tissues lying below the plane of the figure is dotted, 2, cross-sections of pistil pr. 0.15 mm high. The distances between the c.s. are given, 5. cross-section of style in young pistil about 0.5 mm high, 6—14 cross-section of adult pistil. Further explanation in text; 15—16. *Clidemia hirta*, cross-section of ovary at placental level and immediately above. The ovary is not yet delimited from the perianth-tube; 17. *Centradenia floribunda*, cross-section of ovary not yet delimited from the perianth-tube.
locule. Consequently, the corresponding splitting of the reformed ring parts and these ring parts themselves represent the marginal carpel vascular supply. This structure, as stated above, gives rise to a tangentially stretched style canal. In Centradenia floribunda and Clidemia hirta (Fig. 16), on the other hand, the style canal is radially stretched at the base, the vascular ring is not reconstituted above the placenta level and does not split into two little bundles opposite two lobes. In consequence it must be accepted that here the carpel margins are not prominent into the locule.

No opinion has as yet been offered as to the nature of the placenta; it remains to be examined whether this is a structure adherent to the carpel or connected with the axis of the flower. Its double vascular origin, fused to the commissural lateral carpel bundles seems to favour the first suggestion. This being so, the curious fact remains that a placenta like that may develop, rather independently as it seems, into an axis-like structure, covered with ovules on all sides. This matter, however, is left undecided in this study.

In Centradenia floribunda we meet with a cushion-like placenta, which, unlike the one in B. marmorata, is attached to the central column of the ovary for the greater part of its length. This is also true of Clidemia hirta, in which species the placenta is moreover attached by means of a slender sterile base, except for its ends, which extend freely upwards and downwards. On cross-section, the fertile part of this placenta shows two lobes, which are turned back a little and bear the ovules only on their outer surface (Fig. 15). In these two species, the nature of the placenta likewise cannot be discussed before more ontogenetic details will be available.

References