Internal stomata in ericaceous and other unrelated fruits

H. F. BERGMAN

(WITH NINE TEXT FIGURES)

In the examination of some diseased fruits of the cultivated cranberry, *Oxycoccus macrocarpus* (Ait.) Pers., during the winter of 1918–19, the writer observed stomata in considerable numbers in the endocarp or membrane lining the seed cavity (FIG. 1). This condition seemed so anomalous that diligent search through the literature was made in order to find out if the presence of internal stomata had previously been noticed and, if so, in what fruits they had been reported. Very few definite statements relative to internal stomata were found. In the tulip, *Tulipa Gesneriana* L., Czech (**1**, p. 104) reported their occurrence on the margin of the seed, thus confirming (p. 106) an earlier observation of Th. Hartig, and stated that he had found them also on the inner side of an unripe capsule. Schleiden* had already seen them on the integument of the seed in *Canna*. Weiss (**9**, p. 385) makes the following statement concerning stomata: "dem Fruchtknoten fehlen sie fast nie und kommen auch in der Innerauskleidung desselben vor,† desgleichen auf der Testa der Samen." Tschirch (**8**, p. 437) writes as follows: "Spaltöffnungen finden sich überall an der Pflanze, wo die Epidermis erhalten ist, nur dem Wurzeln und den Endosperm fehlen sie ausnahmlos. Man hat sie selbst . . . an der inneren Fruchknotenwand . . . gefunden." Aside from these statements nothing bearing on internal stomata was to be found in the early literature. Within more recent times, however, Winton (**10**), from observations made during the study of the structure of various edible berries used for jams and preserves, records the occurrence of stomata in the epidermis of various fruits.

* See De Bary, Comparative anatomy of the vegetative organs of the phanerogams and ferns, English edition, p. 45, footnote, where the citation, "Schleiden, Beitr. p. 10," is given. Schleiden's work has not been seen by the writer.

† As a footnote here is cited "Krocker, H. De Plantarum Epidermide. Vratislaviae 1833.—'Sie kommen da ganz allegemeine vor.'"

With reference to the structure of the cranberry he states (p. 320) that "although stomata are entirely lacking in the epicarp, it is a remarkable fact that they occur in considerable numbers in the endocarp." He also gives a figure (p. 319, *f. 29*) showing characteristic cells of the endocarp with stomata. FIG. 1 shows a similar condition.

The question immediately arose as to the possible occurrence of internal stomata in other plants, especially in other Ericaceae. Dr. Neil E. Stevens, of the Bureau of Plant Industry, kindly loaned the writer some permanent slides of sections of the fruits of *Epigaea repens* L. An examination was made of a number of sections and stomata were found in the endocarp. At that time no other plants were available, and further observations were left until later.

Among the ericaceous plants which were examined during the summer and autumn of 1919 were wintergreen (*Gaultheria procumbens*, L.), bear berry (*Arctostaphylos Uva-ursi* [L.] Spreng.), Indian pipe (*Monotropa uniflora* L. and *M. Hypopitys*, L.), blue berries (*Vaccinium corymbosum* L., *V. pennsylvanicum* Lam. and *V. vacillans* Kalm), huckleberry (*Gaylussacia baccata* [Wang.] C. Koch), dangle berry (*Gaylussacia frondosa* [L.] T. & G.), mountain cranberry (*V. Vitis-Idaea* var. *minus* Lodd.) and mountain laurel (*Kalmia latifolia* L.). Other species studied were canna (*Canna* sp.), St. John's Lily, (*Crinum asiaticum* L.) and cultivated snowberry (*Symphoricarpos racemosus* Michx.).

In describing the endocarp of the blueberry Winton (**11**, p. 371) says: "This tissue, consisting of a single thin layer of loosely united stone cells, is intermediate between the parenchymatous endocarp of the cranberry on one hand, and the thick stone-cell tissue of the huckleberry endocarp on the other. These stone cells separate readily from one another and are remarkable for their diversity of size and shape." He shows also (p. 371, *f. 288*) a figure of the endocarp of a blueberry (*V. Myrtillus* L.) *without* stomata.

In the three species of blueberries studied by the writer stomata were found in the endocarp, although often much deformed. The stomata are largest in *V. corymbosum* (FIG. 2). In *V. pennsylvanicum* (FIG. 3) they are similar but somewhat smaller. The

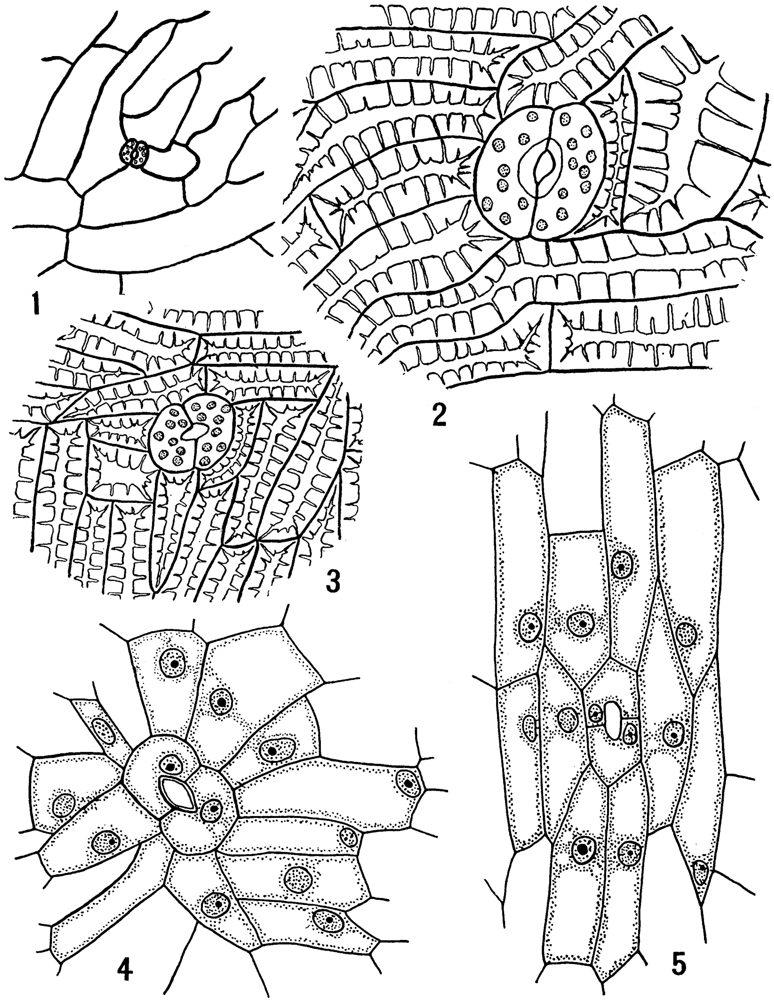


FIG. 1. A group of cells from the endocarp of cranberry (*Oxycoccus macrocarpus*) showing a stoma, × 125.

FIG. 2. A portion of the endocarp of the swamp blueberry (*Vaccinium corymbosum*) showing a stoma, × 380.

FIG. 3. A portion of the endocarp of the low blueberry (*Vaccinium pennsylvanicum*) showing a stoma, × 240.

FIG. 4. A group of cells from endocarp of Indian pipe (*Monotropa uniflora*) showing a stoma, × 190.

FIG. 5. A group of cells from the under side of a scale leaf of Indian pipe (*Monotropa uniflora*) showing a stoma, × 190.

guard cells in all three species contain chloropasts. Stomata also occur in the endocarp of fruits of *Vaccinium Vitis-Idaea* var. *minus** and in the endocarp of *Gaylussacia frondosa*. The outline formed by the guard cells in the last species is generally typical, but the stomata seem to be less well developed than in *Vaccinum* and always closed. Both species of *Gaylussacia* have an excessively stony endocarp.

Almost all authors agree on the complete absence of stomata in *Monotropa Hypopitys*. Thus Rudolphi (**5**, p. 70) says, "sie fehlen . . . bei *Monotropa Hypopitys*, *Ophrys nidus-avis* and *Cuscuta Europaea*." This statement or a similar one may be found in many of the more important works on plant anatomy. On the other hand Porsch (**3** pp. 78–79) quotes Chatin† as the authority for the statement that stomata occur rarely in *Monotropa*, although Chatin, in a special part of his work, asserts the absence of stomata on the stem and scale leaves. Chatin also, according to Porsch, reports the occurrence of stomata on the under side of the scale leaves of *Monotropa uniflora*. Solereder (**7**, p. 489) also says, "stomata are only met with exceptionally (and not in all the Monotropeae) on the axis or on the lower side of the leaf."

Observations were made on a number of plants of *Monotropa uniflora* without finding stomata in the endocarp or elsewhere. Plants of this species, however, collected in Livermore, Maine, July, 4 1919, by Dr. Stevens, showed occasional stomata in the endocarp (FIG. 4) and also on the scale leaves (FIG. 5). These were large and much misshapen, the aperture being often longer on the transverse axis of the stoma than on the longitudinal. Repeated observations of the inner surface of the ovaries of *M. Hypopitys* have failed to reveal the presence of stomata, although they have been found on the under side of the scale leaves.

Stomata were not found in the endocarp of *Gaultheria*, *Kalmia*, *Arctostaphylos*, *Gaylussacia baccata* or *Symphoricarpos*. Later, fruits of *Canna* and *Crinum* were examined and numbers of stomata found in the endocarp (FIGS. 6 and 8). The stomata on

* Material collected by Miss Mary Percival on Mt. Washington, New Hampshire, August 10, 1919. Observations made by Dr. Neil E. Stevens.

† Chatin, Adolphe. Anatomie comparée de végétaux. Paris. 1856–62. Chatin's work has not been seen by the writer.

the integument of canna seed (FIG. 7) are peculiar in having the guard cells very much larger than the surrounding cells. The presence of internal stomata in fruits of the tulip and other monocotyledonous plants is of much interest, since these are very remote in relationship to the ericaceous plants, in which group internal stomata have been most often found. No further observations have been made as to the possible occurrence of internal stomata in fruits of other monocotyledonous plants.

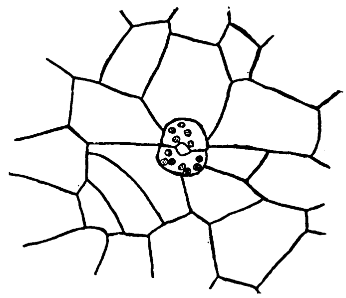


FIG. 6. A stoma from the endocarp of canna with adjacent cells, × 240.

Two points of great importance to be considered in connection with the presence of internal stomata are, first, to determine whether or not they retain their ability to function, second, to account for their persistence inside the fruit. In the attempt to answer the first question a number of observations have been

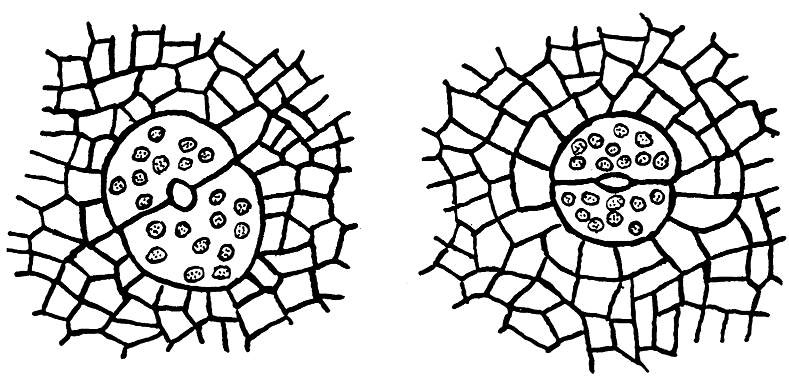


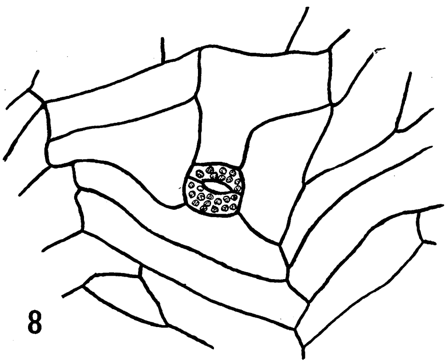
FIG. 7. Two stomata with adjacent cells from the integument of canna seed, × 760.

made on the cultivated cranberry. Berries freshly collected from the plants on clear days were taken at once into the laboratory and portions of the endocarp mounted and examined. Other berries were collected on densely cloudy days, when examinations of the stomata on the leaves of *Gaultheria*, *Arctostaphylos*, *Oxycoccus*, *Maianthemum*, *Taraxacum*, *Trifolium hybridum* and *Plantago major* showed the stomata to be closed. It was found that the internal stomata in cranberries were open as fully when collected on cloudy days as when collected on clear days. Examinations of the stomata in the endocarp of cranberries were also made from material collected in the evening shortly after sundown. The stomata were open in this case also. Stomata of other plants at sundown were found to be nearly, if not completely, closed. Moreover, an occasional stoma in the cranberry may be closed, even when most of them are wide open. Apparently these statements apply also to the blueberry and *Monotropa uniflora*, for in the many examinations of internal stomata from these plants which have been made, the stomata have been found to be open in nearly all cases. Accordingly, it appears that the stomata remain mostly in an open condition and are not functional.

As the internal stomata in the specimens examined apparently no longer retain their ability to function, it remains only to account for their presence. Morphologically a fruit must be considered as a modified leaf or as two or more modified coalesced leaves with or without some accessory parts. From the natural position of leaves on the plant, it is to be expected that the upper side of the leaf would become the inner part or endocarp of the fruit.

It is to be noted, however, that in cranberries and most other ericaceous plants the stomata occur only on the under side of the foliage leaves. We have then the apparent anomaly of a twisting or reversal of position in the fruit. A comparison of the epidermal structure of the fruit with that of the upper leaf surface shows many similarities. The shape and character of the cells in surface view and in cross section show a heavy cuticularized outer wall. Similarly the lower epidermal cells of the leaf show a correspondence with the cells of the endocarp. As far as the similarity of the epidermis of the fruit to the upper leaf epidermis is concerned, it is without much doubt simply an analogy. The lower side of the leaf in becoming modified and transformed into the fruit would of course form the outside layer of the fruit. The epidermis of the fruit and upper leaf epidermis are both exposed to the same conditions and both must protect the plant from undue loss of water. Accordingly it is not surprising that a similarity in structure has resulted in response to identical factors of the environment.

The assumption that the leaf has reversed its surfaces without an actual turning on the axis might apply very well if the epidermis of the fruit only were considered. The explanation does not seem to apply as well to the endocarp. There is apparently no useful purpose which the stomata in the endocarp might serve and to assume that they have developed from a stomata-less surface without a demand seems absurd. There still remains the possibility that in the development of the fruit the leaves which enter into the formation of the carpels have actually turned on their long axis in the process of this transformation. No evidence can be submitted to substantiate either of these suggestions. They are merely offered and left for some anatomist to answer.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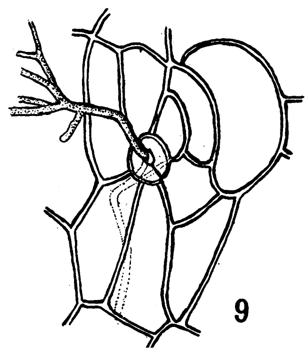
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FIG. 8. A stoma from the pericarp of *Crinum* with adjacent cells, × 190.
FIG. 9. A stoma from the endocarp of cranberry showing a fungus hypha which has come through the stoma and branched out in the seed cavity, × 240.

As these internal stomata apparently serve no purpose their persistence must be regarded as a hereditary continuation of a stomata-producing tendency after the leaf has lost its normal form and function. The persistence of stomata in parts where they are no longer useful is well known. Other examples of this are found in the occurrence of stomata on the axis and scale-leaves of underground stems of numerous plants observed by Hohnfeldt (**2**, p. 48) and in the persistence of stomata on submerged organs of many aquatic plants. Schenk (**6**) calls attention to the significance of heredity in explaining the occasional appearance of stomata on submerged organs as does also Porsch (**4**, p. 132).

It is of interest to note that in several instances in the examination of fungus-infested berries hyphae have been found entering the seed-cavity through the stomata of the endocarp (FIG. 9). This apparently was not accidental as it was observed in several instances and in no case were hyphae found which had penetrated the cell wall.

In conclusion a statement may be made with reference to gaseous interchange. It has been found that a rapid interchange of gas occurs in the respiration of cranberries and blueberries. These fruits have a thick epidermis in which stomata or lenticels are entirely lacking. The epidermis of the cranberry is provided with a layer of cuticle. That of the blueberry is cuticularized, although less so than in the cranberry. Whether or not the rate of respiration in fruits can be correlated with the thickness of the epidermis or with the cuticularized layer in the epidermis and whether a difference can be shown to exist in the rate of respiration of fruits with and without stomata are questions for further study. As stomata are lacking in many fleshy fruits most of which are provided with cuticularized epidermis, we have in such fruits excellent examples of gas interchange through cuticularized surfaces.

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