FLORAL ANATOMY AND MORPHOLOGY OF SOME SPECIES OF THE GENUS VIBURNUM OF THE CAPRIFOLIACEAE

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Previous papers (Wilkinson 1948a, 1948b) have considered the Loniceraeae, Linnaceae, and Sambuceae. This paper will concern itself exclusively with Viburnum, by far the most interesting genus studied, both morphologically and anatomically. It shows the greatest reduction and greatest complexity of any genus studied.

Viburnum differs from Sambucus in its simple leaves and one-stoned drupe. The fourteen species studied fall into seven sections. The two sections—Tinus and Megalotinus—with V. Davidi and V. cylindricum respectively are not represented. Rehder's (1940) taxonomic disposition of the species included in this study is as follows: Sect. Thyrsoma, V. Sieboldii; Sect. Lantana, V. Carlesii, V. Lantana, V. rhipidophyllum; Sect. Pseudotinus, V. alnifolium; Sect. Pseudopulus, V. tomentosum; Sect. Lentago, V. nudum, V. cassinoides, V. Lentago; Sect. Odontotinus, V. dilatatum, V. dentatum, V. acerifolium; Sect. Opulus, V. trilobum, V. Opulus.

Descriptive morphology.—As will be seen the anatomy gives only general support to this grouping. The anatomical characteristics of the groups of species have not become adequately set off to mark clearly the limits of the various groups. The anatomy and morphology do however, give the trend of evolution in the genus and show that the carpellary structure is far more complex than macroscopic examination would indicate.

In the main part of the ovary, there is a single locule with the single fertile ovule pendulous in its uppermost part (fig. 3). In the upper part of the ovary at the level of attachment of the fertile ovule, two more locules become evident. These are small and may contain one or more minute sterile ovules. Above the attachment of the fertile ovule, all three locules merge into a single 3-lobed locule. In this paper, the relatively well developed locule which is seen macroscopically in the body of the ovary will be referred to as the ovule-containing locule, the two small locules as abortive or atrophied locules, and the chamber resulting from the fusion of all three of these as the 3-lobed or compound locule.

The ovule-containing locule is usually excentric (fig. 4, 5, 10). Below the attachment of the ovule, the locule is compressed (fig. 8) and it appears elliptical in transverse section with the elliptical or slipper-shaped section of the ovule lying in the center. Below the ovule, the locule becomes even narrower (fig. 8). It is most open in V. Lentago where it is lenticular in cross section; it is a mere slit (fig. 5) in V. acerifolium, V. Carlesii, V. Opulus, V. rhipidophyllum and V. tomentosum; and it may be so compressed that its place is marked only by a line of separation where the epidermal layers of the two sides of the locule meet in V. cassinoides, V. nudum, V. trilobum and V. Lantana. Where there is a placenta projecting into the lower part of the locule—V. alnifolium, V. dentatum (fig. 4), V. Sieboldii (fig. 1), and V. rhipidophyllum—the locule may be lunar in cross section, though the two ends are often swollen.

The ovule is apparently attached on the center of the side of the ovule-containing locule adjacent to the abortive locules (fig. 6). The attachment of the ovule, i.e., the stalk, and the regions between the two abortive locules and the ovule-containing locule form three masses of tissue, which are gradually separated upward by two narrow furrows (fig. 7). The two furrows are lined on each side by a specialized epidermal layer. The stalk of the ovule may appear as a lobe (fig. 6) with a glandular epidermis projecting into the locule. Above the ovule attachment, the furrows deepen and open into the abortive locules crowded with vestigial ovules (fig. 7). This anomalous structure is thus explained: The tissue between the abortive locules is the placenta and stalk of the fertile ovule; the mass of tissue on each side of this placenta is a sterile placenta. The enlarged fertile placenta is fused below with the two sterile placenta so that its fertile ovule lies in the locule opposite—the locule of another carpel—instead of the locule on one side of it—its own carpel. Above the attachment of the ovule, the fertile placenta gradually recedes toward the wall until it is no more marked than the two sterile placenta (fig. 8, 9). The attachment of the fertile ovule is therefore parietal and the ovary is at this level actually unilocular, though 3-carpellate (fig. 8, 9). Yet because of the excessive development of the fertile placenta and the stalk of the fertile ovule between the two sterile placenta, the fusion of the three placenta, and the abortion of two locules, the ovary superficially appears to be monocarpellate with the ovule attached at the fused margins of the carpel.

The abortive ovules are attached on both sides of the fertile placenta and on both sides of the

[The Journal for July (35:365–454) was issued August 25, 1948]

AMERICAN JOURNAL OF BOTANY, VOL. 35, NO. 8, OCTOBER, 1948

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sterile placentae in *V. Sieboldii* (fig. 15), and in a flower of *V. cassinooides* which has an abortive ovule in the place of the usual fertile one. In the other species and in the fertile flowers of *V. cassinooides*, there are no ovules borne on the sides of the sterile placentae bordering the ovule-containing locule (fig. 15-19). Except in *V. Sieboldii*, therefore, the carpel which is relatively well-developed and whose locule encloses the single fertile ovule, does not itself bear a single ovule. The abortive ovules in the atrophied locules vary in number and position in the different species. They are most numerous in *V. Sieboldii*. In most species, there is at least one ovule on each side of the fertile placenta and one on the side of the sterile placenta bordering the vestigial locules. In many species, an ovule just above and on each side of the fertile ovule seems less atrophied than most of the other defective ovules (fig. 8, 15-19). The frequent presence of weak ovular traces to this pair of ovules further indicates that these two ovules were probably the most recent, phylogenetically, to abort. In more than half the species, flowers are found where all ovules are abortive, though there is usually one ovule that in size, position, and vascular supply, is obviously comparable to the fertile ovule of other flowers.

The abortive locules may appear just below the ovule attachment (specimens of *V. dentatum*, *V. Lentago*, *V. trilobum*); at the same level (*V. acerifolium*, *V. trilobum* and a specimen of *V. dentatum*), or above it as in most species. Moreover, the 3-lobed locule may extend above the separation of the calyx so that the ovary is not entirely inferior (fig. 3, 9). This prolongation of the compound locule above the calyx (fig. 9) is regularly found in *V. dentatum*, *V. dilatatum*, *V. rhitido-

phylum*, *V. tomentosum*, and *V. trilobum*. It is common in *V. acerifolium*, *V. alnifolium* and *V. cassinooides* and occurs occasionally in most of the other species. It is not found in *V. Lantana* and rarely in *V. Lentago* and *V. Sieboldii*.

On the side of the locule to which the fertile ovule is attached, a projecting placenta is sometimes apparent. This is a column of tissue which in transverse section appears as a broad, rounded lobe projecting into the locule. Such a placenta is characteristic of *V. Sieboldii* (fig. 1), *V. alni-

folium*, and *V. dentatum* (fig. 3), and was found also in two flowers of *V. rhitidophyllum*. It attains extraordinary development in *V. Sieboldii* where in two specimens, it is stalked in the lower part of the locule below the ovule (fig. 1). Often in this species, the placenta almost fills the cavity.

In the upper part of the locule, at about the level of the base of the ovule, a groove develops in the center of the placenta. But the ovule is not attached to one of the crests as might be expected; it lies in the groove. That the depression is not caused by the presence of the ovule is indicated by the fact that in *V. Sieboldii* and *V. alnifolium*, the groove extends below the ovule also. The situ-

ation is the same for *V. dentatum*, but the furrow is shallow (fig. 4). In *V. dentatum* (fig. 4) and *V. alnifolium*, the opposite wall of the locule extends toward the groove and tends to close the center of the locule so that just a lunar-shaped opening remains at each end of the locule (fig. 4).

Below the attachment of the ovule, the placenta recedes toward the inner wall so that there is no evidence of it at the region of ovule attachment (fig. 10).

Tanniferous and mucilage-containing cells are characteristic of the ovary. They are more abundant and common in the fruit than in the bud and flower stages, but if found in the fruit are usually present to some extent in the earlier stages.

**Descriptive anatomy.**—Since anatomically as well as taxonomically, *V. Sieboldii* is the most primitive member studied in the genus, it will be used as the basis of the description of the genus. This will make a comparative study possible and make the simplified structure resulting from reductions easier to understand.

The small stele of the receptacle divides usually into five bundles which after giving off traces centripetally proceed to the periphery and run up the wall of the ovary. While characteristic of the genus, five peripheral bundles are not universal. In *V. dentatum* (fig. 4), there are regularly nine or ten; in *V. alnifolium* there are eight to ten. A 2-loculate specimen of *V. Lentago* has eight bundles; two specimens of *V. rhitidophyllum* and *V. Sieboldii* have nine and six bundles respectively. In both the latter species, the specimens with additional peripheral bundles have an enlarged placenta. Such a placenta is not characteristic of *V. rhitidophyllum*, and though it is characteristic of *V. Sieboldii*, the specimens with six bundles have extraordinarily developed placentae. In a sterile ovary there are only four peripheral bundles.

From the five or more bundles below the ovary, one-five small strands approach the center. *V. Sie-

boldii, V. alnifolium, and V. Carlesii* usually have three-five; *V. dentatum, V. Lantana, V. Lentago, V. nudum, and V. trilobum* usually have two or three; *V. acerifolium, V. cassinooides, and V. to-

mentosum* vary from one-three; and *V. Opulus* and *V. rhitidophyllum* have just a single strand. Where there are more than one, the central strands fuse completely and extend up the center of the ovary (fig. 4, 5). In *V. Sieboldii*, however, one of the centripetal strands usually extends up the dorsal side of the ovule-containing locule. This is the dorsal trace of the ovule-containing carpel and extends up the center line of the carpel in the innermost layers of the carpellary tissue (fig. 1, 10). The remaining centripetal strands then unite and form the single central bundle which extends up more or less in the center of the ovary inside the ring of peripheral bundles. The central bundle is composed of the marginal supply of the three carpels of the ovary and bears a definite position with respect to the peripheral bundles. One periph-
eral bundle characteristically lies in the same radius on the same side of the locule (fig. 1, 5, 10). This peripheral bundle will be designated as “P” in the rest of this paper. On the same side of the locule on each side of “P” is another bundle, and on the other side of the locule are the remaining two bundles (fig. 1, 5–7, 10). Where there are more than five peripheral bundles, those in excess of the three are concentrated on the same side of the ovule-containing locule as the central bundle (fig. 4). Only in one flower were all the peripheral bundles found to be distributed regularly around the wall.

In addition to the peripheral bundles and the ventral bundle, (and the dorsal trace in *V. Sieboldii*, in the lower part of the ovary, there may be slight short strands given off by the bundles on each end of the ovule-containing locule as seen in transverse section (fig. 5). These bundles are directed toward the ends of the ovule-containing locule (fig. 5) and usually are short. They are prominent in *V. Lentago* and *V. Lantana* and found occasionally in *V. acerifolium*, *V. nudum* and *V. cassioides*. In other species they appear to be absent.

In the upper part of the ovary of *V. Sieboldii*, at the level of the lower half of the ovule, the central bundle divides. The separation occurs at about this level in *V. cassioides*, *V. dentatum*, *V. Opulus*, and *V. tomentosum*. In *V. acerifolium*, *V. Carlesii*, and *V. tomentosum*, the separation takes place later and may occur below the ovule. The bundle branches at or just below the ovule attachment (fig. 8) in *V. Lentago*, *V. nudum*, and *V. rhizodiphylum*. The level of separation in *V. alnifolium* and *V. Lantana* is variable. In dividing, the central bundle first becomes triangular (fig. 4), then 3-lobed with the arms parallel to the locule becoming increasingly long. Each lobe finally separates from the center. Of the four bundles thus formed, the central one is the ovular bundle, the other three are ventral bundles (fig. 21). The two bundles on each side of the ovular bundle, nearest the locule are the ventral bundles to the sterile placenta. The other ventral bundle in the same radius as the ovular bundle and “P” is the ventral bundle of the fertile placenta (fig. 21). The ventral bundles of the sterile placentae are slight in comparison with the large ovular and ventral bundles (fig. 10–y, y’, 21).

While the ovular bundle is always larger than the ventral bundles of the abortive placentae, it is not always larger than the fertile bundle. It is actually larger than any of the ventral bundles in *V. acerifolium*, *V. alnifolium*, *V. Carlesii*, *V. dentatum*, *V. Opulus*, and *V. rhizodiphylum*; in *V. Sieboldii* and most specimens of *V. Lantana*, it is smaller than the fertile ventral bundle. In *V. cassioides*, *V. Lentago*, *V. nudum*, *V. tomentosum*, and *V. trilobum*, the two are approximately the same size. When the ovular bundle separates, it may be double (fig. 10–o, 15, 20); it may be elongate (fig. 21) as in *V. Carlesii* and *V. acerifolium*; or it may be V-shaped as in *V. dentatum*. Before extending into the ovule how-
ever, it becomes a single cylindrical bundle (fig. 6, 15, 19, 23).

All the ventral bundles proceed in their respective radii toward the wall (fig. 8). There in *V. Sieboldii* and other species (*V. tomentosum*, *V. Lantana* and specimens of *V. trilobum*), the sterile ventral bundles meet bundles derived from the peripheral bundles and unite with them. These bundles derived from the peripheral bundles are lateral traces. In some species (*V. trilobum*, *V. Opulus*, *V. nudum*, and *V. Lentago*), the sterile ventral bundle may reach the position of the sterile placentae (fig. 17, 20) but fade without uniting with the lateral traces; or they may separate but barely reach the position of the placentae (fig. 21), (*V. acerifolium* and some specimens of *V. cassioides*). Sometimes no sterile ventral bundles are present (fig. 22). Where there are no sterile ventral bundles, the central bundle becomes triangular or 3-lobed and only the fertile ventral bundle separates from the large ovular bundle. This is characteristic of *V. Carlesii*, *V. rhizodiphylum* and half the specimens of *V. cassioides*. In these species, except for *V. cassioides*, the ovular bundle is usually larger than the ventral bundle. Sometimes a ventral bundle is given off to only one sterile placenta. In *V. alnifolium* this may fuse with a lateral trace in the placenta; in some specimens of *V. cassioides* it fades on reaching the placenta; and in many specimens of *V. dentatum*, it fades before reaching the placenta. While these various stages in reduction are generally characteristic of the different species, the stage is not constant for the species, for in each species there are to be found exceptions to the stage seemingly characteristic of the species.

The ventral bundle of the fertile placenta as it proceeds toward the wall of the ovary forks (fig. 6–8, 15) in *V. Sieboldii*, *V. cassioides*, *V. nudum*, *V. tomentosum* and some specimens of *V. acerifolium* and *V. Lentago*. However, the two ventral traces which make up the ventral bundle may remain united (fig. 9) as they do in *V. alnifolium*, *V. Carlesii*, *V. dentatum*, *V. Lantana*, *V. rhizodiphylum* and *V. trilobum*. On reaching the wall, the fertile ventral bundle may give off traces centrifugally which extend tangentially toward the above locule on each side (fig. 25) in *V. Sieboldii*, *V. acerifolium*, *V. Carlesii*, *V. Lentago*, *V. tomentosum*, *V. trilobum* and specimens of *V. dentatum* and *V. Lantana*. These are lateral traces. In many specimens of *V. rhizodiphylum*, such bundles separate early, often below the separation of the ovular bundle from the ventral bundle. In *V. Carlesii* the lateral traces from the fertile ventral bundle separate at the level of ovule attachment. No such bundles are given off in *V. alnifolium*, *V. cassioides* and *V. nudum*.

Usually the abortive ovules are without vascular supply, but in *V. Sieboldii*, scattered among the four main bundles are short slight traces (fig. 10–o’, 15). These usually end blindly, but some of them extend into the base of abortive ovules (fig. 15). Their position and direction indicate that they are vestigial.
traces to the abortive ovules. Such vestigial ovular traces are also common in *V. Lentago*, *V. Carlesii* and *V. Lentago* (fig. 16), and occur occasionally in *V. dentatum*, *V. nudum*, *V. tomentosum*, and *V. trilobum*. In *V. Sieboldii*, the abortive ovular traces occur in both the sterile and fertile placentae (fig. 15). In one instance in *V. Sieboldii*, one sterile ventral bundle terminates in a rudimentary ovule. In the single occurrence in *V. nudum* and a flower of *V. trilobum*, the vestigial ovular trace is in a sterile placenta. Where vestigial ovular traces are found in other species, they are in the fertile placenta only (fig. 16). Here they often consist of a pair of bundles given off by the fertile ventral bundle towards a pair of relatively well-developed abortive ovules (fig. 16). In *V. Sieboldii*, there are more often two pairs of abortive ovular traces in the fertile placenta (fig. 10-0, 15).

As the ventral and ovular bundles are separating, bundles are cut off tangentially from the inner side of the peripheral bundles. Each of the two bundles dorsal to the ovule-containing locule gives off a pair of traces or a single bundle which forks. These pairs of bundles extend into the sterile placentae where they fuse with the ventral traces and proceed up the carpels (fig. 25). From "P," lateral traces which usually arise at a higher level than those to the sterile placentae, are given off toward the fertile placenta. They may unite with the ventral traces or bundle, or they may take up their position on each side of them (fig. 9). All these are the lateral traces of the three carpels.

In other species, the separation of the lateral and dorsal traces from the peripheral bundles is not always as definite as described above for *V. Sieboldii*. In specimens with five peripheral bundles, they may be derived from all five or just four of them. Sometimes, as in *V. acerifolium*, *V. cassinoides*, *V. Lentago*, *V. nudum*, and *V. tomentosum*, no lateral traces are given off by "P" (fig. 8; in some species (*V. Carlesii*, *V. rhizidophyllum* and some specimens of *V. dentatum*, *V. Lentana* and *V. trilobum*), "P" does give off lateral traces. Where "P" does not give off lateral traces, they

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**Fig. 1-25. Viburnum.**—Fig. 1. *V. Sieboldii*. Cross section of ovary showing stalked placenta; central bundle; dorsal trace; five peripheral bundles.—Fig. 2. Cross section of base of style showing basic plan of carpellary supply.—Fig. 3. Longitudinal section showing abortive locule in different plane; attachment of fertile ovule; tapering of ovule-containing locule; continuation of locule above fertile ovule and above separation of calyx; recession of fertile placenta; recession of ventral bundle toward wall; union of lateral and ventral traces above fertile ovule; calyx, corolla, stamen and carpellar supply.—Fig. 4. *V. dentatum*. Cross section of ovary showing placenta with shallow groove and pushing in of opposite wall; asymmetrical disposition of the ten peripheral bundles; triangular central bundle.—Fig. 5-9. Cross sections of flower at successively higher levels. Fig. 2 at a level above fig. 9.—Fig. 3. Below ovule showing slit-like locule; disposition of five peripheral bundles; minute secondary strands.—Fig. 6. At region of ovule attachment, just below abortive locules showing relative position and size of three locules; double fertile ventral bundle.—Fig. 7. At region of ovule attachment showing three masses of tissue; abortive locules with ovules; disposition of five peripheral bundles with respect to carpellar bundles; pair of ventral traces; ovular bundle; double fertile ventral bundle.—Fig. 8. Above attachment of fertile ovule showing three placenta of equal size; pair of relatively well-developed abortive ovules on fertile placenta; dorsal, ventral, and lateral carpellar supply; ten peripheral bundles.—Fig. 9. Cross section of base of style showing persistence of locules and abortive ovules above separation of calyx and corolla; three parietal placenta of equal size; fused fertile ventral bundle; three dorsal and six lateral traces.—Fig. 10. *V. Sieboldii*. Below attachment of ovule showing five peripheral bundles; dorsal trace of ovule-containing carpel; large fertile ventral bundle—v; two small sterile ventral bundles—v'; pair of ovular traces—o; four abortive ovular traces—o'.—Fig. 11. Diagrammatic representation of cross section of floral prototype showing parietal placenta; one placenta longer than the other two; ovules attached biserially; each carpel with two ventral traces, two forked lateral traces, and a dorsal trace; ten peripheral bundles.—Fig. 12-14. *V. Lentago*. Cross sections of sterile ovary at successively higher levels.—Fig. 12. Shows no locule; triangular central bundle; peripheral bundles.—Fig. 13. Central bundle has divided into ovular bundle (center) and three ventral bundles.—Fig. 14. Locule present; three parietal placenta; central abortive ovule larger than the others; three pairs of ventral traces; three dorsal traces; ten peripheral bundles.—Fig. 15-19. Diagrammatic representation of series of morphological and anatomical stages in reduction of margins of carpels.—Fig. 15. *V. Sieboldii*. Shows abortive ovules and ovular traces on both sides of all three placenta; ventral bundles in all three placenta; fertile ovular bundle double at its origin;forking of fertile ventral bundle.—Fig. 16. *V. Lentago*. Shows abortive ovules only in abortive carpels; abortive ovular traces only in fertile placenta; ovular bundle fused but wide at origin; ventral bundles in all three placenta.—Fig. 17. Shows weak ventral bundles in sterile placenta; no abortive ovular traces; ovular bundle fused at origin.—Fig. 18. *V. rhizidophyllum*. Shows no ventral bundles in sterile placenta; ovular bundle large and cylindrical; fertile ventral bundle small, fused.—Fig. 19. *V. rhizidophyllum*. Shows no ventral bundles—central bundle enters ovule directly.—Fig. 20-23. Diagrams showing evolutionary stages in reduction of marginal carpellar supply.—Fig. 20. Sterile ventral bundles reach position of sterile placenta; two ovular traces to fertile ovule.—Fig. 21. *V. acerifolium*. Sterile ventral bundles become free but do not reach position of placenta; fertile ovular bundle elliptical and large.—Fig. 22. *V. Carlesii*. Sterile ventral bundles absent; fertile ovular bundle elliptical and large.—Fig. 23. *V. rhizidophyllum*. Sterile ventral bundles absent; fertile ovular bundle elliptical and large.—Fig. 24. Diagram showing vascularization of carpel—two ventral traces; two lateral traces which fork; one dorsal trace; recession of ventral traces from margin of carpel; union of lateral and ventral traces.—Fig. 25. Diagram of the two abortive carpels showing vascularization. Shows fertile ventral bundle (center) giving off lateral traces; dorsal, lateral, and ventral traces. Broken lines represent fusion with peripheral bundles; zigzag lines represent fusion tangentially with ventral traces.
are often derived centrifugally from the fertile ventral bundle (fig. 8, 25) or from adjacent peripheral bundles or both. In specimens with more than five peripheral bundles, the lateral traces may be derived from more than four peripheral bundles.

While in *V. Sieboldii*, the dorsal trace of the ovule-containing carpel usually arises at the base of the ovule; it sometimes separates from a peripheral bundle in the lower half of the ovary. In other species, this dorsal always arises from one of the peripheral bundles in the upper half of the ovary (fig. 3, 8). It arises below the attachment of the ovule in *V. Carlesii*, *V. dentatum*, and *V. tomentosum*; at the level of attachment in *V. alnifolium*, *V. nudum* and most specimens of *V. rhitidophyllum*; and above the attachment of the ovule in *V. acerifolium*, *V. cassinooides*, *V. Lantana*, *V. Lentago*, *V. Opulus*, and *V. trilobum*. Dorsal traces to the abortive carpels are cut off centripetally from the peripheral bundles on each side of "P." Instead of being cut off directly from the peripheral bundles, the dorsal traces, particularly those to the abortive carpels are sometimes derived from the lateral bundles by radial division. All the carpellary traces proceed into the style. Regardless of their number or orientation in the upper part of the ovary, in the style, the universal condition is that of a pair of bundles in each placenta and a bundle at the end of each of the lobes of the 3-lobed styral canal (fig. 2). In flowers that are not 3-carpellate, the basic plan per carpel remains the same.

Most of the peripheral bundles divide radially at about the level of attachment of the ovule and form ten bundles. "P" rarely divides radially. This division may take place below the attachment of the ovule as in *V. Lentago*, *V. trilobum* and one collection of *V. tomentosum*. In *V. cassinooides*, it often takes place at the same level, but in most species where there are five peripheral bundles, the division takes place above the attachment of the ovule, after or at the same time as the lateral and dorsal carpellary traces are being cut off centripetally.

By tangential division, "P" gives rise to a stamen and a sepal trace. The four alternating bundles do likewise. The sepal traces are derived therefore, only from stamen-sepal bundles. They are most extensive in *V. Carlesii* where they are 3-5-branched. They are regularly 3-branched in *V. rhitidophyllum* and specimens of *V. alnifolium* and *V. dentatum*, and least extensive in *V. trilobum* where if present, they are very short sligt bundles. They enter the short calyx tube and proceed towards the teeth. The five stamen and five petal traces enter the corolla tube.

**Atypical specimens.**—Irregularities in the number of members of the floral whorls occur in several specimens studied. A 6-merous fruit of *V. tomentosum* and a bud of *V. acerifolium* have a supply normal for 6-merous flowers based on the supply of 5-merous flowers, *i. e.*, the peripheral bundles divide to form twelve bundles, six of which are stamen-sepal bundles and six petal traces. In a 6-merous flower of *V. dentatum*, however, there are ten peripheral bundles. One of these, a petal bundle, gives off a sepal trace centrifugally and two stamen traces centripetally—one on each side. Both the stamen traces enter the same filament. As a result there are six sepals, six petals, but five stamens. A 4-merous bud of *V. alnifolium* has four petal traces and four stamen-sepal bundles.

One bud of *V. Lentago* has two well-developed locules. The central bundle extends up the septum to the attachment of the ovules where it breaks up into three bundles. The middle bundle is an ovular bundle; the bundle on each side is a ventral bundle. The tissue around the ovular bundle becomes delimited from that of the placenta on each side. The ovular bundle supplies the ovule that comes to lie in the groove of a 2-ridged placenta. This placenta recedes toward the wall upward from the ovule attachment. Its ventral bundle splits and proceeds centrifugally. The other ventral bundle supplies an ovule attached to one side of its placenta. The centrally attached ovule continues higher than the other. Above, two abortive locules develop at right angles to the ovule-containing locules, so that the flower is actually 4-carpellate.

In over half of the species studied, flowers were found with no well-developed locule and no fertile ovule. Two such flowers were found in *V. acerifolium*, four in *V. cassinooides*, three in *V. dentatum*, two in *V. dilatatum*, three in *V. Lentago*, two in *V. nudum*, one in *V. Sieboldii*, two in *V. tomentosum* and one in *V. trilobum*. In most of these, the lower half of the ovary lacks a locule. The central bundle extends up the center of the ovary. In the upper part of the ovary, it becomes triangular (fig. 12) or 3-lobed and finally breaks up into a median bundle and three bundles (fig. 13) which move centrifugally. These three bundles are the ventral bundles (fig. 18). The median bundle is the ovular bundle and as it continues upward, a cylinder of tissue around it becomes distinct from the surrounding tissue (fig. 14). This is followed by the appearance of three abortive locules between the ventral bundles (fig. 14). In the radii with the ventral bundles are parietal placenta and in the center, closing the locules as it were, is the ovule (fig. 14). This ovule is attached to a placenta and more abortive ovules are borne on both sides of all three placentae.

There are many variations in this basic plan. In one specimen of *V. acerifolium*, the ovular bundle fades out before the ovule is delimited. The ovular bundle of two flowers of *V. cassinooides* is minute and insignificant. One fruit has no ovular bundle, just the three ventral bundles and the unilocular area with three sterile placentae and no ovule better developed than the rest of the abortive ovules. A bud of *V. dentatum*, has two ventral
bundles and between them two bundles which unite and extend into the ovule. This is clearly a 2-carpellate flower. In two flowers of *V. Lentago*, one of the ventral bundles has associated with it two slight ovular bundles. These are abortive ovular bundles and it is significant that they are found here as well as in flowers with fertile ovules. The sterile ovary of *V. Sieboldii* has two abortive ovular traces but they are not as distinct as in the sterile ovaries of *V. Lentago*. Two other bundles are unequal in size unite and enter the centrally-located ovule. In *V. Sieboldii*, the sterile flowers of *V. trilobum*, and a flower of *V. cassinoidea*, one placenta extends further into the locule than the other two, though it eventually recedes. This is true even despite the fact that in *V. cassinoidea*, the central ovule is no more prominent than the other aborted ovules. A few sterile ovaries are not 3-carpellate. The central bundle of a flower of *V. dentatum* breaks up into four ventral bundles and an ovular bundle. All the ventral bundles fade out, three of them before the locule is apparent. The ovular bundle extends into the ovule which lies in the center of the 4-lobed locule. This flower has four stamens, one of which has a double trace as described for a 6-merous flower above. In a fruit of *V. dentatum*, a flower of *V. acerifolium* and one of *V. dilatatum*, the central bundle forms two ventral bundles and one ovular bundle. In *V. acerifolium* the ovular bundle enters an ovule. In *V. dilatatum*, the ovular bundle fades out; there are only two placenta and a linear locule. In *V. dentatum*, one of the locules is twice the size of the other and contains many more ovules.

The ventral bundles often fork in these sterile ovaries (fig. 14). They all do in *V. Lentago*, *V. Sieboldii*, *V. tomentosum*, and *V. cassinoidea*. Only two fork in *V. acerifolium* and *V. nudum*, and only one fork in the 2-loculate ovary of *V. acerifolium*. In the 2-carpellate flower of *V. dilatatum* both ventral bundles split.

Two sterile ovaries of *V. cassinoidea* have normal structure except that the “fertile ovule” is rudimentary. One flower not only has the ovule abortive, but lacks an ovular supply. The central bundle breaks up into a huge bundle, the “fertile” ventral bundle which forks, and two smaller bundles, the sterile ventral bundles which migrate to the position of the placenta.

In a fruit of *V. nudum*, the central bundle extends up one end of the locule. From it, moving up the side, a “fertile” ventral bundle (i.e., the ventral bundle analogous to that in fertile ovaries), an ovular bundle, and one sterile ventral bundle are derived. The sterile ventral bundle fades out; the fertile ventral bundle forks and the ovular trace proceeds into the ovule which though abortive, corresponds in position to the fertile ovule of normal flowers.

From the peripheral bundles are derived three dorsal traces (fig. 14). Lateral traces are cut off from the peripheral bundles in *V. dentatum*, *V. Lentago*, *V. Sieboldii* and in the 2-carpellate flowers of *V. dilatatum* and *V. trilobum*. Centrifugal lateral bundles are given off by some of the ventral bundles of *V. dilatatum* and *V. Sieboldii*. Above the locule, the supply continues in the same pattern as in normal flowers.

Discussion.—The variations in the structure of the carpellary cycle are the most varied and the most significant from an evolutionary standpoint. From these variations it is possible to attempt to trace the changes that may have occurred in the history of the pistil of this genus. The evolutionary history has been a complex one indeed. The original ancestor was undoubtedly completely 5-merous. The 4-celled ovary of *V. dentatum* and *V. Lentana*, and the 4-merous flower of *V. alnifolium* are evidence of one of the stages in this reduction. In its more recent history, however, the flower must have been a 5-merous one with a 3-carpellate pistil in which all three carpels were equally developed (fig. 11). The pistil was probably deeply lobed so that adjacent traces tended in time to fuse (fig. 11). The placentalization was parietal at least in the upper part, and the ovules were arranged in biseriate rows (fig. 11). The peripheral bundles in the wall were probably ten, giving off sepal traces at a lower level than they do in the genus today. The carpels were probably 7-traced, or at least 5-traced with the lateral traces forking at the base (fig. 24, 25). There may have been slight short branches from the main traces. Such traces are so variable and found in so few species that they are probably secondary.

The evolution toward the present-day structure of the flower included enlargement and atrophy of organs as well as adnation and cohesion of parts and of their vascular supply. The surviving fertile ovule is probably the lowermost ovule. The absence of sterile ovules or even rudiments of ovular traces below the fertile ovule in even the large number of flowers and species examined is some evidence of this. Moreover, though the abortive locules may appear slightly below the attachment of the fertile ovule (fig. 7) in *V. dentatum*, *V. Lentago* and *V. trilobum*, no abortive ovules are attached below it. Finally, where there are sterile and fertile cells, in other genera of the family, the fertile ovules seem comparable to the lowermost ovule of the sterile carpels. The position of the fertile ovule has changed from the margin of the placenta to the center. The ovary of *V. Lentago* with two well-developed locules is interesting in this respect since one of the relatively well-developed ovules is marginal as is common in primitive placenta; the other is central as is characteristic of the genus. This change in position is apparently very old, for it is impossible to determine to which of the atrophied carpels, the fertile ovule is attached. Its change in position was accompanied by the abortion of the other member of the pair of ovules at its level. Nevertheless, the ovular trace of the aborted ovule has persisted and unites with the
ovular trace of the surviving ovule in supplying it (fig. 15). The V-shaped character of the ovular bundle in *V. dentatum*, its elliptical shape in *V. Carlesii*, *V. acerifolium* (fig. 21), and other species, as well as its general large size denote its double character. The objection may be raised that the ovular bundle is not always larger than the fertile ventral bundle. Where such is the case however, it is often true that the ventral bundle consists of more than ventral traces. It often gives off abortive ovular traces, and more important, it gives off lateral traces centrifugally. In fact, where there are no lateral traces derived from "P" and none from the fertile ventral bundle, it seems highly probable that the forking of the ventral bundle is actually the separation of the lateral traces with which the ventral bundle or traces are united, since it is usually the lateral traces that are strong and well-developed above the locules and since the plan of the carpellular supply above the locules is always the same.

Associated with the development of the fertile ovules is the enlargement of the fertile placenta and the stalk of the fertile ovule. In this expansion the placenta closed the passage between the other two placenta (fig. 7, 15). This was followed by a fusion, first of the placental tissue then of the ventral and ovular bundles. As a result of this fusion, the fertile ovule lies in the locule of a carpel other than that to which it is attached. The fusion of the ventral bundles with the other ventral bundles of the pistil and with the ovular traces resulted in the presence of a single large bundle in the center of the ovary consisting of the marginal supply of all three carpels (fig. 1, 4, 5, 12). Simultaneously, there was probably a fusion of other carpellary bundles to the peripheral bundles. The enlargement of the fertile placenta, however, put the outermost lateral traces of its two carpels at some distance from "P" (fig. 11). Being nearer the fertile bundles, they united with it. This would account for the separation of lateral traces centrifugally from the fertile ventral bundle in some species. The pair of lateral traces nearer "P" united with it or with adjacent peripheral bundles. The excessive development of one placenta and ovule was accompanied by the enlargement of the locule enclosing the ovule. Following this enlargement, the other two locules and placenta with the rest of the ovules attached to them tended to abort. This may have caused a reduction in the circumference of the ovary bringing the peripheral bundles closer together and increasing the chances of their uniting radially. Whatever the cause, the peripheral bundles united and were reduced to five though in some species they are still more than five. "P" was apparently so far from the rest of the peripheral bundles that it did not unite with any of them.

This is the stage of development reached in *V. Sieboldii*. Further evolutionary stages are found within the various species today (fig. 15–23). The next change, probably next in time, since it is characteristic of most of the species of the genus, is the loss of all ovules attached to the ovule-containing carpel (fig. 16). This tendency toward reduction in the number of abortive ovules extends to the abortive locules also, for while they always bear rudimentary ovules, the ovules vary in number and extent of development. They are rather numerous in some species (*V. Sieboldii, V. Carlesii*), but may be so few and so poorly developed as in *V. alnifolium* that they would be difficult to discern without comparative study of other species. Following the abortion of ovules, the rudiments of traces to these ovules tend to disappear, first from the sterile placenta (fig. 16), finally from the fertile placenta (fig. 17). The loss of ovular traces in the sterile placenta is followed by the weakening of the sterile ventral bundles (fig. 17). These at first fail to reach the position of the placenta (fig. 21) and finally do not even separate from the central bundle (fig. 18, 22, 23). The pair of traces to the fertile ovule fuse just beyond their separation from the central bundle. The resulting bundle is V-shaped or elliptical in cross section at first (fig. 21, 22), and finally cylindrical (fig. 18, 19, 23) and gives no manifestation of doubleness. Finally the central bundle separates into two bundles—on an ovular bundle and a ventral bundle (fig. 18, 22, 23). In some flowers of *V. rhidophyllum*, even the fertile ventral bundle is absent and the central bundle extends into the ovule directly. The central bundle shows various stages of fusion at its origin also. It may result from the fusion of several bundles (*V. Sieboldii, V. alnifolium, V. Carlesii*); from few bundles as in most species; or the fusion may extend to the very origin of the various bundles of which it is composed so that there is a single bundle from the base of the ovary as in *V. Opulus* and *V. rhidophyllum*.

The lateral traces in the sterile placenta are always present, but they do not always separate as two distinct pairs in the genus today and they extend farther in some species than in others. Though the lateral traces are present in the fertile placenta of *V. Sieboldii, V. Carlesii*, and *V. rhidophyllum*, derived from both "P" and the fertile ventral bundle, they may separate only from the fertile ventral bundle (fig. 25) (*V. Lentago, V. tomentosum*); or they may be absent (*V. cassioides, V. nudum*). Where they are absent, the two abortive locules have no apparent lateral traces on the margins making up the fertile placenta. In sterile ovaries, lateral traces are often absent.

The dorsal trace of the ovule-containing carpel of *V. Sieboldii* is free at its origin or it separates in the lower part of the ovary (fig. 1, 10). The other two dorsal traces of this species and all three dorsal traces of other species are united most of their length with peripheral bundles and separate only in the upper part of the ovary.

In the non-carpellar cycles, the main evolutionary trend is in the sepal trace from the 3–5-
branched (*V. Carlesii*), to 3-branched (*V. alnifolium, V. dentatum*), to 1-branched (*V. cassioides, V. Lentago, V. Opulus*), and eventually to the complete loss of sepal traces (*V. trilobum*). There are even suggestions of the direction which floral evolution may take in the future. The long locule occupied only in the upper part by an ovule is already reduced to a slit or a line below the ovule. This will undoubtedly close. The one locule in the upper part of a 4-loculate ovary of *Sambucus* (Wilkinson, 1948b) which is entirely filled with its ovule may be the result of such a fusion. The presence of the ventral and ovular bundles of *Lonicera dioica* and *L. semperiorense* (Wilkinson, 1948a) through a mass of tissue at the base of the ovary before reaching the locules is also evidence of obliteration of the locules at the base of the ovary. Moreover, the single fertile ovule in the genus is tending to abort. The flower of *V. casinoides* with abortive ovule in the well-developed locule is an early stage in this abortion. The abortion of all the locules seen in the many sterile ovaries in so many species is a further stage in this abortion. This tendency in reduction of the number of abortive ovules may result in their total loss and eventually in the disappearance of the atrophied locules. The sterile ovaries with a central, relatively well-developed aborted ovule in the center of an abortive 3-carpellate locule (fig. 12–14) and fused to the ovary at its base, show extreme reduction indeed. This tendency toward the abortion of all ovules in an ovary is a tendency toward sterile, possibly petaloid flowers. Such flowers are found in several species (*V. macrocephalum, V. alnifolium, V. tomentosum, V. trilobum, V. Opulus, V. Sargentii*) and in horticultural (snowball) varieties of *V. macrocephalum, V. tomentosum*, and *V. Opulus*. The 2-carpellate flower of *V. dentatum* may represent a stage in the reduction of the number of carpels. The fusion of the marginal carpellary supply has already reached the extreme condition of not dividing into its constituent bundles (fig. 19) though in sterile ovaries, the ventral bundles all separate and are equally well-developed. The reduction in peripheral bundles cannot proceed much farther without affecting the number of members of the non-carpellary whors. The reduction in the calyx supply points to an abortion of the free calyx.

**RELATIONSHIPS.**—From the standpoint of floral anatomy and morphology, *V. Sieboldii* is the most primitive of the species studied. Its internal morphology and anatomy, therefore support its taxonomic position. Its primitive characters are (1) the presence of a huge placenta (fig. 1); (2) the presence of sterile ovules in the well-developed, ovule-containing carpel as well as the atrophied carpels and on both sides of all three placenta (fig. 15); (8) the large number of abortive ovules; (4) the freedom of the dorsal trace of the well-developed carpel through most of its course in the ovary (fig. 1, 10); (5) the division of the central bundle into its constituent traces well below the attachment of the ovule (fig. 10); (6) the separation of the sterile ventral bundles from the central bundle and their continuation in the sterile placentae (fig. 10, 15); (7) the separation of the ventral traces of the fertile placentae and their giving off lateral traces centrifugally; (8) the presence of vestigial ovular traces in the sterile as well as the fertile placentae (fig. 15); (9) the separation of lateral traces from “P.” There are only two characteristics of the species that might be considered advanced—the reduction of the peripheral bundles to five, and the reduction of the sepalsm to a single unbranched trace. In no other species studied, however, are so many primitive characteristics assembled.

In section *Lantana*, *V. Carlesii* and *V. Lantana* both have many primitive characteristics, though in *V. Carlesii* such traits are more numerous: the centripetal strands at the base of the ovary which unite to form the central bundle are the most numerous of any species studied; the central bundle divides at the level of the lower part of the fertile ovule; it separates into a large and usually double ovular bundle and a fertile ventral bundle which gives off lateral traces centrifugally; a pair of abortive traces are derived from the fertile ventral traces; lateral traces are derived from “P.” This species moreover, has the heaviest and most extensive carpellary supply and calyx supply of any species. Nevertheless it is advanced with respect to the fusion the length of the ovary of the traces making up the fertile ventral bundle, and the non-separation of the sterile ventral bundles from the central bundle. The latter condition probably accounts for the unusually large size of the ovular bundle.

*V. Lantana* is almost as primitive as *V. Carlesii*. The ovular bundle is elliptical in cross section; unlike *V. Carlesii*, this species has sterile ventral traces which enter the sterile placentae (fig. 20); centrifugal lateral traces are given off by the fertile ventral bundle which here as in *V. Carlesii* does not split; carpellary traces are derived from all the peripheral bundles; and there are numerous minute secondary strands in the ovary (fig. 5). The species is advanced in the fusion of the central bundle to the level of the point of attachment of the fertile ovule and in the reduction in number of abortive ovules as compared with *V. Sieboldii*.

*V. rhytidophyllum*, placed taxonomically in the same section as *V. Carlesii* and *V. Lantana*, seems rather too specialized to belong in the same group. It is highly advanced in that: the central bundle arises as a fused bundle, coming from a single bundle in the receptacle; the ovular bundle separates from the fertile ventral bundle just before entering the ovule; it is cylindrical with no evidence of its double or compound nature (fig. 18, 19, 28); no ventral bundles are given off to the sterile placentae (fig. 18, 19, 28); and the ventral bundle does not fork but may fade out or may not
even separate from the central bundle (fig. 19). Evidence of a certain degree of primitiveness is the fact that lateral traces separate from the central bundle centrifugally before it divides into ovular and ventral bundle. Such early separation is found in no other species. Moreover, two atypical specimens have placentae, nine or ten peripheral bundles, and a central bundle derived from five centripetal traces at the base of the ovary.

V. alnifolium in the section Pseudotinus is less advanced than V. rhidophyllum, but more advanced than V. Carlesii or V. Lantana. It is characterized by nine-ten peripheral bundles; the central bundle results from the union of three-five traces in the receptacle; there is a placenta; and the sepal is 3-branched. On the other hand, the vestigial ovules in the atrophied locules are the fewest and most abortive of any species studied; the sterile ventral bundles rarely become free from the central bundle (fig. 22); the fertile ventral bundle is slight and does not fork or give off lateral traces; and the carpellary supply is rather light.

V. tomentosum of the section Pseudoporus is in some respects more primitive than V. alnifolium. There are strong sterile ventral bundles; abortive ovular traces are found in some specimens; the carpellary traces from the peripheral bundles are often derived below the attachment of the ovules and are heavier than those of V. alnifolium, though not as numerous as those of V. rhidophyllum.

With respect to floral anatomy and morphology, the rest of the sections show little uniformity as to stages of evolution. Instead, one species is usually most primitive, while the rest vary in the stage of advancement. In section Lentago, V. Lentago is much less advanced than the other species. In fact, it is scarcely more advanced than V. Lantana. The locule is the most open of the species studied; the sterile ventral bundles become free; there are vestiges of ovular traces to the abortive ovules (fig. 16); the fertile ventral bundle separates into its constituent ventral traces and tends to give off lateral traces centrifugally; and the carpellary supply is rather strong. In one flower the central bundle is double. In V. cassinooides, though the sterile ventral bundles become free, they do not always reach the position of the placenta (fig. 21) and are not always both given off. The ventral bundle forks however, as in V. Lentago. The sterile ventral bundles of V. nudum barely reach their placenta and the carpellary supply is not very heavy.

In the section Odontotinus, V. dentatum has rather many primitive anatomical and morphological characters for a species having such a high taxonomic position. These characteristics are the presence of an enlarged placenta (fig. 4); the eight to ten peripheral bundles (fig. 4); the three centripetal strands at the base of the ovary which form the central bundle; the large V-shaped or double ovular bundle and its division well below the attachment of the ovule; the weakness or non-separation of the sterile ventral bundles; the presence of abortive ovular traces; the derivation of lateral traces from “P” in some specimens; and the 3-branched sepal traces. In evolutionary rank, anatomically and morphologically, the species seems closer to the more primitive members of the genus than to the more highly evolved members. It is in fact much less advanced than V. rhidophyllum being on a level with V. Lantana and V. Carlesii. V. acerifolium resembles V. dentatum only in the level of division of the central bundle. There are usually two ventral bundles which barely reach the abortive placenta. Of V. dilatatum, not enough fertile ovaries were studied to allow a comparison with the other members of the section, but the species does not seem to be as primitive as V. dentatum.

In the section Opulus, V. trilobum seems the most primitive of the two species included. Its central bundle arises from two or three centripetal bundles at the base; abortive ovular traces are found in some specimens; and lateral traces separate from the fertile ventral bundle centrifugally. In contrast, the central bundle of V. Opulus is single at its origin; there are no lateral traces derived from the fertile ventral bundle or from “P” and the carpellary supply is on the whole rather slight. Nevertheless, with respect to calyx supply, V. trilobum is the most advanced of the species studied for at times there are no free sepal traces.

It would seem therefore that in several sections, one of the species is quite primitive while some may be as advanced as species in more specialized sections. Grouping the species on the basis of their internal morphology and their vascular anatomy, they would fall into five groups. V. Sieboldii would stand alone as the most primitive, V. Opulus as the most advanced. The group of primitive species, though not as primitive as V. Sieboldii, would include V. Carlesii, V. Lantana and V. dentatum. A group of less-primitive species would include V. alnifolium, V. tomentosum, V. Lentago; and the group of more advanced species would include V. rhidophyllum, V. nudum, V. cassinooides, V. acerifolium, V. dilatatum and V. trilobum.

**SUMMARY**

Fourteen species of *Viburnum*, representing all but two sections of the genus are described. The ovary has a large excentric locule containing the fertile ovule. Above the attachment of the ovule are two abortive locules. These merge with the well-developed locule above the ovule attachment. It is then apparent that the fertile ovule is attached to the placenta common to the two sterile carpels. This placenta is enlarged and fused with the two sterile placentae most of the length of the locule. As a result of this enlargement and fusion of the placentae and abortion of two locules,
the fertile ovule lies in the locule of the carpel opposite, not in the locule of its own carpel. Vestigial ovules are usually present in the abortive carpels and are usually absent in the carpel containing the fertile ovule. The carpel with the well-developed locule, therefore, is usually sterile, though it contains the single fertile ovule in the flower. The vascular supply of the ovary consists of five peripheral bundles and a central bundle. The central bundle usually divides in the vicinity of the ovule attachment, primitively, into three ventral bundles and an ovular bundle. Reduction stages occur in the various species showing the loss of one, then both sterile ventral bundles, followed eventually by the disappearance of the fertile ventral bundle. The ovular bundle may be double at its origin, but it fuses before entering the ovule. The ovular supply, therefore, like that of the fertile ovules in the Linnaceae, is double. Some species show vestiges of ovular traces to some of the abortive ovules. Lateral and dorsal carpel-lary traces for the three carpels are variously derived from the peripheral and central bundles. Four of the peripheral bundles divide at the top of the ovary. In all, ten bundles are formed,—five petal traces, five stamen-sepal bundles. In many of the species, flowers occur with no fertile ovule, though one abortive ovule is relatively better-developed than the rest. The supply is similar to that of the normal ovary. The relatively well-developed abortive ovule is delimited in the upper part of the ovary around the ovular bundle in the center. It emerges in the center of a 3-lobed locule which contains even more reduced vestigial ovules attached to the three placentae. It is evident that there has been enlargement and atrophy of organs, and adnation and cohesion of parts and their vascular supply in the evolution of the genus. Reduction stages are found in the dorsal and marginal carpellary supply; the supply to fertile and abortive ovules; the number, position, and development of abortive ovules; the peripheral bundles; and the sepal traces. Comparative study of the internal morphology and vascular anatomy of the flower indicates that V. Sieboldii is the most primitive; V. Opulus, the most advanced. Also primitive are V. Carlesii, V. Lantana and V. dentatum. More advanced are V. rhitidophyllum, V. cassinoides, V. acerifolium, V. trifolium and others.

**THE DOMINANT ROLE OF THE EPIDERMIS IN LEAVES OF ADIANTUM**

Robert B. Wylie

The cuticle of foliage leaves protects in some degree the epidermal layers as well as underlying tissues. These living epidermal cells except in extreme xeromorphs may share in certain functions of the mesophyll. Of interest in this connection is the common occurrence of chloroplasts in the outer layers of many fern leaves belonging to the Polypodiaceae. Less-appreciated, however, are the striking modifications of these epidermal layers when serving as chlorenchyma. While some of them have normal tabular epidermal cells, many show marked specializations, particularly of the upper layer, which are evidently related to the photosynthetic activity of these cells. The following paper outlines the functional importance of the epidermal layers in leaves of certain Adiantum ferns.

Haberlandt (1882) in his classical paper on chlorenchyma mentioned the “armpalisade” type of epidermis in a few ferns, including *Adiantum trapeziiforme*, and figured a section through its upper epidermal cells showing their inner lobes. Presently other northern European botanists took up the study of fern leaves, both native and introduced. Benze (1887) surveyed the anatomy of fern leaves particularly with respect to evidence for adaptions to climate and habitat. In discussing the epidermis he stressed its importance for water storage as well as for photosynthesis. Vinge (1887) published a preliminary report on the leaf histology of ferns and later (1889) a more extensive paper on the general anatomy of a considerable number of Polypodiaceae. While this dealt primarily with the blade tissues, he considered epidermal specializations and placed twenty-six species in a group marked by definite inner bulgings of the upper epidermal cells. Petersohn (1889) studied particularly the mesophyll of native ferns and grouped them into four categories, one of which dealt with forms showing “armpalisade” without distinction as to the tissue giving rise to these specializations. He also gave attention to the numerous ferns of this group showing modifications of the upper epidermal cells. Knös (1902) contributed measurements on cell size and considered cellular structure as well as tissue relations. He noted Vinge’s earlier paper but omitted reference to his second and more comprehensive publication. Knös listed several species having protrusions from the inner walls of epidermal cells, but published no figures. He included helpful data on

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1 Received for publication February 9, 1948.