

The Mechanism of Stomata.

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THE movements of stomata have been familiar to botanists for more than a century. From all points of view, anatomical and physiological, the stomata have received more constant and lasting attention probably than any other single vegetative structure in the plant. And yet recent literature on the subject is most contradictory, not only as to the mechanism of their movements, but even as to the conditions which influence their opening and closing. On the theme proper of this paper—the relation between the structure of stomata and their movements—our knowledge is incomplete but harmonious, and I am therefore happily spared the necessity of controversy. But as this takes for granted the occurrence of movement under certain conditions, we must first determine what these conditions are, and how, aside from the structure of the stomata, the conditions are met.

The earliest attempt at a solution of these problems seems to have been that of von Mohl¹, who described the thickening of the walls of what he regarded as a typical stoma, and

¹ H. v. Mohl, Welche Ursachen bewirken die Erweiterung und Verengung der Spaltöffnungen? *Bot. Zeit.*, xiv (1856), 697, 713.

[*Annals of Botany*, Vol. XVI No. LXII. June, 1902.

added (p. 702): 'Diese ungleichförmige Wanddicke muss auf die Veränderungen dieser Zellen, wenn sie Wasser endosmotisch einsaugen oder abgeben, von Einfluss sein.' He determined that stomata freed from pressure of neighbouring cells opened in light and closed in darkness; but did not believe that stomata on uninjured leaves moved likewise by their own activity. Passing over Müller's¹ work, most of which has not stood the test of time, the next important contribution is Schwendener's², which described in detail the thickening of the walls of several stomata, and showed clearly the relation of their structure to their movements: the structure being constantly such as to permit an increase in turgescence of the guard-cells to open the pore; and the movements of the guard-cells being made more independent by thinner parts of the outer wall, next to the guard-cells, acting as hinges.

Leitgeb³, as von Mohl had less emphatically done, ascribed greater activity to the surrounding, and less to the guard-cells; his view being that if stomata closed at night the guard-cells were forced together by the increasing turgescence of the subsidiary or epidermal cells. But Leitgeb found stomata shut on brightly illuminated plants which had transpired freely, when the pressure against the guard-cells was presumably not greatest; and also observed a disappearance of solid matter in guard-cells before the pore opened. Schaefer⁴ showed conclusively for certain stomata (*Amaryllis*, *Aconitum*, &c.) that their movements were independent of the surrounding cells; for they closed in darkness and remained closed even if isolated from other cells; and opened in a saturated atmosphere, when the pressure of the neighbouring cells must

¹ N. J. C. Müller, Die Anatomie und Mechanik der Spaltöffnungen, III. Jahrb. f. wiss. Bot., viii (1872), 75-116.

² S. Schwendener, Ueber Bau und Mechanik der Spaltöffnungen. Monatsber. d. Akad. d. Wiss. zu Berlin, 1881, p. 833.

³ H. Leitgeb, Beiträge zur Physiologie der Spaltöffnungsapparate. Mitth. Bot. Inst. Graz, i (1886), 123-184.

⁴ R. Schaefer, Ueber den Einfluss des Turgors der Epidermiszellen auf die Function des Spaltöffnungsapparates. Jahrb. f. wiss. Bot., xix. (1888), 178-205. Berlin Dissertation.

have been at its maximum. As my own experiments will show, stomata open in bright light when under water. Von Mohl's assumption, that light influenced the stomata by photosynthetically increasing the amount of osmotically active material in the guard-cells, has usually been concurred in by those who ascribed to them the chief activity in their movements. Schellenberg¹ maintains that absence of CO₂ suspends the action of light; but Darwin's² results are the direct opposite.

As to the factors which directly affect stomata, it is generally agreed that abundant moisture, in the plant and in the air, tends to open the pore. When the plant transpires too actively the stomata begin to close, before the wilting is discernible (Leitgeb, Darwin). Von Mohl's statement, that if the epidermis of most plants, with the stomata open, be mounted in water the stomata promptly close, is not true of all with motile stomata (for instance, not of *Medeola*, nor, as von Mohl saw, of many Orchids). When it occurs it is because the structure of the epidermal cells lets them take up water more rapidly than the guard-cells can, and after a time the pore reopens (Schaefer, l. c., p. 189), with sections thick enough to include some of the mesophyll, so that the water does not come into immediate contact with the inner wall of the epidermis, this preliminary closing is prevented. According to Müller, Kohl³, and Darwin, closed stomata are opened by a rise in temperature; Schwendener could not substantiate this, and Leitgeb found it true in light but not in darkness.

The influence of light is to open the pore, which tends to close in darkness, and the closure at night has sometimes been regarded as wellnigh universal. The most generally recognized exceptions to this rule are halophytes, hydro-

¹ H. Schellenberg, Beiträge zur Kenntniss von Bau und Function der Spaltöffnungen. Bot. Zeit., liv (1896), 169-185.

² F. Darwin, Observations on Stomata. Proceedings of the Royal Society, lxiil. (1898), 413-417. Philos. Trans., Royal Soc., cxc (1898), 531-621: pp. 608-610.

³ F. G. Kohl, Zur Mechanik der Spaltöffnungsbewegungen. Bot. Beibl. z. Leopoldina, 1895.

phytes, and plants with nyctitropic leaves (Stahl¹, Darwin). The stomata of such hydrophytes as have them must, in general, be regarded as at least slightly motile (Leitgeb, Haberland², Darwin); Kohl and Schellenberg would regard most of them as entirely closing the pore. Stahl³ is the most positive supporter of the view that even among terrestrial plants nocturnal closure is no general rule. For the study of transpiration, his method—testing for escaping water—is certainly better than direct microscopic examination of the stomata. But when the stoma is itself the subject of study, direct observation is the only conclusive method; and comparatively few stomata have as yet been *seen* open at night. We owe these largely to Leitgeb. I shall assume then that most stomata are motile, and that the pore is more or less completely closed in darkness.

Greater precision than has hitherto been observed in the use of terms is prerequisite to an analysis of the mechanism of the movements. Turgescence and turgor, have been, used in this connexion indiscriminately for the osmotic pressure which the dissolved material in the cell-sap can exert, and for the condition of turgidity. Restricting turgescence to the latter sense, let us distinguish the former as turgor; the word is already most familiar in that use—to indicate the osmotic power of the cell-sap, usually measured by plasmolysis. The turgor in the guard-cells must vary, being increased by light⁴ or heat. The turgescence depends upon the turgor and also upon the available supply of water. In direct sunlight and proper warmth, in spite of the increasing turgor, the evaporation of water may lessen the turgescence of the guard-cells,

¹ E. Stahl, Ueber den Pflanzenschlaf und verwandte Erscheinungen. Bot. Zeit., lv (1897), 71-109.

² G. Haberlandt, Zur Kenntniss des Spaltöffnungsapparates. Flora, lxx (1887), 97-109.

³ E. Stahl, Einige Versuche über Transpiration und Assimilation. Bot. Zeit., liii (1894), 117-145.

⁴ This assumed variation in turgor needs careful study: a difference in turgor by day and by night has never been measured. Nor are the osmotically active substances known. Kohl tells us that the action of diastase opens the pore; but diastase, like sugar, is unknown in guard-cells.

causing the pore to close. The turgescence of the subsidiary and other epidermal cells must vary, but there is no reason to suspect that their turgor does so, except inappreciably with the temperature.

To distinguish between the entire opening between the guard-cells and the narrowest part of this opening, where it closes, I have decided, reluctantly, to call the former the rift, and the latter the pore. To use 'pore' for one and 'pore proper' for the other is quite unsatisfactory. 'Centralspalte' serves for the pore, when it *is* central, but it forced Haberlandt¹ to the negative description of the stoma of *Polytrichum* as 'ohne Centralspalte,' and no English word will translate it.

Hinges in the outer wall, next the guard-cell, were recognized by Schwendener (1881) as necessary to permit the lateral movement of the guard-cell. A similar thin line on the inner wall is called an inner hinge (Haberlandt, 1887). Besides these lateral hinges, which may extend a part or the whole of the side of the guard-cell, Westermaier² recognizes similar thin places at the ends as polar hinges. In all of these places it is most necessary, from the mechanical standpoint, to distinguish between mere thin lines, which will bend but not give way, and therefore are fixed axes of revolution—real hinges—and broad bands of thin wall, often the entire wall of the subsidiary cells, which permit movement by the guard-cells, but which are not fixed axes deserving to be called hinges at all. The difference in the movements permitted by the hinge and by the thin band is obvious. More details as to the hinges and their relation to the mechanism of stomata will accompany the treatment of the stomata themselves.

The pressure that may be exerted against stomata is of two very different kinds. That of the neighbouring cells,

¹ G. Haberlandt, Beiträge zur Anatomie und Physiologie der Laubmoose. Jahrb. f. wiss. Bot., xvii (1886), 359-498.

² Max Westermaier, Ueber Spaltöffnungen und ihre Nebenapparate. Schwendener Festschrift, 1889, p. 63-80.

increasing with their turgescence, cannot be guarded against by a hinge, for the latter must permit movement in one direction as well as in the other; this is true even in the possible case that the wall acts as a spring, because any movement is from a temporary state of equilibrium, disturbable in either way, else the motility of the stoma is interfered with. In many leaves, chiefly succulents, the stomata would be subjected to much greater, and probably irresistible pressure resulting from shrinking of the entire leaves with *loss* of turgescence; but this pressure would be exerted against the guard-cells by the walls, and they (the guard-cells) are protected against it by thin bands¹. Without such protection the stomata would be forced to shut, as probably occurs in the instance of *Chrysoma*², whose cross-section shows only a hinge.

In stomata whose outline changes with their movements, and only in these, the turgescence of the contiguous cells must be a factor in determining the state of equilibrium, open, closed, or intermediate. But because the pore closes with excessive transpiration when turgescence in the leaf is least, because the contents of the guard-cells furnish a clue to changes in turgor which is wanting in the neighbouring cells, because some stomata do not change their outline (surface view) in their movements, because isolated stomata usually move like those on uninjured leaves, and because the forms and structures of the guard-cells are explicable and intelligible on this ground only, the conclusion cannot be escaped that the turgescence of the neighbouring cells is a passive factor, the active one being, as Schwendener and his students have maintained, the turgescence of the guard-cells.

We are now ready to turn to a study of the structural devices by which an increase in the turgescence of the guard-cells accomplishes the opening of the pore. The types

¹ W. Benecke, Die Nebenzellen der Spaltöffnungen. Bot. Zeit. (1892), 521, 537, 553, 569, 585, 601.

² F. E. Lloyd, Some points in the anatomy of *Chrysoma pauciflosculosa*. Bull. Torr. Bot. Club., xxviii (1901), 445-450.

already familiar—those of *Amaryllis*, *Helleborus* and the Gramineae¹, described by Schwendener, Haberlandt's *Mnium* type, and the peculiar case of *Azolla* as explained by Schaefer—will be taken up in appropriate places in a sequence intended to show their relations to one another and to the various other forms to be described.

When we say that the guard-cell becomes more turgescient we mean that its volume is forcibly increased. As the cell begins to take up water, the pressure against all units of area of the wall is the same. Therefore the greater walls sustain the greater pressure; or in other words, the greatest pressure is exerted in the direction of the least diameter of the cell. To bend a wall requires less pressure than to stretch it, because in bending only one of its faces is stretched. If, then, the wall of an anisodiametric guard-cell be reasonably thin throughout, or in large part, an increase in turgescence will be accommodated without any stretching of the wall, by an equalization of the diameters, the cell becoming more nearly spherical. Stomata meeting these conditions should be regarded as structurally simple because the lack of great local thickening leaves them in so far like cells of the epidermal tissue. We will consider first stomata of little depth, which enlarge, with increasing turgescence, at right angles to the surface of the leaf.

MEDEOLA VIRGINICA, L.

The stomata of *Medeola* are irregularly scattered over both surfaces of the leaves. The epidermal cells are very large, with remarkably sinuate walls. The stomata are likewise large, of rather irregular outline, usually not quite as wide as long, though occasionally wider, as in Fig. 1. The very obtuse angles making the irregularity seen in surface view mark either the points of connexion with the stoma of the walls between the epidermal cells, or more often peculiar outgrowths or folds of the wall into the lumen of the epidermal

¹ S. Schwendener, *Die Spaltöffnungen der Gramineen und Cyperaceen*. Sitzber. Berl. Akad. Wiss., 1886, I, 65-77.

cell. Such folds occur only where the cells are in contact with stomata, and more often from the sides of the latter. The folds frequently leave what appear to be intercellular spaces next the guard-cells or in the end of the fold: I have been unable to determine the extent of these spaces in cross-section, even with serial sections cut in paraffine, but they certainly do not pass the external wall. In cross-section (Fig. 2) the stomata are conspicuously shallow. The walls are equally thin throughout, except for a narrow ridge of entrance and a place which cannot nearly always be detected, representing the ridge of exit. In very thin sections it appears that the lumen projects somewhat toward the ridge of entrance.

To study the changes in guard-cells with variations in the width of the pore, I cut surface sections of the leaf with the razor. Such sections keep the stomata subject to any tensions the underlying mesophyll may exert upon it, directly or indirectly; and spare them the violence inflicted by stripping the epidermis off alone. The leaf of *Medeola* is so spongy throughout and the stomata are so large that a little less accuracy in measurement is the only objection to studying them in place. Their appearance and behaviour are exactly the same in the sections. This is not necessarily true of all stomata, but it helps me to believe that the objections of Benecke and Kohl to work done with sections are not practically important. At any rate, on plants where it cannot be determined that there is or is not a difference it is because they cannot be studied in place, so that resort to sections, when one would measure all dimensions, is compulsory. The sections were made from leaves in bright diffuse light. They were mounted in water, drawn very carefully with a camera lucida, closed by running glycerine under the cover, and drawn again: the drawings were measured. All measurements are stated in mikrons. Even approximately accurate measurements of depth, by focussing with the micrometer screw adjustment as is feasible with many stomata, are impossible with *Medeola* for want of marks to focus on. And I was unable to make satisfactory use of Schellenberg's

method, using thick cross-sections. It is very easy to make certain that there is a decrease in depth when the pore closes, but not to measure it. The dimensions determined were:—

	I.		II.	
	Open.	Closed.	Open.	Closed.
Length of stoma	62	62	59	59
Width of stoma	46	46	47.5	47.5
Width of guard-cell	20	22 +	21	23 +
Width of pore	6	1.5	5 +	1
Width of outer vestibule . . .	11	10		

The pore of most of the stomata does not quite close: so transpiration through the stoma must take place at night. Still it is a motile stoma the width of whose pore varies more than 4μ . The length and width of the entire stoma do not change. But the closure of the pore is effected entirely by a flattening out of the guard-cells. In this process the outer vestibule is narrowed; and, as may be seen on sections viewed from within the leaf, the lines representing ridges of exit move nearer together. The whole process when the pore opens is therefore a becoming round of each guard-cell, in which all parts of the wall except the very narrow back seem to be equally concerned.

Since the pore opens at most only as much as the guard-cells become narrower—the dorsal wall being subject not to a push but to a pull from the guard-cell—it is essential that this wall be quite rigid. Though the walls are thin, this is accomplished by the outgrowths already described, which are therefore a most important feature of the apparatus. The rigidity of the ends is insured in part by the wall between the guard-cells, and by the walls between the epidermal cells, which strike the guard-cells irregularly, and in part by folds of the wall, which, however, are of much less frequent occurrence here than on the dorsal walls. The rigidity of the ends seems more essential to stomata of some other mechanical types than to these, and will be found provided for in various ways. But reinforcement of the dorsal wall is a want peculiar

to stomata of fixed outline. Solereder¹ describes what I take for a similar peculiarity of the wall of *Erodium cicutarium* and *Geranium Londezii*, figuring the latter. On California material of *E. cicutarium* however I find no such structure. The stomata of *Pyrola secunda*, L., bear a superficial resemblance, but the mechanism is altogether different. Linsbauer² describes and figures what seems to be the same structure on *Lycopodium complanatum*, L., var. *thyoides*, H. B. K. It is not present on our American *L. complanatum*, the dorsal wall of whose guard cells is too thick to require reinforcement. Leitgeb (l. c.) describes projections from the wall into the lumen of the guard-cell, of *Galtonia* and some other plants.

It may be of interest to add to this account of the stoma of *Medeola* that while only a part of the guard-cells show plasmolysis in 4 per cent. KNO_3 (tested during day), the pore begins to narrow in 1 per cent., and in 1.5 per cent. closes entirely if it does so at all.

The nearest approach to the stoma of *Medeola* hitherto described is that of

MNIUM CUSPIDATUM,

made familiar by Haberlandt³. The *Mnium* stoma approximates mechanically that of *Medeola*, agreeing in that the total area is constant, the pore opening with an increase in the depth of the guard-cells: but it falls short of the type, as Haberlandt's measurements and diagram show, in that the outer (upper) wall is rigid, so that the width of the anterior vestibule is fixed, the movement being executed entirely by the ventral and inner walls.

The stoma of

FUNARIA HYGROMETRICA

differs from that of *Medeola* to the same extent as does that of *Mnium*, but in this case the inner wall is rigid (Fig. 3),

¹ H. Solereder, Systematische Anatomie d. Dicotyledonen. Stuttg., 1898-9, p. 193.

² K. Linsbauer, Beiträge zur vergleichenden Anatomie einiger tropischen Lycopodien. Sitzungsber. d. k. Acad. d. Wiss. Wien, civ. i (1898), 995.

³ L. c., 1886: Physiol. Pflanzenanat., 2nd ed., p. 390.

leaving the movement to be performed by the ventral and outer walls. The closure is incomplete, and is effected about equally by the central part of the ventral wall and by the ridge of entrance. I measured the pore from ridge to ridge. These measurements were made on a rather small stoma.

	Open.	Closed.
Length of stoma	45	45
Width of stoma	35	35
Width of pore	5	3
Depth of guard-cell	13.7	8.4

The chief peculiarity of this stoma, as is well known¹, consists in the partial resorption of the wall between the guard-cells, leaving them in open contact at both ends of the rift. As Haberlandt pointed out (l. c. p. 465), and direct observation shows, this does not interfere with the mechanism of the stoma. As practically all stomata are symmetrical both shut and open, the variations in turgescence must be the same in both guard-cells. So far as movements are regulated by variations in the turgescence of the guard-cells alone, it can therefore make absolutely no difference in their movements whether or not the guard-cells communicate.

It is surprising that the relation between the shape of the stoma in surface view and the mechanism should hitherto have been overlooked. In those that we have been considering, the width of the guard-cells was necessarily in considerable excess over the depth. The length was limited because any possible variation in volume at the ends is wasted, and so interferes with the sensitiveness of the stoma. For these reasons, stomata with this mechanism are conspicuously broad: the limit to the ratio of breadth to length is fixed by the danger that the bulging of the outer and inner walls should be interfered with by the end walls. There are a vast number of stomata so shaped that the depth increases with

¹ W. Ph. Schimper, *Recherches anatomiques et morphologiques sur les mousses*, Strassburg, 1848; Haberlandt, l. c., 1886. Similar stomata occur on various other mosses.

an increase in turgescence; and so long as the total width of the stoma does not decrease, the increase in depth contributes to the opening of the pore. But there are comparatively few whose pore is opened by this factor alone. In many stomata of the types next to be considered there is some increase in depth, but it is not considerable and may be neglected in describing them.

SAGITTARIA VARIABILIS, ENGELM (Figs. 5, 6).

The stoma of *Sagittaria* is conspicuously narrow. The one drawn is a fair specimen; the ratio of width to length is 1 : 2.6. Looking at the stoma as a whole, which I have sought to justify by the discussion in connexion with *Funaria*, it is evident that with increasing turgescence this stoma would widen, and if possible shorten. In cross-section it is seen that closure is effected by the middle of the ventral wall and by the ridge of entrance. If the guard-cell were to be regarded as composed of two halves, one of them having thick, the other thin walls, the halves would be an outer and an inner, rather than a ventral and a dorsal. If now the entire stoma widens as its turgescence increases, the outer wall, instead of stretching, will draw back the sides of the pore, opening it. While the wall between the guard-cells does not prevent them from acting as if it were not present when the action depends on excess of length over breadth, it does, by refusing to stretch so long as an increasing volume can be accommodated more easily by a change in shape of the stoma, make it necessary to consider the guard-cells individually with respect to depth: they are deeper than wide. A limited shortening of the stoma is possible without compressing or distorting this wall, from the shortening of the rift as it widens. Schwendener (l. c. p. 845) says the outer vestibule of the stoma of *Amaryllis* shortens in widening; if this does not shorten the entire apparatus, the wall between the guard-cells must be singularly elastic. Leitgeb reports a considerable shortening of the stoma as it widens. Schaeffer (l. c. pp. 199-204) has justified the assumption that

the presence of this wall is inessential, and spared me the obligation to give statistics in this case of *Sagittaria* by making an apparatus representing a stoma of

AZOLLA CAROLINIANA

on the same mechanical principles, except that it had corners which were withdrawn as the sides bulged out. It is obvious that only a widening of the middle part of the stoma will result in opening the pore. An increase in the width of the ends would be disadvantageous, and the thick walls at the ends of the guard-cells of *Sagittaria*, as compared with their other walls, may be construed as to prevent this. The stoma of *Canna* has the ridges a little more thickened than those of *Sagittaria*: according to Weiss¹, its ratio of breadth to length is 1 : 3.49. His table contains three others more slender than that of *Sagittaria*, but I cannot speak for their mechanism. The ratio of axes of the stoma of *Luzula campestris* is 1 : 2.84. It and that of *Lilium superbum* represent a transition to the type of

AMARYLLIS.

In the stomata hitherto considered some stretching of the walls was possible, and in *Sagittaria* undoubtedly occurred. In the type to which we have now come, the stretching of the dorsal wall is the most conspicuous feature. I can add nothing to Schwendener's exposition of its mechanism (l. c. 1881). The stomata of this type are broader than that of *Lilium superbum*, deep, usually large, and freely motile. *Amaryllis formosissima* (Schwendener's subject) is stated by Weiss to have the ratio of breadth to length 1 : 0.93, it being the broadest stoma in his table; but his material must have been unusual in that respect. The thickening of the wall of the guard-cell is almost confined to the angles of the ventral face, so that with increasing turgescence the dorsal wall alone will be stretched and become more convex, drawing open the pore as in the case of *Sagittaria*. The stoma

¹ A. Weiss, Untersuchungen über die Grössen- und Zahlenverhältnisse der Spaltöffnungen. Jahrb. f. wiss. Bot., iv, 196.

of *Smilax glauca*, Walt. (Figs. 7, 8), represents this type very well. As is true of *Amaryllis*, the dorsal wall is so thin that it readily collapses in glycerine¹. The stoma of the stem of *Polygonum sagittatum*, L. (Fig. 15), also belongs here; the presence of a thin outer wall on the adjoining cell, instead of a thick wall with a hinge, makes the stoma more freely motile. The stomata of *Dracaena* sp. and of *Euonymus atropurpureus*, Jacq. (Fig. 10) are also of this type, in that the thickening is largely confined to the ventral half of the guard-cells, but the thickening is so excessive that motility is comparatively limited.

A great number of stomata combine the features of the types of *Medeola* and *Amaryllis*, so that in opening the pore the depth increases and at least a part of the dorsal wall becomes more convex. Most commonly the inner part of the stoma executes the movement, the outer walls moving little if at all. These are features of the type of

HELLEBORUS,

whose mechanism has also been fully explained by Schwendener (l. c. 1881, pp. 856-7). The stoma of *Aplectrum hyemale*, Nutt. (Fig. 11), represents this type, which is most familiar because, though one of the most complicated, it is used in various general texts as a plan from which to explain the mechanism of stomata in general. It differs most conspicuously from *Amaryllis* in that the entire inner wall, as seen in median cross-section, is strongly thickened, so that it will neither stretch nor bend. The dorsal is thin, somewhat convex, and oblique, slanting in and toward the pore. The greater diameter of the lumen—not necessarily of the entire cell—as seen in cross-section is parallel to the surface: accordingly with increasing turgescence the greatest pressure is exerted to deepen the cell. This can be done at first without stretching any wall, but merely by bending them where they are thin, if the inner wall moves backward until

¹ Not however, in my experience, until it has ceased to be stretched; cf. *Zeitgeb.*, p. 152.

the dorsal wall is straighter and perpendicular to the surface: as the inner wall moves backward and inward the pore of course opens. The inner wall of the subsidiary or other contiguous cell is usually thin throughout, and attached to the inner dorsal angle of the guard-cell, more or less at a right angle to the surface. This provides that it shall offer no considerable resistance to the movement of the guard-cell; and also, as Schwendener (1889) observes with reference to the Gramineae, by giving the deep subsidiary cell a free and elastic inner wall, removes its turgescence as an obstacle to the movement of the guard-cell (cf. Fig. 55).

It has usually been assumed that a hinge belonged to the wall of the subsidiary cell. Haberlandt (l. c., 1886, p. 466) says that a hinge is often present on the outer wall of the guard-cell of Mosses, near the dorsal side; but the rest of the description—walls inequally thickened, thicker ventrally, and back walls more or less thin—fits the type of *Amaryllis*, with which a hinge in such a place would be useless. Linsbauer (l. c., p. 1000, Fig. 7) figures the guard-cell of *Lycopodium Phlegmaria* with a hinge on the inner wall. In stomata of the type of *Helleborus*, as the pore opens by an inward and downward movement of its sides, the hinge representing the axis of a cylinder in whose periphery the side of the pore moves, it is evident that the nearer to the ridge of entrance the hinge is placed the more the sides of the pore will move backward, and the less, inward. Accordingly the hinge is practically always brought forward on to the outer wall of the guard-cell, the dorsal part of which remains thin for this reason. This is well illustrated by *Ipomoea hederacea* (Figs. 54, 55). The same advantage is gained if the pore is situated deep down in the rift, as far as possible inside the level of the hinge. In *Helleborus* and other stomata of its type the pore is therefore well inside the middle of the rift, almost down to the beginning of the inner wall. This principle is carried still farther in the stoma of *Viburnum prunifolium*, L. (Fig. 14), in which closure is effected by the ridge of exit.

ACHILLEA MILLEFOLIUM (Figs. 15, 16, 17).

Achillea and many other plants have stomata strikingly like those of *Helleborus*, but different in the one very important particular that the breadth of the lumen of the guard-cell does not exceed the depth. In the thickening of the walls and in the hinges they agree with *Helleborus*, and sometimes in a moderately oblique dorsal wall as well. The stomata of this pattern are all very small, and, while motile, do not open wide, and are therefore not good subjects for experimental study. As I would construe these stomata, they operate in part by a stretching of the dorsal wall, as in *Amaryllis*; but another factor must be recognized, at the ends of the guard-cell. The lumen there is deeper than broad, and hence widens with increasing turgescence. On its ventral face each guard-cell opposes the other, so that the increase in breadth must be by the retreat of the dorsal wall. When both ends of the dorsal wall are forced backward all of it must go, opening the pore; but as there is a hinge in the outer wall only, the inner alone is free to move bodily backward, and the resulting movement is exactly as in *Helleborus*. The responsibility of the union of the ends of the guard-cells in this mechanism demands a considerable size there, and the result is that the pore is short compared with the length of the stoma.

The study of numerous examples has convinced me that in stomata of the *Helleborus* type the ends almost always act somewhat in this same way, except as the direction of the axes makes the movement of the dorsal wall be obliquely backward and inward. Thus in the stoma represented by Fig. 12, the longest axis being $a-a'$, the greatest pressure will be at a right angle to it, and the dorsal wall will be forced in the direction of β . While the operation of the *Helleborus* stoma would be intelligible without this assistance from the ends, it is probably no inconsiderable factor. Haberlandt is right in recognizing that the type of *Helleborus* is a combination of those of *Mnium* and *Amaryllis*; it may

also contain elements of that of the Gramineae. Only the (dynamic) characters of the types of the Gramineae and of *Amaryllis* are present in that of *Achillea*. In some stomata of both of these types, in *Aplectrum* and *Lobelia* for instance, the inner wall is thickened at least dorsally very nearly to the end of the guard-cell. This gives the ends an advantage in controlling the middle part of the cell; and *Aplectrum* has a longer rift in proportion to the length of the stoma than any other of its type that I have seen.

POLYGONATUM BIFLORUM (Figs. 18, 19)

has stomata whose mechanism is such as has just been described—probably intermediate between *Helleborus* and *Achillea*—but which is entirely inverted. The outer wall is the more evenly thickened across its surface. The outer walls of the adjacent cells are at a right angle to the surface of the leaf where they strike the guard-cells; the dorsal walls incline ventrally towards the surface; and the pore is above the middle of the rift.

The restriction of the active part of the guard-cells to their ends, which is partly accomplished in *Achillea*, is complete in the stomata of

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and Cyperaceae, which have been thoroughly treated by Schwendener (1889). In median cross-section (Fig. 20) the outer and inner walls of the guard-cells are very thick, the lumen being reduced to little more than a mere slit. The subsidiary cells are much deeper than the guard-cells, and have thin outer and inner walls. In longitudinal section (Fig. 21) the guard-cells are seen to be enlarged and thin-walled at the ends; cross-sections there (Fig. 22) show the depth to be much greater than the width. With increasing turgescence the ends of the guard-cells widen, and the retreating dorsal wall carries with it the thick, passive middle part of the cell, opening the pore. In surface view (Fig. 23), these stomata are usually slender and straight-backed. Near each end of the guard-cell is a well-marked area, always easily

recognized, which represents the thin-walled part of the cell. The dorsal and polar walls are usually not far from perpendicular to the surface, though the dorsal are sometimes inclined a little inwardly towards the rift, and the polar in the other direction. The inward inclination would give the guard-cell an inward as well as a backward movement in opening the pore; which will be an advantage when the outer wall of the subsidiary cell is considerably thicker than the inner, or attached at less of an angle to the surface. But the movement of the guard-cells is typically horizontal.

In the Ericaceae the dorsal and usually the polar walls incline strongly ventrally inward; and in mature stomata, when the thickening is such that the median part must be quite rigid, they retain a slight motility, which is then mechanically of the type of the Gramineae. But, as will be shown later, they are of the type of *Achillea* when more active. *Euphorbia dentata*, Mx., has stomata on the back of the leaf very suggestive of those of the Gramineae, except in not being deep at the ends. The deep, thin-walled epidermis makes subsidiary cells unnecessary. The stomata of the stem are as near *Amaryllis* as to *Achillea*, while those of the upper surface are intermediate in structure between those of the stem and those on the back of the leaf, making a fair series of connecting forms on the one plant.

Among the Gramineae themselves it is common for the outer wall of the subsidiary cell to be thicker than the inner, as in Fig. 30, and it is always attached at an angle less favourable to free movement. The result must be that the inner part of the guard-cell is forced backward more easily than the outer. If this difference in the ease of movement becomes very considerable, the result will be a stoma standing in the same relation to the grass type that *Mnium* does to *Medeola*. The *Achillea* type will be midway between this stoma and that of *Amaryllis*, as the *Helleborus* is a combination of those of *Mnium* and *Amaryllis*.

THE GYMNOSPERMAE.

From the work of Hildebrand¹, Kraus², Strasburger³, Mahlert⁴, and Klemm⁵, it has long been recognized that the stomata of all Gymnosperms constitute a well-defined morphological type. They occur individually at the bottom of depressions, the wall just above them showing a more or less thin hinge. In median cross-section (Fig. 24) the lumen is shallow, and there can be distinguished, as Kraus says, only an outer thick and an inner thinner wall. Both walls are too thick to be bent—not to suggest stretched—by a pressure from the contents. They are strongly lignified and, where exposed to the air, cutinized. The part remaining cellulose varies in different genera. It does not look probable to me that there is any considerable movement of water through this wall (cf. Schwendener, 1881, p. 836), the ends of the guard-cells affording a readier passage. A cross-section at the end of the stoma throws the needed light on the mechanism. The outer wall is narrow, and the dorsal wall inclined about 45°, making the cell almost a right-angled triangle in section, the dorsal wall being the hypotenuse. The walls are thin throughout, except for a part of the dorsal. When the guard-cell takes up water the dorsal wall will be forced in the direction indicated by the arrow in Fig. 25, carrying with it the thick-walled part of the cell and opening the pore. The thickened line running along the dorsal wall helps the active ends to move the passive middle zone, and so permits a longer rift. The very oblique polar walls and hinges already mentioned facilitate the free movement of the guard-cells in the manner just described.

¹ F. Hildebrand, *Der Bau der Coniferen-Spaltöffnungen und einige Bemerkungen über die Vertheilung derselben*: Bot. Zeit. xviii (1860), 149-152.

² G. Kraus, *U. d. Bau d. Cycadeenfiedern*: Jahrb. f. wiss. Bot. iv (1865), 305-346.

³ E. Strasburger, *Ein Beitrag zur Entwicklungsgeschichte der Spaltöffnungen*: Jahrb. f. wiss. Bot. v (1866), 297-342.

⁴ Mahlert, *Beiträge zur Kenntniss der Laubblätter der Coniferen, mit besonderer Berücksichtigung des Spaltöffnungsapparates*: Bot. Centralb. xxiv (1885), 54, 85, &c.

⁵ P. Klemm, *Ueber den Bau der beblätterten Zweige der Cupressineen*: Jahrb. f. wiss. Bot. xvii (1886), 498-540. I have been unable to see Strübing's Königsberg thesis, of 1888, on this subject.

That the mechanism of the Gymnosperm stomata has remained so long unexplained is probably due to the difficulty of directly observing their movements. Their being overlapped by other cells is less of an obstacle to direct measurement than the bubble which persistently clings in the depression outside the pore, where the waxy surface prevents its removal by water. Moreover, on old evergreen leaves the walls become so thick even at the 'hinge' that movement is impossible; this is the case on the leafless stems of *Ephedra*. The deciduous leaves of *Ginkgo* and *Larix* have motile stomata, whose movement can be observed and measured if a surface-section is exposed to the light for several hours in water from which the gas has been partly driven off, so that it will dissolve the air from the outer respiratory chamber. They will close in alcohol or glycerine. The widest open pore I have observed measured 3.5μ ; they close completely. Measured by focussing from the outer wall of the adjacent cell to the dorsal line of the lumen of the guard-cell—from x to x in Fig. 27—the depth of *Larix Europaea* was found to be 15.2μ in water, 19μ in alcohol. The dorsal wall of the guard-cell moved downward at the same time as towards the rift in closing. Another stoma changed depth a little more.

Stomata of similar mechanical structure are not confined to the Gymnosperms. It seems to me, as it does to Westermaier (l. c. p. 77), that the stoma of *Iris*, as it is described by Schellenberg (l. c. p. 172), is more like that of a Conifer than like that of *Helleborus*. The stoma of *Allium vineale* (Figs. 28–30) is in all essentials—hinges, shape of guard-cells, pitch of walls, and distribution of thickening—like that of a Conifer: the walls are not so much thickened and not lignified. Schwendener figures the stoma of *A. Cepa* as between this one and *Amaryllis*. In the pitch of the walls, the stoma of *Polygonatum*, described above, approaches the Coniferae. The stomata of *Botrychium* will be described later.

The grass type is more motile than the Gymnosperm, because in it the direction of enlargement of the active ends is vertical to the sides of the pore, while the movement in

the Gymnosperm stoma is inclined perhaps 45° . The plan of *Medeola* presented by a stoma whose activity is restricted to the ends of the guard-cells will evidently permit no great motility. I have found it fully worked out, so that the greatest diameter of the thin-walled end is quite horizontal, only in *Osmunda Claytoniana*, L. (Figs. 31–33), and *O. regalis*, L. Stahl (l. c. 1894, p. 123), from his cobalt test, decided that the stoma of *O. regalis* was non-motile; but, while the pore does not close, its width varies somewhat. What movement occurs is an increase in the depth of the cell, in which, judging from the sections, the ends must be the active part.

In the stomata which have now been described I have intended to include a sufficient number of forms so that the various mechanical devices by which the width of the pore is made subject to the turgescence of the guard-cells should be illustrated by individual stomata, which it is convenient to call types: and also to make clear the relation of these types. As is to be expected, there are complete series of intermediate forms connecting all these types—a limit to the profitable description of which might easily be reached. There are, however, a number of individual peculiarities, as of the stoma of *Equisetum*, which have so far been passed over only for the sake of consecutiveness in types. The ecological grounds for the development of the different types can be estimated, except *a priori*, only by ascertaining in a considerable number of instances what types occur under various environments. It will also be of some interest to see to what extent any relation can be traced between the taxonomic position of plants and the mechanism of their stomata.

The Mosses, so far as they have motile stomata, seem generally to rely on an increase in the depth of the guard-cells to open the pore, agreeing in mechanism with *Mnium* or *Funaria*, more often the latter. They have been best studied by Haberlandt (1886) and Bünger¹, in whose work there is nothing to criticize, unless it be that Haberlandt did not seem

¹ Bünger, Beiträge zur Anatomie der Laubmooskapsel, Bot. Centralbl. xlii (1890): 193, 225, 257, 289, 321, 352.

to quite appreciate the general occurrence among them of the mechanical type he was first to explain.

The stomata of *Anthoceros laevis*, L., and *A. punctatus*, L. (Figs. 34, 35), have walls of rather uniform thickness, except dorsally, where the wall is too thick to be likely to be displaced by any pressure from the guard-cell. The depth of the lumen is equal to the width. I fixed my material without examining it fresh, and can only suppose from the structure of the stoma that it is inactive. The thin polar areas and the absence of hinges make it likely that the width of the pore is influenced by the shrinking or swelling of the entire sporogonium, with variation in its turgescence. These stomata are usually exceptions (Fig. 35) to De Bary's general rule¹ that at most the guard-cells are of equal height with the epidermal cells.

The stomata of *Botrychium ternatum*, Swtz., *B. simplex*, Hitchcock, and *B. Lunaria*, Swtz., are strikingly like those of the Coniferae. *B. ternatum* has the same form in all sections, with the characters a little less extreme. The wall is cellulose; and the outer respiratory chamber is just deep enough to make a place for the characteristic hinges. The stomata become rigid in autumn. The following measurements were obtained on a grown leaf in spring:—

	Open.	Closed.
Width of stoma	38	36
Width of guard-cell	17	16.5-17
Width of pore	4	2.5
Length of stoma	55	55

At the same time there was the same downward movement of the dorsal wall as in the stoma of *Larix*. In one extreme case of a stoma whose pore changed 4μ , this perpendicular movement was 5μ . These stomata of *B. ternatum* are noticeably straight-backed in surface view; and those of *B. simplex* are even more so, like the conifer type. *B. Lunaria* rivals many Conifers in the thickness of the walls in median cross-section.

¹ Comparative Anatomy, English translation, p. 36.

The restriction of the active part of the guard-cells to the ends in *Ophioglossum pendulum* is illustrated by Figs. 36 and 37, made from a stoma which had probably become rigid with age. Campbell¹ says of this species, 'The upper walls of the guard-cells are thickened irregularly': as his figure shows, this irregularity consists in leaving the thin areas at the ends, familiar in the Gramineae. The same restriction of motility to the ends, with a most excessive thickening of the middle, characterizes the stoma of *Angiopteris* (Figs. 38, 39). The deep and narrow ends would permit such a movement as in the Gramineae, insured more perfectly by the thick lines running to the ends: but the insertion of the outer and inner walls of the subsidiary cells is such that the outer part of the guard-cell, where the ridge of entrance constitutes the pore, will execute most of the movement.

In the Polypodiaceae I have examined there is in all an approach to what Haberlandt² calls the type of swimming plants, in that the ridge of entrance is well developed, while the ridge of exit is inconspicuous or not present. In *Dennstaedtia punctilobula*, Bernh. (Figs. 40, 41), this thickening of the ridge of entrance has gone far enough to give the stoma a rigid appearance, but it is really motile. Opening seems to be effected by a movement of the ridge of entrance outward as well as backward, such as must occur in lesser degree in the case of *Angiopteris*. The guard-cells of *Dennstaedtia* are thin-walled and shallow at the ends. In the following table the depth is measured from the ridge of entrance down to the deepest dorsal focus. The stoma was closed by displacing water with alcohol.

	Open.	Closed.
Width of stoma	30	28.5
Width of guard-cells	13.5 and 14	14 and 14.5
Width of pore	2.5	0
Length of stoma	44	45
Depth	17	14

¹ D. H. Campbell, *Mosses and Ferns*, 1895, p. 233.

² L. c. 1887, *Physiol. Pflanzenanatomic*, p. 401.

The first effect of the alcohol is to widen the pore, which then gradually closes, the sides becoming apparently straight before they meet. The increase in depth at the ends, which is partly responsible for opening the pore of this stoma, works to better advantage than in the stoma of *Osmunda*.

In other Fern stomata, with less thickened ridges, variations in depth are responsible for more of the movement. In median cross-section the guard-cells are shallower, as well as more equally thin-walled. These measurements are of the stoma of *Aspidium acrostichoides*, Swtz. :—

	Open.	Closed.
Length of stoma	57	57
Width of stoma	46.5	46
Width of guard-cell	20	23
Width, ridge of entrance	4	3
Width of pore	7 (about)	0
Width, ridge of exit	12	11

It is noticeable that while the ridge of entrance marked the narrowest part of the rift when open, the pore was closed by the thin wall inside. In other stomata of the same plant the ridges of entrance met one another in closing. And this occurs on most of our Ferns, except that the closing is often imperfect. In the stoma measured for the last table, the change in total width was less than 1μ , which may be regarded as the share of the *Amaryllis* type in this case. The stomata of some other Ferns—*Asplenium montanum*, Willd., *A. pinnatifidum*, Nutt., *A. platyneuron*, Oakes, and *Camptosorus*—are more slender, and the walls between the adjacent cells strike their backs: and the variations in the width of the entire stoma are not quite so inconspicuous. *Pellaea atropurpurea*, Link, on the other hand, has stomata of pronounced *Medeola* type. The 'free' situation of the stomata of *Niphobolus*¹ and some species of *Aneimia*² makes no peculiar demands on their mechanism.

¹ K. Giesenhagen, Ueber die Anpassungserscheinungen einiger epiphytischer Farne: Schwendener-Festschrift, 1899, p. 1; Die Farngattung *Niphobolus*, Jena, 1901, p. 85, literature there.

² Strasburger, l. c. 1866, p. 327; F. Hildebrandt, Ueber die Entwicklung der

The stomata of *Marsilia quadrifolia* are very like those of *Asplenium*. Two other Filicineae have stomata too well known to be entirely passed over here—*Salvinia natans* and *Azolla Caroliniana* (Figs. 42, 43). I have had fresh material of neither. The stomata of both remain open in formalin and alcohol. The mechanism of *Azolla* has been explained by Schaefer (l. c.), with whose material mine agrees in having the guard-cells as deep as broad. I agree again with Schaefer, Haberlandt (l. c. 1887), and Mettenius that the wall between the guard-cells is partly dissolved, which Strasburger¹ denied. As to *Salvinia*, it is agreed even by Kohl (l. c.), who concedes so much for no other stoma, that it is rigid.

The stomata of *Lycopodium lucidulum*, Mx., and *L. complanatum*, L., have thickened ridges which give the appearance of the *Amaryllis* type to sections. The dorsal wall, however, is thick, so that in surface view the stoma appears surrounded by an irregular heavy band—which is not quite so thick in *L. obscurum*, L. The shape of the lumen, with an observation of the movement, shows that the stoma is nearest the type of *Medeola*, but with the activity restricted largely to the dorsal half. The stoma measured was of *L. lucidulum*.

	Open.	Closed.
Length	49	49
Width of stoma	51	51
Width of guard-cell, average	24	25
Width of pore	3	1
Width, between ridges of entrance	14	13

The decrease in depth was about 7 μ . These stomata remain motile on leaves several years old. I have not found the walls lignified (cf. Linsbauer, l. c.).

The mechanism of the stoma of *Selaginella apus*, Spring, is similar to that of *Lycopodium*, though closure is effected by the ridge of entrance, as in *Dennstaedtia*. The stoma of

Farnkraut-Spaltöffnungen; Bot. Zeit. xxiv (1866), 245. The mature stoma was described by Oudemans in 1865.

¹ E. Strasburger, Ueber *Azolla*, Jena, 1873, p. 35.

S. rupestris, Spring, is much deeper, and with the ridge of exit well developed, being in both respects like the *Amaryllis* type.

The remarkable superficial aspect of the stomata of *Equisetum* has made them a frequent subject of note (literature in de Bary, l. c.), and some unsound speculation. In two modern texts it is stated they consist of two pairs of guard-cells, one over the other, a notion disproved by a study of their development by Strasburger thirty-six years ago (l. c., 1866, pp. 318-22). In cross-section (Fig. 46) it is at once evident that the lumen of the guard-cell has two very unequal diameters, and will therefore, like that of *Medeola*, tend to become round with increasing turgescence. The ventral and inner walls are practically all one, with a ridge of exit too little thickened to affect the mechanism. The outer wall is restricted to the ridge of entrance, which constitutes the pore, and is placed where it looks like a continuation of the wall between the guard-cell and the overlying subsidiary cell. The extensive convex dorsal wall is thin except for the thickened strips running across it from the pore, projecting into the lumen of the subsidiary cell. These strips do not stiffen the wall lengthwise of the guard-cell, and will themselves be bent by less pressure than would stretch them. Now if the pore be closed—by which I mean of course as nearly so as it becomes—and the turgor of the guard-cell increases, water will enter it from the subsidiary cell, as indicated by the arrow. To compensate for this movement of water, the wall must move in the opposite direction. This must bend the wall, but need not stretch it. Obviously the thickened strips, attached to more than one wall and presumably fixed fast at the back side, will exert a direct pull on the ridge of entrance and widen the pore. There is a conspicuous hinge in the wall above the ridge. While the guard-cells are often in contact with no other cells than their subsidiary cells, and so must be supplied with water through them, this is of course not essential to the operation of the stoma.

Of the Gymnosperms enough has been said. And of the Glumiferae it need only be stated that in the four Scirpeae¹ I have examined—*Cyperus rivularis*, Kunth, *Fimbristylis capillaris*, Gray, *Scirpus Cyperinus*, L., and *S. polyphyllus*, Vahl—median cross-sections show the thickening typical of other sedges. The stomata of *Juncus acuminatus*², Mx., are mechanically more like those of sedges than like those of *Luzula*, in spite of their curved dorsal wall. In some species of *Luzula*, Westermaier finds the thin polar areas in surface view, but they are invisible in my *L. campestris*, DC.

The stomata of the Liliaceae and their relatives have the one common character that they are large, and therefore convenient subjects of study, so that they were in almost exclusive use by the earlier investigators. The same character makes them an excellent subject of study from the mechanical side. That there is no particular type characterizing the Liliaceae, as might be inferred from references by Schwendener (1889) and Westermaier, is perfectly evident from the illustrations I have already used—*Medeola*, *Lilium*, *Smilax*, *Dracaena*, *Polygonatum*, and *Allium*. The enumeration of more kinds emphasizes the diversity. *Disporum lanuginosum* has the stomata broad, but also deep, combining the characters of *Amaryllis* and *Achillea*. The movement is mostly by the inner half, and is facilitated by the contour of the neighbouring cells inside the ends of the guard-cells (Fig. 47). *Uvularia perfoliata*, L., has clumsy stomata, nearest *Helleborus*. Those of *U. grandiflora*, Smith, suggest *Iris*. *Erythronium Americanum*, Ker., is nearer *Achillea* than any other type. *Clintonia umbellata*, Torr., has a mixture of *Amaryllis* and *Mnium* characters. The same is true of *Smilacina racemosa*, Desf., while *Maianthemum Canadense*, Desf., is nearer *Amaryllis*. *Convallaria majalis*, L., also has them of the *Amaryllis* type on young leaves; on leaves a year old they are thickened so as to resemble those of *Helleborus*, but are little, if at all, movable. Those of *Myrsiphyllum* are not distinguishable

¹ Cf. Schwendener, 1889, p. 71.

² Schwendener, 1889, p. 77; Westermaier, l. c. p. 78.

from those of *Smilax* (Figs 7, 8). Those of *Trillium erectum*, L., approach the *Medeola* type. *Dioscorea villosa*, L., has them similar, but the inner wall is thicker, and the dorsal wall slants as in *Helleborus*. Schmidt¹ describes and figures the stoma of *Conostylis graminea* in cross-section as like that of a grass.

Iris cristata, Aiton, has such stomata as Schellenberg describes for *Iris*, but according to Westermaier not all the species are alike. *Hypoxis erecta*, L., has stomata the slant and thickening of whose walls is suggestive of *Achillea*, though the ventral angles are noticeably thickened, and the stoma is long enough to act by its shape alone.

Lemna polyrrhiza, L., has the ridge of entrance as on other floating plants, the dorsal wall thin, and the whole stoma slender, appearing motile: but I have not examined it alive and it is open after death. *Acorus Calamus*, L., and *Symplocarpus foetidus*, Salisb., have stomata of the *Amaryllis* type, but deeper than the type and narrower, and therefore needing the ventral angles less thickened. Those of *Arisaema triphyllum*, Torr., are of the *Achillea* type.

Of the Orchidaceae, *Aplectrum hyemale*, Nutt., has already been mentioned as an illustration of the type of *Helleborus*. *Goodyera pubescens*, R.Br., comes nearer the type of *Amaryllis*; which is better represented by *Spiranthes gracilis*, Big., and *S. cernua*, Richard. The latter has a notable outer 'hinge'. *Cypripedium acaule*, Ait., approaches the *Medeola* type; and *Orchis spectabilis*, L., exemplifies it fully.

It will economize space if the stomata of Dicotyledones are merely listed, with their characters:—

Platanus occidentalis, L. Like *Quercus rubra*, L., Figs. 12, 13.

Quercus imbricaria, Mx. Different only in not being quite so wide.

Pilea pumila, Gray. Narrowed to the type of *Achillea*.

Codiaeum, sp., the green-house 'Croton.' *Helleborus* type,

¹ K. Schmidt, Ueber den Blattbau einiger xerophilen Liliifloren: Bot. Centralb. xlvii (1891), 1, 33, 97, 164, p. 100.

with the hinge back of the guard-cell; and the line where dorsal and inner walls meet thickened to the end.

Viola ovata, Nutt. *Achillea* type.

Viola blanda, Willd., var. *palustriformis*, Gray. *Achillea* type, but thickened less than typical.

Claytonia Caroliniana, Mx. *Medeola* type; surface view almost round; in contact with several cells.

Erodium cicutarium. *Helleborus* type.

Anemonella thalictroides, Spach. *Medeola* type, in spite of thickened walls; ends and sides of guard-cells locally reinforced.

Caltha palustris, L. Slightly flatter than *Anthoceros* (Fig. 53) in cross-section, very large.

Delphinium tricornis, Mx. *Amaryllis* type.

Aconitum uncinatum, L. *Achillea* type.

Caulophyllum thalictroides, Mx. *Helleborus* type.

Capsella bursa-pastoris, Moench, *Helleborus* type, narrow.

Dentaria diphylla, Mx. Like *Capsella*, but less thickened. Both of these Cruciferae are about as near *Achillea* as *Helleborus*.

Desmodium Dillenii, Darl. Narrow: *Amaryllis* or *Sagittaria* type on leaf, with subsidiary cells.

Cassia Marilandica, L. Like *Desmodium*. Stem without stomata.

Geum vernum, L. *Helleborus* type, dorsal walls quite oblique.

Saxifraga Virginica, Mx. Nearest *Amaryllis*; but inner wall thicker than outer.

Chrysosplenium Americanum, Schwein. *Medeola* type, with suggestion of *Amaryllis*; sometimes angular.

Liquidambar styraciflua, L. Like type of the Gramineae in the depth of the subsidiary cells; and thin ends of guard-cells very evident in surface view. In median cross-section like *Achillea*.

Hamamelis Virginiana, L. Like *Liquidambar*, but more thickened.

Cuphea viscosissima, Jacq. *Helleborus* type.

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Oenothera linearis, Mx. Type of *Achillea*.

Passiflora lutea, L. Like *Anemonella*.

Eucalyptus globulus. Cotyledon. Like Halophytes: much thickened, and no part of ventral wall thin: probably rigid. Character less extreme on leaf.

Opuntia Rafinesquii, Engelm. Leaf. Many stomata rigid or abortive, but some motile. *Amaryllis* type, but with features of *Achillea*.

Hydrocotyle Americana, L. Type of *Achillea*: slender, with oblique dorsal walls.

Osmorrhiza longistylis, DC. Type of *Achillea*.

Nyssa sylvatica, Marsh. Like the Ericaceae, but thickening ceases less abruptly at ends.

The Ericaceae. With the exception of *Arctostaphylos Uva-Ursi*, Spreng., of which I have had only herbarium material whose stomata are as figured by Westermaier (l. c. Fig. 4) and are certainly very nearly rigid, the stomata of all the Ericaceae I have examined are mechanically very much alike. These subjects have been *Azalia nudiflora*, L., *Rhododendron maximum*, L., *Gaultheria procumbens*, L., *Oxydendrum arboreum*, DC (Figs. 48–51), *Andromeda polifolia*, L., *Pyrola secunda*, L., and *Chimaphila umbellata*, Nutt. In sections these agree essentially with those of *Vaccinium*, which impressed Westermaier by their resemblance to the grass type. The thickening is so distributed as to leave the thin polar areas familiar in surface view in the Gramineae. But the ends are not much deeper than the middle, the dorsal walls are not at all straight and are usually oblique in cross-section, the inner wall is much thicker than the outer, very deep subsidiary cells are not often present, and in most Ericaceae, *Oxydendrum arboreum* and *Gaultheria procumbens* being exceptions, more than one cell opposes the back side of each guard-cell. Older stomata of some of these plants are slightly motile; others apparently not at all so. Movement which is undoubtedly like that of *Achillea* is very clear when they are younger and less thickened. The following measurements were made June 1, on a young

leaf of *Asalia nudiflora*, after exposure to direct sunlight, submerged:—

	Open.	Closed.
Length	25	25
Width of stoma	19	14
Width of guard-cell	8	7
Width of pore	3	0

Fig. 53 shows the structure of a stoma of about the same age.

Fig. 52 is of a still younger one, the rift not yet open, but the thin areas already visible.

Cyclamen, sp. (cultivated). *Helleborus* type.

Convolvulus sepium, L. Like *Ipomoea hederacea* (Figs. 54, 55). The stomata on the stems of both of these are nearer the *Amaryllis* type.

Phlox divaricata, L. *Helleborus* type. The reinforcement of the outer part of the end walls is shown by Fig. 56.

Gentiana Andrewsii, Griseb. *Helleborus* or *Achillea* type; not very uniform, but always greatly thickened; thickenings at ends variable; most commonly as in Fig. 57.

Obolaria Virginica, L. Many abortive and angular: those which develop, somewhat like *Anthoceros*, with internal ventral corner thicker.

Chelone glabra, L. Between *Helleborus* type and the stomata on the cotyledon of *Eucalyptus*.

Physostegia Virginiana, Benth. *Achillea* type. In the stomata of the *Labiatae*, with a subsidiary cell around each end of the stoma, the wall between these, striking the dorsal wall of the guard-cell about its middle, is thin and curved, usually about 90°: in *Mentha viridis* the curve is double, 90° each way. This curve probably decreases its resistance to the movement of the stoma.

Mentha viridis, L. *Helleborus* type.

Salvia lyrata, L. *Achillea* type.

Lamium amplexicaule, L. *Achillea* type.

Nepeta Glechoma, Benth. *Achillea* type.

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Mitchella repens, L. Nearer *Achillea* than to *Helleborus*.

Houstonia ciliolata, Torr. *Achillea* type.

Houstonia caerulea, L. *Achillea* type. Ends, in surface view, suggest those of *Funcus*.

Cephalanthus occidentalis, L. *Achillea* type: slender.

Campanula Americana, L. *Helleborus* type, but rather narrow.

Lobelia puberula, Mx. *Achillea* type. Thickening of dorsal edge of inner wall runs to end; rift rather long.

Taraxacum officinale, Weber. *Helleborus* type.

Senecio aureus, L. *Achillea* type. The subject was the radical leaf of a marsh variety.

Helenium autumnale, L. *Achillea* type: thickening and length of rift as in *Lobelia*.

Eupatorium ageratoides, L. f. *Helleborus* type.

Eupatorium coelestinum, L. *Achillea* type.

The number of stomata that I have had time to investigate would not warrant positive conclusions of any value in systematic botany; but it is sufficient to show that no such conclusions could be expected from a wider range of study, except in such groups, like the genus *Equisetum*, as are sharply defined in other ways, morphological and ecological. The Glumiferae and Gymnospermae are such groups. The difference between the *Achillea* and *Helleborus* types, though a very great mechanical one, is insignificant morphologically, depending on the relative depth and width of cells, which are very flat or very deep in neither case; and it is not surprising that the two should often occur in the same genera, and that there should be every intermediate stage between them. The series of divisions leading up to the formation of the stoma is sometimes a character of taxonomic value, and the mechanism must to some extent be correlated with it. Thus the presence of anticlinal walls against the dorsal wall makes desirable some type better prepared to overcome local resistance than is the *Amaryllis*.

Stomata of the *Medeola* type would not have to overcome this resistance; but they must be large in order that the

necessary changes in total curvature may not involve an impracticable bending of any unit of wall; and the stomata which are surrounded by subsidiary cells formed regularly from the same initial cell are from their origin likely to be small. The stomata of the *Amaryllis* type must also be large to permit the needed curvature of the entire guard-cell, as is of course equally true of *Sagittaria*. A stoma of the Conifer type must be below the general level of the epidermis. Outside the very specialized type of the Gramineae there remain only the *Helleborus* and *Achillea* types, which on mechanical grounds could be expected to occur among the very numerous Dicotyledones with small stomata.

The size of the stoma usually corresponds somewhat to that of the epidermal cells (*Salvinia* is a conspicuous exception). And the mechanism of the stoma must be correlated with the size and the depth and the thickness of the walls of the neighbouring cells. When the subsidiary cells are small, so that a small change in volume might demand a difficult change in their form, or when anticlinal walls oppose the movement of the guard-cells, it is some advantage of the *Helleborus* and *Achillea* stomata that only the inner half must overcome this resistance; and that this inner half has a firm wall which can be forced against any single point of resistance with the whole force of the turgescence of the cell.

To some extent more direct ecological adaptations of the stomata can be seen. If Dicotyledones are examined in late summer, in the height of the season of the large gamopetalous orders, as to their stomatal mechanism, the *Helleborus* or *Achillea* type will be found with scarcely an exception. This is true of trees at all times. But if the season of study is early spring, when *Claytonia*, *Hepatica*, *Anemonella*, *Saxifraga Virginica*, &c. are collected, the *Amaryllis* and *Medeola* types will be much in evidence. The Monocotyledones with similar stomata are characteristic spring plants. *Delphinium* and *Aconitum* show a difference that I cannot construe otherwise than as an adaptation to the season. The frequent difference between the stomata of spring and summer plants

suggested that by progressive thickening and a feasible change in the hinges a stoma might easily pass from the *Amaryllis* to the *Helleborus* or *Achillea* type. But this has not been found to occur. The stomata of *Quercus imbricaria*, *Dentaria diphylla*, *Lamium amplexicaule* and *Salvia lyrata*, and the *Azalea* already figured, all show their characteristic thickening before the guard-cells separate.

The ultimate ground for the difference between the predominant types of stomata in early spring and in summer lies of course in the need of protection against drought in summer. It does not follow that pronounced xerophytes can never have stomata of the *Amaryllis* or *Medeola* type. The stomata of *Equisetum* are nearest the *Medeola* type, but are protected by their position. The occasional difference between the stomata of the stems and leaves of the same plant may be partly due to the different demands on the smaller number present on the stems, and should be correlated with the larger and longer epidermal cells common on stems, instead of being ascribed altogether directly, as by Westermaier, to the tensions on the tissues of stems. This difference has already been described on *Euphorbia dentata*. Specialized subsidiary cells appear in cross-section only on the stems, or much better developed there, on many plants; for instance, *Lobelia puberula*, *Campanula Americana*, *Eupatorium coelestinum* and *Chelone glabra*. The surface-view of the *Chelone* stem shows several cells in contact with the dorsal wall of each guard-cell, in the walls between which are thin places, analogous to hinges in that they are to remove resistance to the movement of the guard-cells. The leaf of *Lobelia* shows a similar structure, but less clearly. On the stem of *Lamium* the walls between the subsidiary cells strike the dorsal wall nearer the end, instead of about midway as on the leaf. On *Ipomoea*, *Convolvulus*, *Campanula*, and *Salvia* (the species as in the list above) the stomata of the stem show a tendency toward the *Amaryllis* type, in the thickening.

It would be ridiculous to undertake to tell in detail why each plant makes use of its particular stomatal mechanism.

And to some extent the conditions under which the various types are advantageous have already been indicated. The stomata of *Mnium*, *Funaria*, *Equisetum*, the Gymnospermae, and the Glumiferae have so limited and well-defined a range of occurrence that it may reasonably be supposed that on inner grounds which have become very firmly hereditary they are not now among the devices possible to most plants. The four types of *Amaryllis*, *Medeola*, *Helleborus*, and *Achillea* have so wide and discontinuous a distribution that it is evident that in the development of individual orders or genera, or even species, there is often a possibility for selection among them. When the environment and structure of a plant are such that it is desirable that the stoma be very sensitive, then the guard-cells must be large and have thin walls, so that they can transpire and lose their turgescence before the rest of the leaf feels the loss of water. Such stomata are of the *Amaryllis* and *Medeola* types, especially the latter. Very likely the character of the epidermis most frequently determines the choice between these two types: if it is deep the *Amaryllis* type with its deep guard-cells will be natural; if shallow, the shallow *Medeola* guard-cells. Beyond this, it may perhaps be said that the *Amaryllis* stoma demands large neighbouring cells which can readily accommodate the movement of the guard-cells. And when the epidermis contains chlorophyll, as in most of our Ferns, its turgor may vary somewhat with that of the guard-cells; the *Medeola* structure makes the turgor of other cells indifferent mechanically, though it may still influence the supply of water to the guard-cells. The *Medeola* stoma has the least area of contact with other cells, by which it can receive water, and is therein most sensitive. Stomata of the *Helleborus* and *Achillea* types have the free walls of the guard-cells so reduced in area and so thickened that transpiration from them is not likely to close the pore so long as the mesophyll is well supplied with water. They will occur on plants which guard against loss of water sufficiently in other ways, so that too great sensitiveness of the stomata might result in inadequate

transpiration, as well as interfere with photosynthesis. Of the two, the *Achillea* type, being narrower, has less outer and inner wall, and a narrower strip on the ventral wall is likely to remain thin. So long as other factors, ecological but not mechanical, do not interfere, it is therefore the less sensitive.

In conclusion, it may prove a convenient summary of part of the work in this paper if the mechanical types of stomata are concisely tabulated. Of the numerous combinations and intermediate forms, there are included here only the two which it is convenient to regard as types—*Helleborus* and *Achillea*.

The pore opens by—

1. A change in shape, rather than by stretching the walls, in which the change is

(a) An increase in the depth of the guard-cell, in which there is chiefly concerned—

The entire wall (except the dorsal)	<i>Medeola</i> (<i>Equisetum</i>).
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The inner half	<i>Mnium</i> .
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The outer half	<i>Funaria</i> .
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The dorsal half	<i>Lycopodium</i> .
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The ends	<i>Osmunda</i> .
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(b) An increase in the width of the slender stoma *Sagittaria*.

2. Stretching the thin dorsal wall *Amaryllis*.

3. A change in shape, with or without much stretching, at the ends of the guard-cells which forces the dorsal wall, with the passive middle part of the cell—

Directly backward	The Gramineae.
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Upward and backward	The Coniferae.
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4. Combinations of the types of

<i>Amaryllis</i> and <i>Mnium</i>	<i>Helleborus</i> .
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<i>Amaryllis</i> and the Gramineae	<i>Achillea</i> .
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EXPLANATION OF THE FIGURES IN PLATE XIII.

Illustrating Mr. Copeland's paper on the Mechanism of Stomata.

All the figures are of stomata. Unless the contrary is stated, cross sections are across the middle of the pore.

- Fig. 1. *Medeola Virginica*, L. Surface. $\times 380$.
- Fig. 2. " " Cross section. $\times 380$.
- Fig. 3. *Funaria hygrometrica*, Sibth. Cross section. $\times 380$.
- Fig. 4. " " " Surface. The inner dotted line bounds the respiratory chamber. $\times 380$.
- Fig. 5. *Sagittaria variabilis*, Engelm. Surface. $\times 510$.
- Fig. 6. " " " Cross section. $\times 510$.
- Fig. 7. *Smilax glauca*, Walt. Surface. $\times 510$.
- Fig. 8. " " " Cross section. $\times 1020$.
- Fig. 9. *Polygonum sagittatum*, L. Cross section. $\times 1020$.
- Fig. 10. *Euonymus atropurpureus*, Jacq. Stem. Cross section. $\times 510$.
- Fig. 11. *Aplectrum hyemale*, Nutt. Cross section. $\times 510$.
- Fig. 12. *Quercus rubra*, L. Cross section. $\times 1020$.
- Fig. 13. " " " Cross section near end of stoma. $\times 1020$.
- Fig. 14. *Viburnum prunifolium*, L. Cross section. $\times 1020$.
- Fig. 15. *Achillea millefolium*, L. Surface. $\times 700$.
- Fig. 16. " " " Cross section. $\times 700$.
- Fig. 17. " " " Cross section near end. $\times 700$.
- Fig. 18. *Polygonatum biflorum*, Ell. Cross section. $\times 760$. O. W. = outer wall
- Fig. 19. " " " Surface. $\times 760$.
- Fig. 20. *Zea Mais*. Cross section at $\beta-\beta$ of Fig. 21. $\times 760$.
- Fig. 21. " " Longitudinal section of a guard-cell. $\times 760$.
- Fig. 22. " " Cross section at $\alpha-\alpha$ of Fig. 21. $\times 760$.
- Fig. 23. " " " Surface. $\times 760$.
- Fig. 24. *Tsuga Canadensis*, Carr. Cross section. $\times 510$.
- Fig. 25. " " " Cross section of end. $\times 510$.
- Fig. 26. " " " Longitudinal section. $\times 510$.
- Fig. 27. " " " Surface. $\times 510$. The main focus is above the stoma.
- Fig. 28. *Allium vineale*, L. Surface. $\times 510$. The main focus is above the stoma.
- Fig. 29. " " " Cross section. $\times 510$.
- Fig. 30. " " " Longitudinal section. $\times 510$.
- Fig. 31. *Osmunda Claytoniana*, L. Cross section. $\times 700$.
- Fig. 32. " " " Section across end. $\times 700$.
- Fig. 33. " " " Longitudinal section. $\times 700$.
- Fig. 34. *Anthoxeros punctatus*, L. Surface. $\times 380$.
- Fig. 35. " " " Cross section. $\times 760$.
- Fig. 36. *Ophioglossum pendulum*. Cross section. $\times 380$.
- Fig. 37. " " " Section across end. $\times 380$.

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- Fig. 38. *Angiopteris*, sp. Cross section. $\times 760$.
 Fig. 39. " " Section across end. $\times 760$.
 Fig. 40. *Dennstaedtia punctilobula*, Bernh. Surface. $\times 510$.
 Fig. 41. " " " Cross section. $\times 1020$.
 Fig. 42. *Asolla Caroliniana*, Willd. Surface. $\times 1020$.
 Fig. 43. " " " Cross section. $\times 1020$.
 Fig. 44. *Lycopodium lucidulum*, Mx. Cross section. $\times 700$.
 Fig. 45. *Equisetum arvense*, L. Surface. $\times 510$.
 Fig. 46. " " Cross section. $\times 510$.
 Fig. 47. *Disporum lanuginosa*. Surface. $\times 700$. The main focus is below the stoma.
 Fig. 48. *Oxydendrum arboreum*, DC. Surface. $\times 1020$.
 Fig. 49. " " Cross section. $\times 1020$.
 Fig. 50. " " Section across end. $\times 1020$.
 Fig. 51. " " Longitudinal section. $\times 1020$.
 Fig. 52. *Asalia nudiflora*, L. Surface. $\times 1020$.
 Fig. 53. " " Cross section. $\times 1020$.
 Fig. 54. *Ipomoea hederacea*, Jacq. Surface. $\times 760$.
 Fig. 55. " " Cross section. $\times 760$.
 Fig. 56. *Phlox divaricata*, L. Surface. $\times 760$. The focus is near the outer wall.
 Fig. 57. *Gentiana Andrewsii*, Griseb. Surface. $\times 760$.





