ANATOMICAL STUDIES ON POTATO-WART[1]

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Considerable progress has been made in recent years in the study of the causal organism of potato-wart, but our knowledge of the anatomical structure of the tumor is still limited to brief accounts found in earlier publications. A study of the histology of the tumor, though primarily of interest to the anatomist, will indirectly advance other phases of research in connection with the wart disease.

The wart appears as a proliferation of meristematic regions of stem, stolon, and tuber. An examination of a partly mature plant, grown under conditions favorable for infection, will give a picture such as is presented in Plate 1. Warts are seen to have developed abundantly on all underground parts except the roots. The tumors vary in size from minute undifferentiated protuberances to intricate branch systems. The largest warts have developed on the underground stalk and terminally on stolons, while the smallest appear on tubers, usually as the result of belated infections.

The typical wart is nearly spherical in form and gives the impression of a solid structure with modified peripheral parts. These external modifications, however, are the visible external expression of deeply seated changes so intricate (Pl. 2, E) that only the aid of the microscope will reveal their component parts. The wart, indeed, consists fundamentally of depressed, antler-shaped branches or metamorphosed leaves, partly grown together and branching profusely near the periphery. Since the planes of branching change constantly, symmetrical expansion of all the component branches in a centripetal manner is impossible; as a result the parts are greatly malformed and bear but little resemblance to any normal organ of the plant.

When tuber infection is belated and conditions are generally unfavorable for the development of the parasite the growth of the wart comprises only a superficial modification of the parts attacked (Pl. 3, C, D). While this type of wart may be found on any diseased plant it constitutes the only type which is developed on semiresistant varieties.

Wart formation on aerial organs is uncommon, but occasionally stem buds close to the surface of the ground become infected. Since in these buds leaf differentiation has usually gone past the embryonic stage, even the stimulating effect of the parasite can not altogether change the subsequent development of these organs. The result is a malformed leaf with a lamina little expanded but thickened (Pl. 2, B).[2]

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[2] Mr. Freeman Weiss reports having found a small, roughly spherical wart originating from the midrib of the lower surface of a leaf 12 to 14 inches above the ground; it contained both resisting spores and sori in various stages of development.

The color of the wart below ground is that of the stolon and young tuber, commonly an ivory white. In varieties which produce highly colored tubers, like the Australian Blue, the color of the wart will also be that of the tuber. When developing above ground, the parts exposed to the sun develop chlorophyll and aid in assimilation. Toward the end of the growing season, or earlier, the warts show signs of decay. The color changes from white to a dark brown and finally to a dirty black. At the time the potatoes are ordinarily dug, most large warts have disintegrated, leaving only unsightly vestiges on the infected tubers. Small warts, according to Johnson(*6*),[3] may enter a dormant state and form the source for new infections the following season.

ANATOMY

A cross section of a young wart or of the peripheral part of an older one shows a centrally located vascular strand (Pl. 2, D) and a broad band of cortical tissue whose peripheral cells harbor the resting spores of the parasite (Pl. 4, B). The epidermis, where still intact, is composed of delicate cells isodiametric or with the longer axis in the radial direction. A periderm is not developed, although occasionally a shorter or longer band of cork cells is noticeable immediately below the zone of spore-containing cells, or may surround in concentric layers some deep seated resting spores. The walls of the cells containing the resting spores, as well as the neighboring cells, become lignified and suberized, and since the heavy walls of the resting spores undergo like changes, a lignin stain applied to a section of the wart makes the fungus infected area discernible to the naked eye and permits of ready differentiation with the aid of the microscope.

The cortical tissue (Pl. 5), which comprises by far the largest part of the wart, is composed of simple, large parenchyma cells. The cells are crowded with starch grains. Sugar is always present in varying amounts, and also tannins, primarily in newly infected regions, where, under the influence of the parasite, cellular activity is at its height. Other cell inclusions are more conspicuous by their absence. Calcium oxalate and protein crystals which are usually found in the peripheral region of the normal tuber are usually wanting. Protein crystals have been observed only in the outer cortical cells of the host—never in typical wart tissue.

Modifications of the normal type of storage cells of the wart are frequently observed and consist in their transformation into sclereids. They have been found abundantly in the aerial parts of the potato plant affected with blackleg (*2*) and normally in small numbers in the cortex of the underground stem and in the parenchyma tissue of dormant eyes.

The vascular tissue is centrally located, and only in transition regions is there found a siphonostele inclosing a large pith. The relative position of xylem and phloem is, at best, only approximate. Especially where the vascular elements are greatly reduced, the phloem and xylem appear independent of each other and with no definite orientation with respect to the axis of the organ. In small branches of the wart, however, phloem groups may be observed in close proximity to the xylem and may even surround it so completely as to give the effect of a typical amphicribral bundle. While the arrangement of the vascular tissue is certainly a departure from the normal type, it must be remembered that similar, if not identical, conditions exist in normal organs, such as the tuber (*1*).

[3] Reference is made by number (italic) to "Literature cited," p. 967.

The phloem groups abut directly on the cortex. There is no endodermis; and only groups of small-celled tissue, the homolog of a pericycle, may delimit the phloem from the storage tissue. The phloem groups are small and widely scattered; sometimes a sieve tube with a single cambiform cell may constitute an entire group. Often, however, the groups are larger and attain the size of the inner phloem of the tuber. The relative number of sieve tubes and parenchyma cells is approximately that found in the phloem of the underground organs and is small compared with the aerial parts. When stained with chlorozinciodid the side walls of the sieve tubes in contact with cortical cells show a network of fine, dark-staining bands inclosing areas of lighter color. Since there is an obvious need for rapid movement of food from the storage parenchyma to the growing region of the wart, the extensive pitting of the sieve tube with these storage cells appears as a functional adaptation; the converse relation, however, may also hold.

The xylem is composed of narrow, porous elements with secondary thickenings in the form of rings and close spirals. The end walls of the cells are chiefly oblique, being sometimes, however, strictly transverse. Since the course of the vascular tissue is very irregular and since branching and anastomosing takes place frequently, the xylem cells are commonly atypical. This diversity of form finds expression in abnormal wall sculpture, excessive slope of the end walls, and a general irregular form of the element as a whole. Typical fibers and pitted vessels are wanting. Narrow parenchymatous elements of variable length often separate the xylem from the cortex. Besides being smaller, these elements differ further from typical cortical cells in being devoid of starch. The walls of the xylem elements remain cellulose for a long period. This fact and the conspicuous absence of fibers and tracheids shows that the tissue is adapted primarily for conduction and not at all for support. Such qualitative reductions in vascular tissues are common in simple galls and appear to be adaptations for changes in function. Bally (*3*) believes that the adaptation in case of the wart is for water storage rather than for conduction. It might be questioned, however, whether conduction is second in importance to water storage in wart tissue; and may we not, from morphological considerations, expect only simple protoxylem elements in a tissue as simple, as well protected and as rapidly growing as that of the wart? Both xylem and phloem cells advance independently close to the peripheral region of the wart, a fact which further tends to emphasize the necessity for rapid movement of plastic materials as well as of water. Individual sieve tubes and protoxylem cells may be observed even in small warts, which makes it difficult to tell which of the vascular elements are differentiated first and whether phloem cells or xylem cells are more important in the early growth of the organ. Although normally elements that are essentially vascular rarely terminate a bundle, in the wart tissue individual sieve tubes and also ringed protoxylem cells have been observed to advance to the periphery of the organ unaccompanied by parenchyma cells.

The older basal part of the wart and more especially the transition region show a gradual approach to the normal structure. There is a steady increase in supporting tissue and improved provision for conduction of larger quantities of water. We may then expect to find fibers and pitted vessels in increasing numbers, and indeed we do. Withal there is a complete though gradual transition from the normal to the wart tissue, and although in its simplest form the wart shows both qualitative and quantitative reduction of tissues, there exists, nevertheless, a marked similarity between structure of normal host and wart, and this is shown not only in similarity of position of the tissues with reference to each other but also in their practical identity as regards the essential composition of the vascular tissue.

MORPHOLOGICAL NATURE OF THE WART

From anatomical analysis the wart is a homoplastic growth with quantitative reduction in vascular tissue and increase in storage parenchyma. The likeness is even more marked and reaches a point of complete identity if we choose to compare reduced host tissue with transition regions in the wart. But even if we accept this conclusion, there still remains the answer to the question as to the nature of the wart in its entirety and its relation to the normal organs of the plant. To arrive at a satisfactory conclusion it will be necessary to follow briefly the early ontogeny of the wart and to consider the nature of the stimuli which initiate the abnormal growth.

A newly infected bud shows the surface covered with small pustules which in sectional view (Pl. 4, A) are found to consist of a small-celled tissue rich in protoplasm and very turgid. Certain of these protuberances show a slight depression with a brownish center in which is found a prosorus or summer sporangium of the parasite. These areas of new growth, according to Curtis (*4*) and Bally (*3*), have resulted from the stimulating effect of the fungus. Since the epidermal walls of these pustules are very delicate, and since new summer spores are formed and mature in rapid succession, new infections occur, and as a consequence new centers of growth are formed in direct proportion to the number of new infections. The finely adjusted stimulation which results in the formation of a progressively increasing area of meristematic tissue permits of an uninterrupted development of the parasite and the formation of large numbers of resting spores which under suitable conditions remain viable in the soil and form a latent source of infection for years to come.

In semiresistant varieties wart development remains superficial. The growth slightly resembles scab pustules, though the infected areas are somewhat more elevated (Pl. 3, C, D). In susceptible varieties, on the other hand, the warts are extensive structures (Pl. 2, A, D, C, E; 3 A, B) and only in their topography bear resemblance to the former kind. Percival (*8*) assumes that the wart is "a malformed branch system stimulated by the parasite to grow irregularly and before its natural time." A study of Plate 3, B, suggests no objection to such a theory, and a consideration of the anatomy of the vascular system seems only to lend additional support. However, granting that the stimulating effect of the fungus may result in a shortening or complete elimination of the rest period of the young bud, may we not expect a similar phenomenon in potato plants which are semiresistant to the wart? Yet this is not the case. Furthermore, an analogy with "witches'-broom" formation in Pteris (*5*) indicates that it may be unessential, however, to presuppose the existence of buds in order to initiate growth of extensive though somewhat abnormal foliar organs; that, in fact, the stimulus exerted by the fungus is sufficient to bring about cell division and initiate organ formation in meristematic regions of plants. In the potato, too, extensive wart formation often results from the infection of an outer bud scale which has normally completed development. The association of the fungus with reactive host cells is sufficient to initiate new growth. But the same parasite in the subsequent development of the new organ acts as inhibitor and modifier and thus alters the appearance of the new structure completely. Early developmental studies and the comparative ease with which the pathogene is identified have left no doubt that the wart, as a whole, is normal host tissue and that only the peripheral regions contain typical traumatic cells. An analogous case is presented by Dr. E. F. Smith (*9*). The growth resulting from inoculation is composed of normal host tissue and not of parasitized cells, as viewed by Levine (7). The present impossibility of demonstrating the crowngall pathogene in the tissues, however, gives only presumptive evidence, but a consideration of the reaction of host and parasite in case of the wart of potato should give, if analogy be worth anything, a strong support to the theory defended by Doctor Smith.

The wart can be considered a foliar branch system. The existence of various types of warts seems to be bound up with the relative susceptibility of the host, the nature and extent of the primary infection, and such factors as tend to modify plant growth in general.

LITERATURE CITED

(1) ARTSCHWAGER, Ernst F.
1918. ANATOMY OF THE POTATO PLANT, WITH SPECIAL REFERENCE TO THE ONTOGENY OF THE VASCULAR SYSTEM. *In* Jour. Agr. Research, v. 14, p. 221–252, 4 fig., pl. 27–47. Literature cited, p. 251–252.

(2) ———
1920. PATHOLOGICAL ANATOMY OF POTATO BLACKLEG. *In* Jour. Agr. Research, v. 20, p. 325–330, 1 fig., pl. 57–58. Literature cited, p. 330.

(3) BALLY, Walter.
1911. CYTOLOGISCHE STUDIEN AN CHYTRIDINEEN. *In* Jahrb. Wiss. Bot. [Pringsheim], Bd. 50, p. 95–156, 6 fig., pl. 1–5.

(4) CURTIS, K. M.
1921. THE LIFE-HISTORY AND CYTOLOGY OF SYNCHYTRIUM ENDOBIOTICUM (SCHILB.), PERC., THE CAUSE OF WART DISEASE IN POTATO. *In* Phil. Trans. Roy. Soc. London, ser. B., v. 210, p. 409–478, 1 fig., pl. 12–16. Literature, p. 462–464.

(5) GIESENHAGEN, K.
1892. UEBER HEXENBESEN AN TROPISCHEN FARNEN. *In* Flora, Bd. 76, p. 130–156, pl. 12–13.

(6) JOHNSON, Thomas.
1909. CHRYSOPHLYCTIS ENDOBIOTICA, SCHILB. (POTATO-WART OR BLACK SCAB), AND OTHER CHYTRIDIACEAE. *In* Sci. Proc. Roy. Dublin Soc., v. 12, p. 131–144, pl. 9–11. List of authorities quoted in the text, p. 144.

(7) LEVINE, Michael.
1919. STUDIES ON PLANT CANCERS. I. THE MECHANISM OF THE FORMATION OF THE LEAFY CROWN GALL. *In* Torrey Bot. Club, v. 46, p. 447–452, pl. 17–18.

(8) PERCIVAL, John.
1909. POTATO-WART DISEASE: THE LIFE HISTORY AND CYTOLOGY OF SYNCHYTRIUM ENDOBIOTICUM (SCHILB.) PERCL. *In* Centbl. Bakt. [etc.] Bd. 25, p. 440–447, 3 pl. Literature, p. 445–446.

(9) SMITH, Erwin F.
1921. EFFECT OF CROWNGALL INOCULATIONS ON BRYOPHYLLUM. *In* Jour. Agr. Research, v. 21, p. 593–598, pl. 101–110.

PLATE 1

Color photograph showing wart infection on underground stalk, stolons, and tubers. (Photograph by Freeman Weiss.)


A Hoen & Co Baltimore

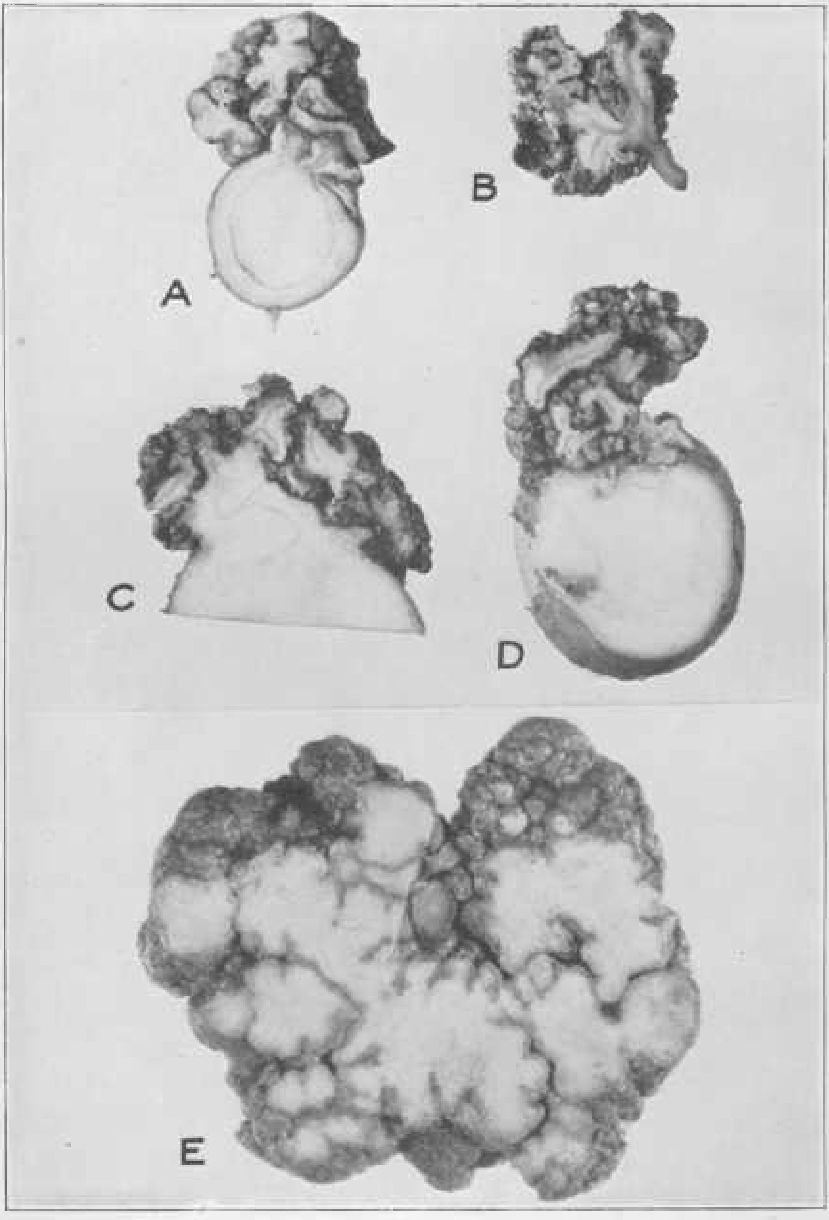

A
B
C
D
E

PLATE 2

A.—Sectional view of large wart developed from terminal bud of tuber.

B.—Sectional view of aerial wart. Note general appearance of wart and central location of vascular tissue.

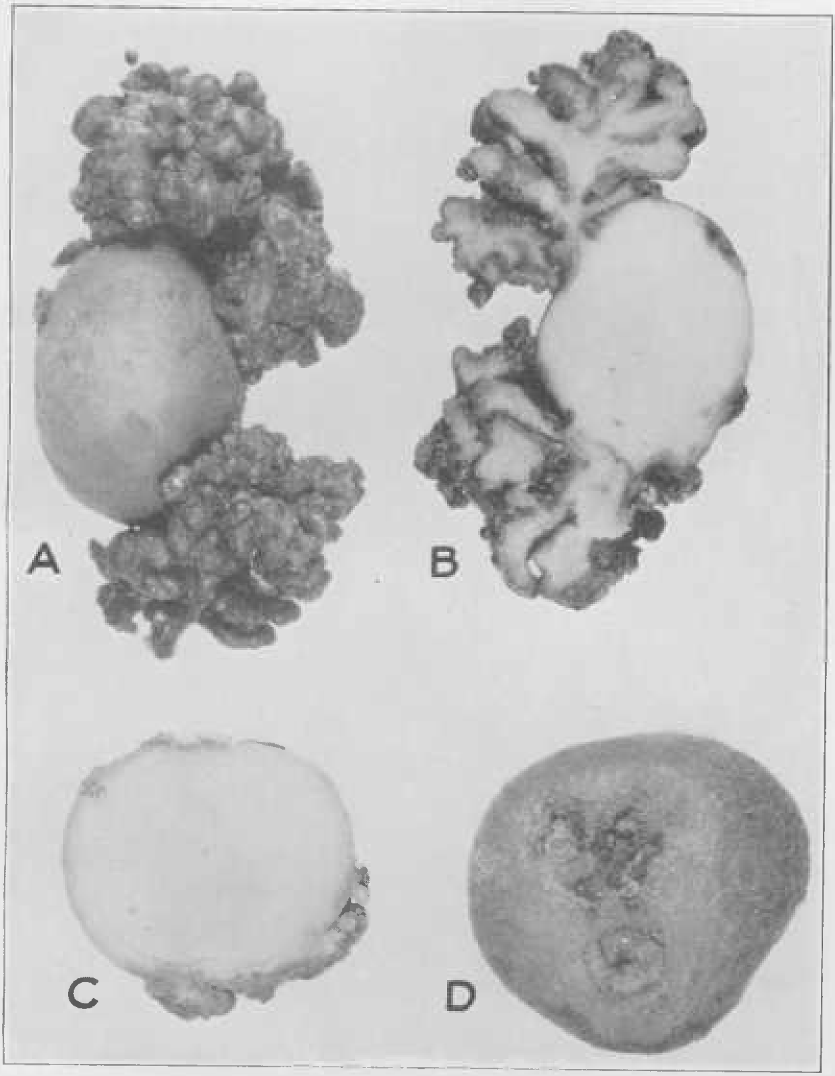
C.—Sectional view of large wart on tuber. The vascular tissue shows the arrangement which is typical of petiolar or midrib bundles.

D.—Sectional view of large wart on tuber. The apparent solid structure is an aggregate of compressed, modified leaves.

E.—Sectional view of large wart on stolon. The branching is often so intricate that only the aid of the microscope will reveal the component parts.

PLATE 3

A.—Surface view of large wart on tuber.
B.—Sectional view of the same wart, showing characteristic branching.
C.—Sectional view of wart on a semiresistant variety.
D.—Surface view of the same wart.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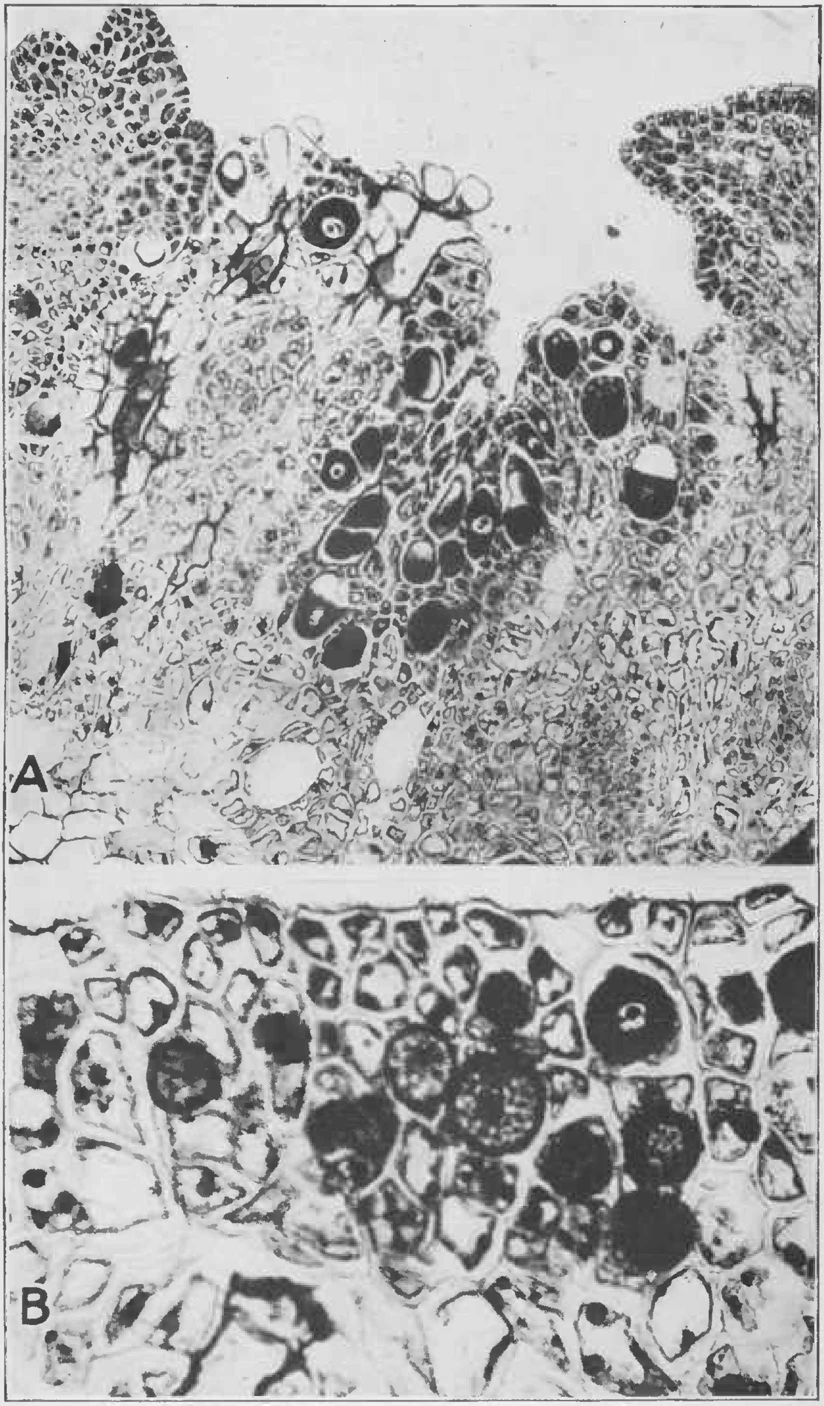
A
B

PLATE 4

A.—Section through the peripheral region of young wart, showing resting spores, summer sori, and new centers of growth which have resulted from the stimulating effect of the parasite.

B.—Section though an older part of a wart, showing structure and position of resting spores.

PLATE 5

Section of young wart, showing general appearance of tissues and location of spore-bearing cells.