THE ORIGIN AND DEVELOPMENT OF THE GALLS PRODUCED BY TWO CEDAR RUST FUNGI

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The question of the origin of the outgrowths caused by *Gymnosporangium Juniperi-virginianae* Schwein. and *Gymnosporangium globosum* Farlow on *Juniperus virginiana* L. has never been settled satisfactorily. The galls produced by *G. Juniperi-virginianae* have been studied by several workers but there still exists considerable difference of opinion as to the method of their origin. The excrescences caused by *G. globosum* have been studied but little.

While making observations on these galls incident to the preparation of another paper the writer became interested in their method of origin. Observations were made throughout two summers and the earliest stages of the development of these galls were studied in the field and later microscopical studies were made. The results of these observations and studies together with a résumé of the literature on the subject are given below.

G. Juniperi-virginianae

Farlow (1880) states that prior to the time of writing it had been generally accepted that the cedar apples originated in the young cedar stems but that so far as he could ascertain they were deformed leaves. Sanford (1888) studied the pathological histology of the galls produced by this fungus and decided that the galls are modified cedar leaves, while Wörnle (1894) after also studying these galls histologically concluded that they originated from the stem. Heald (1909) thinks that the cedar apples originate from the stem in the axis of a leaf. Kern (1911) places *G. Juniperi-virginianae* among the foliage inhabiting species and Coons (1912) states that while he has never observed or produced infection artificially it is evidently a leaf infection. Reed and Crabill (1915) claim that the cedar apple is nothing but a hypertrophy of a cedar leaf infected by the fungus *G. Juniperi-virginianae.* Giddings and Berg (1915) picture minute galls situated near the end of cedar leaves, hence apparently originating from the leaf. Steward

(1915), after having studied the histology of these growths, concludes that they originate as modified axillary buds; the leaf tissue becoming involved later.

The writer's observations go to show that the cedar apples caused by this species usually break through the upper or inner side of the leaves, the first evidence of infection being the discoloration of the whole or a part of a leaf, followed later by a swelling usually from the upper surface but more rarely from the sides. The young galls grow rapidly and assume the characteristic shape and color very early in their development. It was found that when the infected leaves were removed the galls remained attached (Pl. XII, Fig. 1). This led to the belief that they must be in very close association with the leaf and perhaps originate from it. Specimens such as are pictured by Giddings and Berg (1915) and Coons (1912), where the galls are located near or even beyond the center of the leaf, were found in considerable abundance (Pl. XII, Figs. 2 and 3). This strengthened the theory that these galls originate from the leaf. If these galls originated in the stem or as modified axillary buds with separate fibro-vascular systems it would be reasonable to suspect that in the very young stages at least the gall would be more firmly attached to the stem than to the leaf. A single gall has been found by the writer which has the appearance of having originated from the stem and it may be true that this mode of origin also exists, although it is certainly not the common method about Ithaca, New York. The writer has had the privilege of examining young galls from West Virginia and Wisconsin and the method of origin herein described was also found in those galls.

Before proceeding with a discussion of the internal anatomy of these galls a brief description of the structure of the healthy cedar leaf and stem will be given. The cedar leaf is attached to the stem throughout a large part of its length, only the apical portion being free. In cross section the leaf is triangular in outline at the apex but gradually becomes four-sided toward the base. The epidermis consists of a single layer of somewhat flattened, elongate cells with the outer wall covered by a thick layer of cutin. The epidermal layer on the upper or inner side of the leaf is broken by numerous stomata. Beneath the epidermal layer is a hypodermis on all the sides except the upper. For the most part this consists of a single layer of sclerenchymatous cells. This may however be reinforced at certain places, principally at the corners and in the region of the resin duct, by additional cells

of the same character. The central part of the leaf is occupied by a single fibro-vascular bundle of the collateral type. This is composed of a small group of scalariform tracheids and a group of phloem cells about equal in size. Just back of this bundle near the base of the leaf is a resin duct. The remainder of the tissue of the leaf is made up of parenchyma cells. The parenchyma cells near the upper or inner surface below the stomata are globose in shape and are loosely arranged, forming a tissue similar to mesophyll in appearance. The outer layers of cells are elongate, the long axis being perpendicular to the surface forming a palisade tissue. The structure of the very young stems which bear the young cedar apples is only slightly different from that of the leaf except of course that the fibrovascular system consists of a medullated central cylinder which is split up into several collateral bundles by the presence of leaf gaps. The cortical tissue of the stem and the parenchyma cells of the leaf are so much alike that it is impossible to distinguish between them. The parts of the stem not covered by leaves are protected by an epidermal layer similar to that of the leaf.

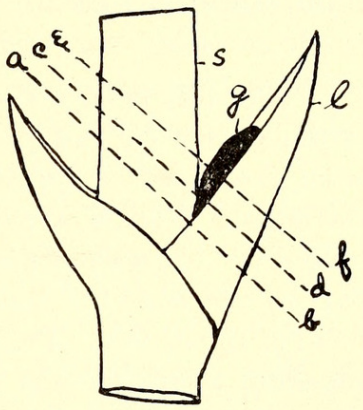
One of the first and most conspicuous things which may be observed in a longitudinal section of a stem bearing a young gall (Pl. XII, Fig. 4) is the position of the gall as compared with that of the opposite leaf. It is evident in every case that the gall occupies a position identical with that of the leaf on the opposite side of the stem. There is no sign of an axillary structure of any kind. Usually the leaf whose position the gall occupies and on which it develops becomes distorted beyond recognition except that there is evident a portion of its tip. A section through the leaf bundle at the base of the gall shows clearly that the vascular bundles of the gall arise from this leaf bundle. This is best studied in galls which have originated some distance from the axil of the leaf as shown in Plate XIII, Figures 1 and 2. In these figures it will be seen that the gall has been formed by the production of a large number of parenchyma cells from the parenchyma of the leaf, and by the vascular bundles which have arisen from the leaf-trace bundle. Examination of serial sections of such a gall precludes the possibility of the existence of any separate vascular bundle in the leaf from which the gall bundles might have arisen. In cases where the gall lies at or near the base of the leaf and from external appearances might possibly be axial in nature, serial sections show no vascular supply derived from the stele except the normal small leaf trace or its

modification. Stewart (1915) decided that the gall bundles are derived from the central cylinder entirely separate from and above the leaf-trace bundle. He illustrates this in Figure 1 of his paper, where he shows at K a section of an axillary bud from which he states the cedar apple is formed. The writer has in only one case found a structure similar to that represented by Stewart. In this case (Pl. XV, Fig. 1b) the structure in question is a section of one side of a terminal bud. An examination of all the sections in the series reveals the presence of the embryonic leaves. The young gall (*g*) beside this bud shows distinctly the difference in the appearance of a true gall and a bud. Evidently Stewart has mistaken a normal axillary bud for a young gall. The writer was permitted to examine some of Stewart's slides and this convinced him that Stewart was mistaken in thinking these structures to be young galls. A careful search of these slides failed to reveal the presence of mycelium in the buds. Stewart admits that "the fungus has not entered the stem at this stage," but concludes that these axillary buds are young galls because structurally these two seem to him alike. So far as seen by the writer this worker's sections show no cases which, when carefully interpreted, as discussed below, demonstrate the axial nature of the gall.

The excrescence caused by *G. Juniperi-virginianae* in its earliest stages consists simply of a few large parenchyma cells similar to those of the leaf. Often no distinct epidermal tissue is apparent at this stage but before the galls enter the winter condition a few layers of cork cells are laid down. The time at which this exterior covering is formed varies in different galls. The beginning of such a layer of cork cells is evident in some very young stages while in other cases galls nearly mature show almost no sign of its development.

That the fibro-vascular system of the gall originates from that of the leaf is evident from the study of the very young stages. How this takes place may be seen in Plate XIII, Figures 1 and 2. The leaf-trace bundle first shows an increase in size beneath the enlarged portion of the leaf. Soon strands of vascular tissue are found leaving the leaf bundle at almost an angle of ninety degrees and passing into the young gall. The vascular tissue of the gall develops rapidly and very early in the development there is present a large amount of conductive tissue in the gall. This same method of origin of the vascular tissue of the gall can be traced in those growths which occur near the base of the leaf. In this case, however, the leaf-trace bundle is very materially

affected by the gall and it soon becomes developed to such an abnormal extent that its identity is nearly or quite lost. Reed and Crabill (1915) give a good diagrammatic drawing of the bundle of a young gall originating near the stem. Stewart (1915) thinks that had Reed and Crabill made transverse instead of longitudinal sections of this infected leaf they would have found two bundles entering the gall rather than one. Such sections of numerous galls have been made by the writer and in no case has more than the one abnormally large bundle been found. In Plate XIV, Figures 1, 2, and 3 are shown sections from a series cut from an infected leaf, the gall being formed near the axil. A section taken a little way above the junction of the leaf and stem is represented in Figure 1 (line *a–b*, text figure 1). Here it is evident that the vascular bundle has been affected since it has more than doubled in size. A section taken farther from the stem is illustrated in Figure 2 (line *c–d*, text figure 1). This shows the bundle split into three parts by the intercalary formation of large cells filled with resin. These segments of the vascular system later branch out and become diffused throughout the gall (Fig. 3) (line *e–f*, text figure 1). A photograph of a stage somewhat comparable to Stewart's text figure is shown in Plate XIV, Figure 4. The central cylinder of the stem is shown at *a* and passing off from this is the greatly enlarged and modified leaf trace bundle breaking up and passing out in all directions in the gall. In Plate XIII, Figure 3, is shown a transverse section of the stem at *s* with two leaves at *l* and *l'*. From one side of leaf *l* a gall (*g*) is being produced. The vascular system of leaf *l* is much enlarged and from it strands of vascular tissue (*v*) extend into the gall (*g*). These figures check the opinion of Reed and Craybill concerning the single bundle supply. In cases where the gall occurs near the leaf base the increase in vascular tissue occasioned by its presence enlarges the leaf trace even through the cortex. At the base of the gall its vascular tissue frequently takes the form of an irregular hollow cylinder



TEXT-FIG. 1. Diagrammatic drawing of a portion of a cedar twig with two leaves attached. Lines *a–b*, *c–d*, and *e–f* show the approximate positions from which the sections illustrated in Plate XIV, Figs. 1, 2 and 3 respectively, were taken. *s*—stem, *g*—gall and *l*—leaf.

simulating that of a branch. To interpret correctly, especially in longitudinal sections, the enlarged and irregular base of the leaf trace (a mass of tissue sometimes even near its base partially broken up, and dividing soon into two masses, the larger upper one simulating a branch stele) serial sections are clearly absolutely essential. It is quite probable that Stewart has drawn his conclusions from individual sections. It is easy to see, further, how in this case a longitudinal section that is not quite median might lead to erroneous conclusions.

Sanford describes exactly the same condition that the writer has found in numerous cases. The writer therefore concludes with the majority of investigators along this line that in most cases at least and probably in all cases the gall is foliar, and does not represent a transformed branch.

G. GLOBOSUM

There has been no controversy in regard to the origin of the gall produced by *G. globosum*. Heretofore most workers have assumed from the external appearance of the old galls that they originate in the stem. Farlow (1880) who first named this fungus states that unlike *G. Juniperi-virginianae* it does not break through the central part of the leaf, but bursts through the stem at the point of attachment of the leaves. Pammel (1905) states that the galls break through the stem where the leaf is attached. Kern (1911) described the telial stage of this species, as being caulicolous. Stewart (1915) gives an account of histological studies made which he interpreted as showing beyond a doubt that this cedar gall originates from the limb as has always been supposed.

In order to make more careful observations on this subject a small cedar tree about four feet high and bearing numerous cedar apples was selected and all the galls removed early in April (1914) in order that they might not be confused with other galls appearing later.

This tree was kept under close observation and on July 25 the first young gall was visible. No aecia were mature at this time. The young galls seemed to be composed of modified portions of leaf rather than stem tissue. These galls were tagged and their development followed throughout the summers of 1914 and 1915. They grew very slowly and in late autumn were not more than two millimeters in diameter. The following spring (1915) these cedar apples sporulated, thus showing that this fungus, like *G. Juniperi-virginianae*, requires nearly two years for the completion of its life cycle.

On March 19, 1915, several small cedar trees were planted in pots in the greenhouse and on April 7 several leaves were found on these trees from the surface of which telial horns were developing (Pl. XV, Fig. 2). One or more were seen to come from the upper surface of the infected leaves which were swollen very little or not at all. These telial horns resembled those of *G. globosum* in shape and color and the spore measurements corresponded to those of that species. Inoculations were made on Crataegus leaves with some of these spores and the characteristic aecia of *G. globosum* developed; thus showing that the original determination was correct. Later similar specimens were found in nature. Often the infected leaves are yellowed throughout a certain portion of their length and the telial horns develop from those discolored areas. These tentacles may be found developing from any part of the upper surface or side of the leaf. Sections of some of these leaves showed them to be completely permeated with mycelium which in some cases at least did not extend to the base of the leaf. Infection must have undoubtedly occurred in the leaf.

Having observed that galls of *G. globosum* sometimes originate in the leaf, more careful observations were made to determine if possible whether this is always true. A great number of galls of this species were examined both during the autumn and winter of 1914 and 1915 and during the summer of 1915. Hundreds of galls were examined and in every case the foliar origin was found. These galls, however, usually develop near the base of the leaf and displace a certain part of it. As the galls continue to develop the terminal portion of the leaf remains attached to the gall and may be found here for some time. A careful study of Plate XV, Figs. 3 and 4 will make this point clear. A large amount of variation occurs. In some cases the gall may grow out from the upper surface of the leaf as do the galls caused by *G. Juniperi-virginianae*, or they may burst out of the side. A close inspection of older galls showed in nearly every case the dead tip of the original leaf still intact (Pl. XV, Figs. 3, 4, 5 and 6).

The gall grows slowly and is perennial, forming spores for several years. In the early stages these galls are nearly mahogany red in color as compared with the green color of the minute galls of *G. Juniperi-virginianae*. The red color gradually changes to grayish brown in the older galls. The shape of these galls is more or less globose from the beginning and often flattened on the side next to the stem (Pl. XV, Fig. 4). When the gall becomes older, it displaces the leaf

as stated above and as it continues to develop from year to year it becomes firmly attached to the twig, appearing to have originated in the twig (Pl. XV, Fig. 5 and Pl. XVI, Fig. 3).

In case of the above mentioned infected leaves where there was scarcely any swelling, the infection presumably took place in the summer of 1913 but was not apparent in the late summer or fall of 1914 and first became obvious in the spring of 1915. That the fungus had been developing in the leaf for some time seems certain when it is considered that in nineteen days after the trees were removed to the greenhouse telial horns had been produced. For some unknown reason the characteristic stimulation of cellular activity did not occur and when the mycelium reached the spore-bearing age, spores were produced.

Other cedar trees brought into the greenhouse early in the spring of 1914 produced cedar apples during the spring of 1915. These were scarcely more than telial horns coming directly from the leaf as in the other cases described. These were probably infected in the fall of 1913 and the mycelium was able to live in the leaf from that time until the spring of 1915, or approximately two years before causing any noticeable effect on the host.

These small galls developing on the leaf at considerable distance from the stem seldom reach any great size, probably due to their distance from the stem and a consequent lack of sufficient vascular tissue development.

A study of a large number of serial sections through the stem and young gall shows a condition such as is apparent in Plate XVI, Figures 1, 2, and 3. Plate XV, Figure 7, shows a section of a cedar leaf which had a slight discoloration but almost no swelling. The leaf when sectioned was found to be permeated with mycelium. A corky exterior layer K is already being developed in the gall shown in Plate XVI, Figure 1. The resin duct *r* is present and the vascular bundle is the leaf-trace bundle somewhat enlarged. Figure 2 shows much the same condition. Figure 3 illustrates a still more advanced stage. In this section the tip of the old leaf still remains visible at the apex and the corky exterior covering is well developed. The gall has become closely attached to the stem similar to the condition found in old galls where the stem tissue is probably also involved.

Summary

The galls produced by *G. Juniperi-virginianae* and *G. globosum* on *Juniperus virginiana* originate as modified leaves.

The vascular systems of the galls are composed of the enlarged and modified leaf-trace bundles.

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LITERATURE CITED

Coons, G. H. Some Investigations of the Cedar Rust Fungus, Gymnosporangium Juniperi-virginianae. Nebr. Agr. Exp. Sta. Rept. **25**: 215–246. 1912.

Farlow, W. G. The Gymnosporangia or Cedar Apples of the United States. Boston Soc. Nat. Hist. Anniv. Mem. **1880**: 1–38.

Giddings, N. J. and Berg, A. Apple Rust. W. Va. Agr. Exp. Sta. Tech. Bull. **154**: 1–73. 1915.

Heald, F. D. The Life History of the Cedar Rust Fungus, Gymnosporangium Juniperi-virginianae Schw. Nebr. Agr. Exp. Sta. Rept. **22**: 105–133. 1909.

Kern, F. D. A Biologic and Taxonomic Study of the Genus Gymnosporangium. N. Y. Bot. Gard. Bull. **7**: 392–494. 1911.

Pammel, L. H. The Cedar Apple Fungi and Apple Rust in Iowa. Iowa Agr. Exp. Sta. Bull. **84**: 1–36. 1905.

Reed, H. S. and Crabill, C. H. The Cedar Rust Disease of Apples Caused by Gymnosporangium Juniperi-virginianae Schw. Va. Agr. Exp. Sta. Tech. Bull. **9**: 1–106. 1915.

Sanford, Elmer. Microscopical Anatomy of the Common Cedar Apple (Gymnosporangium macropus). Annals of Botany **1**: 263–268. 1888.

Stewart, Alban. An Anatomical Study of Gymnosporangium Galls. Amer. Journ. Bot. **2**: 402–417. 1915.

Wörnle, P. Anatomische Untersuchung der durch Gymnosporangium-Arten hervorgerufenen Missbildungen. Forst. Nat. Zeitschr. **3**: 129–172. 1894.

EXPLANATION OF PLATES XII–XVI

Plate XII

Fig. 1. Young galls caused by *Gymnosporangium Juniperi-virginianae* showing their axillary position and their relation to the leaf. The two galls at the right were removed by pulling on the tips of the leaves to which they are attached. Compare the method of origin here with that shown for *G. globosum* galls in Pl. XV, Fig. 3.

FIG. 2. Mature gall of *G. Juniperi-virginianae* developed from the upper surface of the leaf and producing one telial horn.

FIG. 3. Three mature galls of *G. Juniperi virginianae* with telial horns partly gelatinized. These galls have evidently developed from the upper side of the leaves upon which they occur.

FIG. 4. Longitudinal section of stem and leaves of young cedar twig showing the relation of the gall (*g*) to the leaf (*l*) which bears it and to the leaf on the opposite side of the stem.

PLATE XIII

FIG. 1. Young gall (*g*) forming on the leaf (*l*) at a considerable distance from the stem (*s*). The vascular tissue in the young gall is very abundant and arises from the leaf-trace bundle (*t*).

FIG. 2. A young gall borne near the tip of the leaf showing the vascular development as in Fig. 1. The letters correspond to those in Fig. 1. The connection of the vascular tissue is more readily visible.

FIG. 3. A transverse section of a stem (*s*) with two opposite leaves (*l* and *l'*). A gall (*g*) has developed from the side of leaf *l* and vascular strands (*v*) are derived from the enlarged leaf-trace bundle at *t*.

PLATE XIV

FIG. 1. Section through a leaf (*l*) with a basal gall, the section taken as shown in diagram and transverse to the leaf trace. The vascular bundle (*v*) is considerably enlarged. Only one bundle is present, supplying both leaf and gall. This precludes the possibility of a separate origin of the vascular system of the gall, *i. e.*, of the axial nature of the latter. (See text figure 1.)

FIG. 2. Section of the same leaf (*l*) as shown in Fig. 1 but taken farther from the stem (*s*). The vascular bundle has broken into three distinct segments.

FIG. 3. Section from the same leaf as in Figs. 1 and 2 but taken still farther from the stem. Here the vascular tissue has become much diffused.

FIG. 4. Transverse section of a medium-sized gall (*g*) and the stem which bears it (*s*). The leaf on the opposite side of the stem is shown at *l*. The vascular tissue of the gall originates as one large strand at *a* which finally breaks up into a fan-like system of bundles. How this takes place is made clear by a careful study of Figs. 1, 2, and 3.

PLATE XV

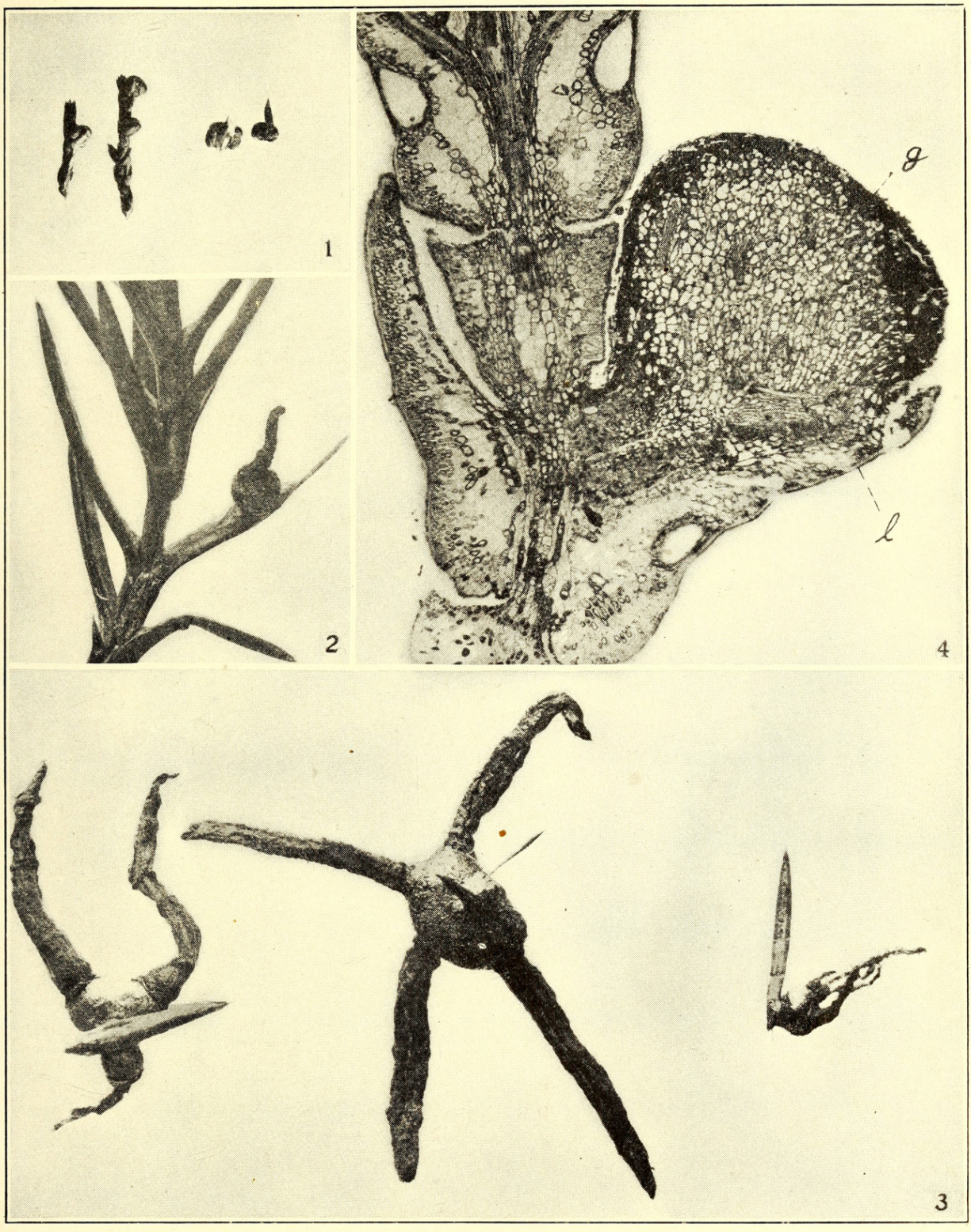
FIG. 1. Longitudinal section of young stem (*s*) showing terminal bud (*b*), young gall (*g*) and leaves (*l*). The bud (*b*) has identically the same appearance as the young gall shown by Stewart (1915) in Fig. 1 of his paper. There is no mycelium in this bud while mycelium is abundant in the gall beside it.

FIG. 2. Telial horns of *G. globosum* issuing directly from the leaf.

FIGS. 3 AND 4. Young galls of *G. globosum* originating from leaves, the tips of which are apparent at the top of the galls. The white appearance of the upper portion of the galls is due to fragments of the leaf tissue.

FIGS. 5 AND 6. Mature galls showing the remains of the leaves from which they originated. The galls shown in Fig. 5 have fruited more than once.

FIG. 7. A transverse section of a leaf which was slightly discolored and very slightly swollen at the base. The leaf is permeated with mycelium throughout nearly



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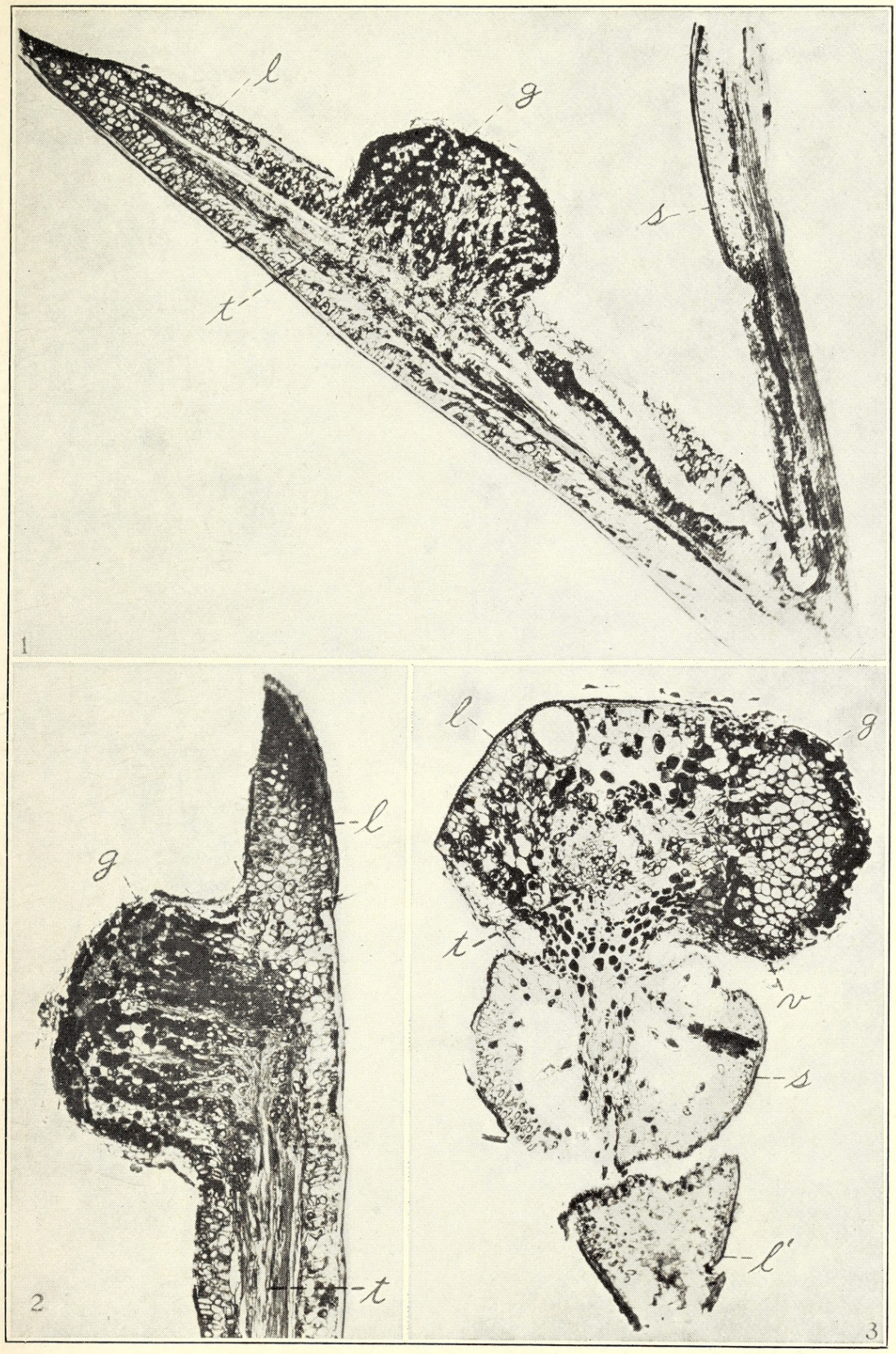

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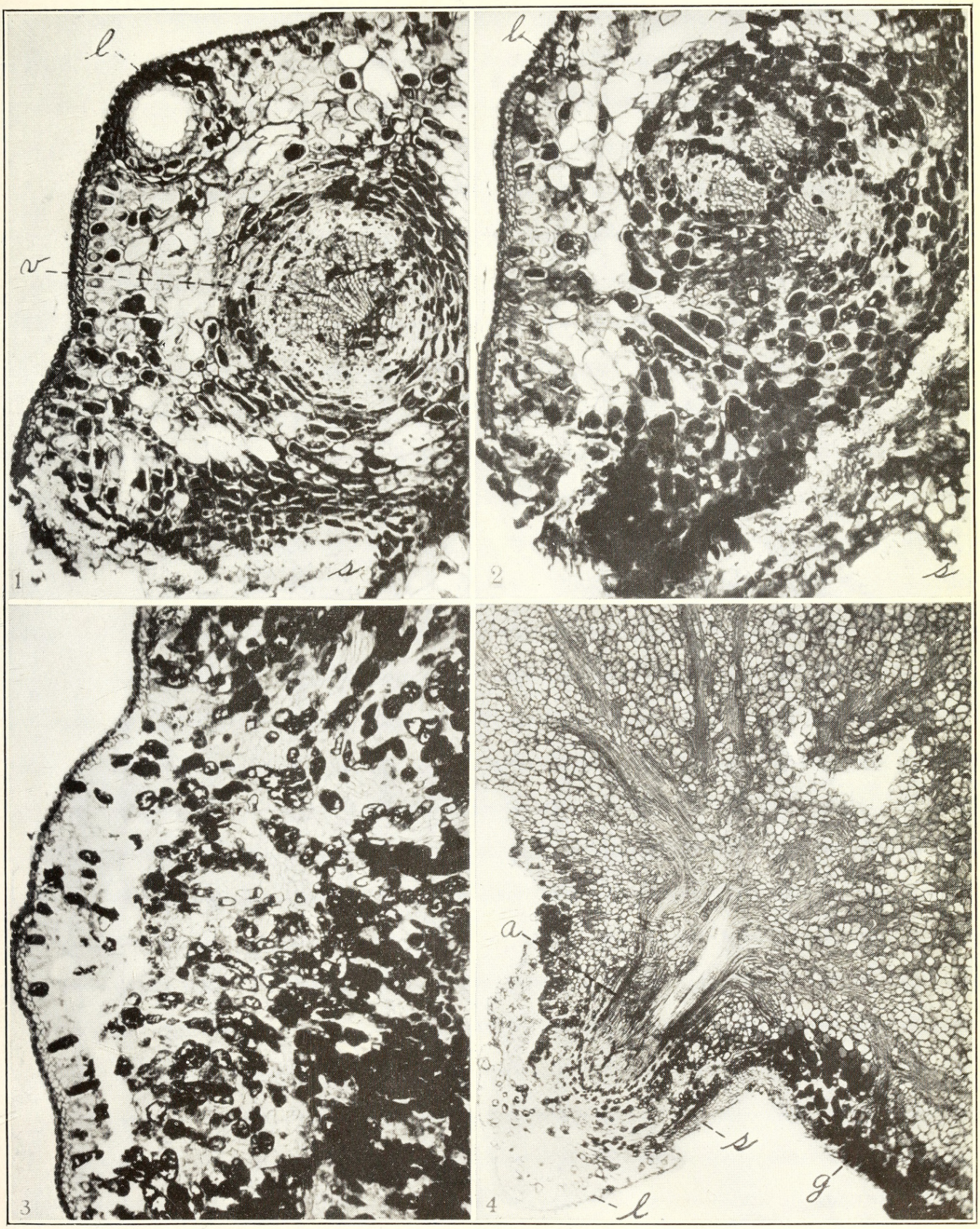

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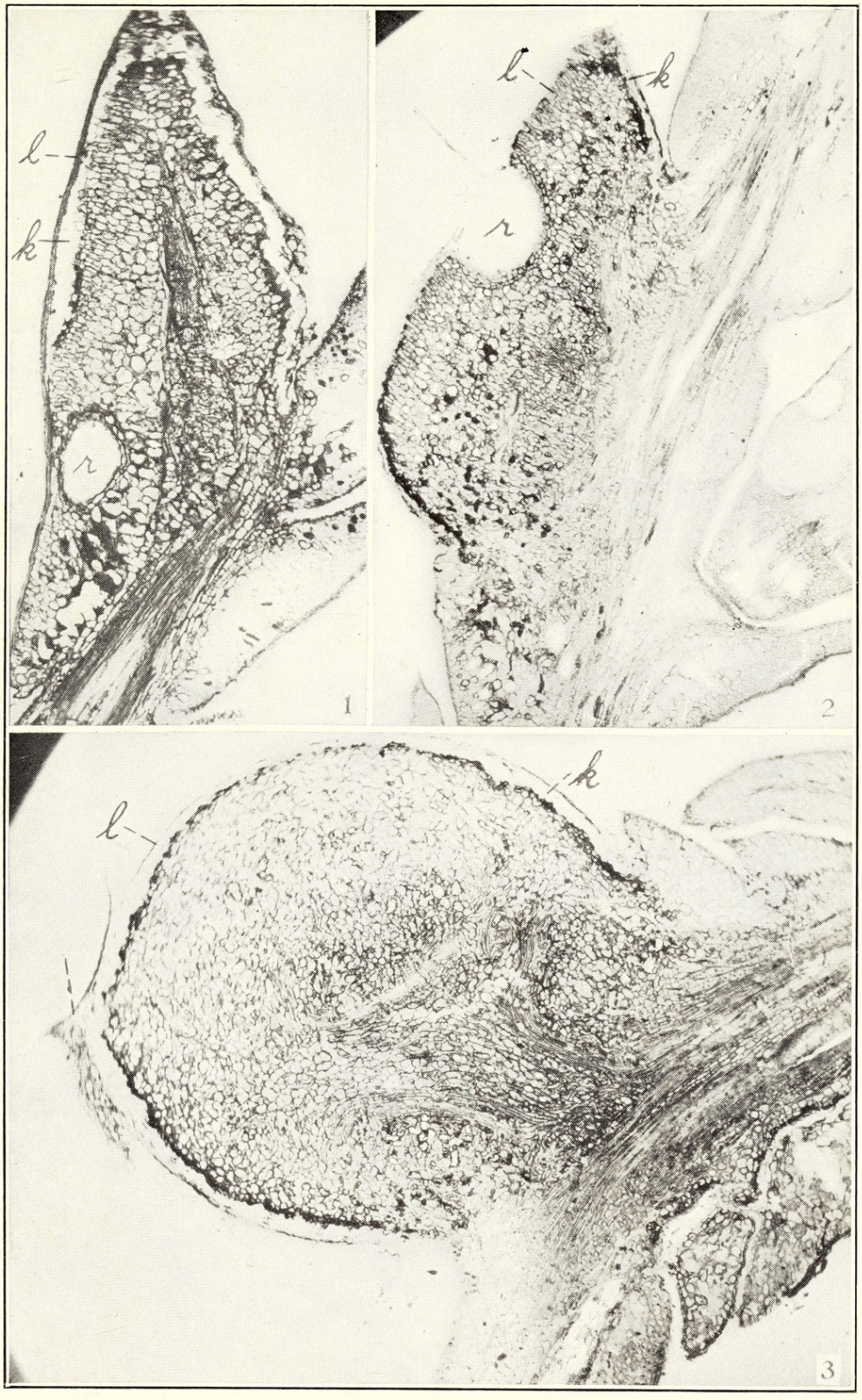

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its entire length. A layer of cork has been laid down in the cortical tissue as denoted by the dark line extending from the base to about the center of the leaf (see *a–b* in photograph).

PLATE XVI

FIGS. 1 AND 2. Sections of leaves (*l*) affected with *G. globosum* showing resin ducts (*r*) and their relation to the stems. The white area beneath the epidermis (*k*) in both galls is the corky covering which develops very early in galls caused by this fungus.

FIG. 3. Section of a gall in a more advanced stage than represented in Figs. 1 and 2. The tip of the leaf is evident at *l* and the corky layer (*K*) surrounds the gall on all free sides. The gall is firmly attached to the stem and it can easily be seen how the condition shown in Pl. XV, Fig. 5, develops.