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REPORT

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Agricultural Experiment Station,

Agricultural and Mechanical College,

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Contents:

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The Bulletins of this Station will be sent free to any farmer in the State, on application to the Director.

SCIENCE CONTRIBUTIONS

FROM THE

Agricultural Experiment Station,

Alabama Polytechnic Institute,

AUBURN, ALA., - - - - DECEMBER, 1889.

VOL. I., NO. I.

A Preliminary Report upon the Life History and Metamorphoses of a Root-Gall Nematode, *Heterodera radicicola* (Greeff) Müll., and the Injuries caused by it upon the Roots of various Plants.

By GEO. F. ATKINSON.

Whenever subjects of any special scientific interest arise in the original re searches of the Departments, it is purposed to publish them under the name of "Science Contributions".

BULLETIN NO. 9,

OF THE

AGRICULTURAL EXPERIMENT STATION,

Agricultural and Mechanical College,

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NEMATODE ROOT-GALLS.

By GEO. F. ATKINSON.

I.

INTRODUCTORY.

The purpose of the present paper is to put in the form of a preliminary report the results of some investigations made this autumn, in the neighborhood of the Experiment Station, upon the nature and cause of the abnormal growths found upon the roots of various plants. These deformities are popularly termed "root-knot". Soon after entering upon my new field of labor here, my attention was called to the subject by the Director, Prof. J. S. Newman who showed me tomato plants the roots of which were exceptionally "knotty."

The investigations were begun the first of October, 1889, and continued for about six weeks when the subject matter of this preliminary report was sent to the press.

At the time the work was undertaken I was unaware that a Bulletin was being published by the Division of Entomology, U. S. Agr. Dept., under the direction of Dr. C. V. Riley, embodying the results of investigations made by Dr. J. C. Neal of the Florida Experiment Station. The first notice I had of this work was from INSECT LIFE*.

That work† has since been distributed, and has reached me just about the time of going to press. Unfortunately there are many errors in the part dealing with the structure and life history of the nematode, though some of the economic suggestions possess value. It is but just to Dr. Riley to say that he is not personally responsible for the errors contained in the Bulletin, since he states in an introductory paragraph (loc. cit.) that the nematodes "do not, in a Zoölogical sense, strictly belong to the Division work. * * * The Bulletin makes no pretense to be a scientific treatise

*Vol. II., No. 3, Washington, 1889.

†Bulletin No. 20. Division of Entomology, U. S. Dept. of Agr., The Root Knot Disease of the Peach, Orange, and other Plants in Florida, Washington, 1889,

on the life history of these worms, but is in the main an effort to ascertain a suitable remedy. The general literature on the subject has not been at Dr. Neal's command, and my time is so fully occupied otherwise that I can do little or nothing at present in the way of identification of species or of comparing Dr. Neal's results with those of European investigators, which, as a matter of fact, are of little practical importance."

The conditions this autumn at Auburn have been quite favorable for determining a number of interesting facts relating to the development and transformations of this nematode, as well as the duration of a life cycle showing the number of successive generations in a year.

II.

EXTERNAL CHARACTERS OF THE DISEASE.

By a reference to Plates I., II. and III. the external characters of the disease can be seen. These Plates represent respectively "knotted" specimens of the roots of the Irish potato, tomato, and parsnip and salsify. Plates I. and III. are natural size; Plate II. is reduced to two-thirds natural size. All are from average specimens. The abnormal growths on the tomato root appear as irregularly fusiform, knotty, or nodulate enlargements, two to ten times the natural diameter of the roots. The surface of the gall is at first smooth, more or less undulate, or papillate, but becomes later roughened, scurfy, or cracked and finally decay of the tissues sets in. The tap root and the earlier lateral roots were attacked early in the season and when the photograph was taken they were partially decayed and falling to pieces. When the roots begin to die they send out new roots in the efforts of the plant to recover from the effects of the disease. These roots in turn are attacked and deformed as represented in the figure. Other plants were found with the tap root still alive, very much enlarged and cracked, and the disease in an active state. The enlargements of the roots of the Irish potato are similar in form to those of the tomato, though on specimens I have examined they are not so large or numerous. The surface of affected tubers first presents minute elevations usually at the point on the surface corresponding to a lenticel. The minute elevation soon grows to be quite a large convex elevation and finally cracks. In the seed potato in the figure, Plate I., the cracks can be seen, while on the young potato represented in the upper left hand corner the projections are still quite smooth. These characters of the disease in the tubers will be referred to again.

There is great variation in the form of the galls even on the roots of a single species. Plate V., figures 31 and 32 represent respectively the galls on the roots of the cotton plant and peach. The fibrous roots of the peach possess short ovoid, usually lateral galls; sometimes they are symmetrical. As the root becomes older and the disease spreads the external appearance is more as represented by the larger root in the figure, the surface irregularly enlarged, roughened and cracked.

This description of the external characters of the disease will serve to introduce the subject. A more detailed comparison of the variations in different plants will be given below.

III.

MICROSCOPIC CHARACTERS.

Upon examination the enlargements proved to be the galls produced by the presence of a nematode worm, *Heterodera radicicola* Müll.* (*Anguillula radicicola Greeff*†, *Anguillula arenaria N.*‡ *ex parte*). If we cut directly across one of these tomato root galls, make a very thin shaving from the cut end and prepare it for examination with the microscope the micro-characters of the disease will be revealed. Fig. 36, Plate VI., represents such a preparation magnified. *a* and *b* represent two female cysts; *a* is mature, *b* is in an earlier stage of development. If the female cyst is very old the cavity in the tissues of the root will be seen to be occupied by young thread-like worms—the larvæ—and eggs in different stages of development, floating in a semi-fluid, granular, gelatinous substance, the amorphic remains of the parent worm.

*Mittheilungen über unseren Kulturpflanzen schädliche, das Geschlecht Heterodera bildenden Würmer, Landwirthschaftliche Jahbücher. Band XIII., Hef I., S. 1-42, Berlin, 1884.

†Sitzungsbericht. der Marburg Gesell. z. Beförd. d. Naturwiss. 1872, S. 169.

‡Bulletin No. 20, U. S. Department of Agriculture, Division of Entomology, Washington, 1889.

See fig. 37, Plate VI. If the knife in making the section should pass through a young female cyst, the cavity would seem to be occupied by granular protoplasm and numerous small fat globules, or as in many instances is the case, the long tubes of the uterus and ovaries with young ova in different stages of development may be seen. If the knife should pass by the side of the animal without injuring it the cavity would then contain a perfect animal variable in form according to age or the character of the surrounding tissues of the root. See fig. 29, *a* and *b*, Plate V.; figs. 36, *a* and *b*, 40, *a*, and 41, *a*, Plate VI.

In order to understand the real nature of the cysts and the effect produced upon the growth and structure of the deformed root, it will be well to note the form and general characters of the mature female cyst, and then follow with a detailed account of the development, transformations and habits of the sexes, which forms one of the most wonderful and interesting subjects it has ever been my lot to investigate.

IV.

GENERAL CHARACTERS OF THE MATURE FEMALE CYST.

I have selected the mature female cyst as a preliminary study because of its comparatively large size as compared with the males or young, because it is so much more easily found than the males, and almost any one who has a low power microscope at hand can demonstrate with ease the general characteristics here given.

When the galls on the roots of some plant, which has tender tissues like the roots of the tomato, are badly cracked and in the incipient stages of decay if one is broken there will usually be seen whitish, or dull yellowish irregularly oval bodies, from one-fourth to one-half of a millemetre (one-hundredth to one-fiftieth of an inch) in diameter, that are easily differentiated with the unaided eye from the discolored and broken surrounding tissue. Usually the unaided eye can detect also the head end projecting as a minute point on one side giving to the object the appearance of a minute "gourd", or "crooked neck squash", or a minute inflated bladder. With the aid of a small hand glass at least this peculiarity of form can be seen. These are the gravid female cysts.

Placing some of these cysts so that they can been seen under the microscope and magnifying them about 100 times they will appear something like figs. 34 and 35, Plate VI; or 27, Plate IV. The resemblance now to a small "gourd" is easily seen. The head is at the small end. In the mouth hole can be seen a short slender cylindrical spear broadend at the base which ends in three short lobes. This spear is hollow, the anterior end lies in the mouth opening at the middle point of the head end of the animal. It is capable of extension at the will of the animal and is moved by pairs of muscles directly attached to it. Fig. 34, *a*, Plate VI. The spear of the male nearly agrees in form. This is represented more highly magnified in plate IV., fig. 21z, *c*, and fig. 25, *a*. In this latter figure only two of the lobes at the base of the spear are represented. The mouth opening is cylindrical and behind broadens into the mouth hole.

In the males the anterior end of the exsertile spear is supported by six lamellæ the ends of which form the anterior end of the head and fit around the spear. A front view of the arrangement of the lamellæ presents a radial, stellate figure, which is shown in fig. 24, Plate IV., drawn also from the male. The œsophagus begins at the base of the exsertile spear. The anterior part is a long slender tortuous channel which looks like a dark line reaching to near the swelled portion of the cyst where is the middle part of the œsophagus. The middle part of the œsophagus is an ovoid or ellipsoidal transparent muscular bulb, which has a fibrillate structure, the fibrillæ radiating from the centre. Seen in side view this bulb looks very much like a small wheel. In Plate VI. fig. 34, *b* is the bulb, or middle part of the œsophagus. The slender tortuous channel forming the anterior part is represented connecting this with the base of the spear *a*. The posterior part of the œsophagus connects with the alimentary canal, neither of which are represented in the figure, as the mass of fat globules usually renders the body too opaque at this age.

Were it not for a slight movement of the apparatus just described, or a trifle "nodding" of the head there would be nothing to suggest what we ordinarily consider a sign of life. Occasionally even while the cyst is under microscopic examination the exsertile spear is thrust slowly out at the mouth, and then drawn back, at the same time the anterior part of the œsophagus being connected with it is also moved. Sometimes the apparatus slides far enough so that the tortuous anterior part of the œsophagus is straightened and the bulb is moved a little forward and backward. Sometimes there appears also a slight sidewise movement of the anterior part of the head, a sudden "jerkey" motion. This sidewise movement of the head is probably from force of the habit of the worm in its larval stage when movement from place to place is accomplished by a constantly changing tortuous motion of the body. Müller* speaks of an expansion and contraction of the middle part of the œsophagus which he has observed. By this means nutriment from the plant is sucked in through the lumen of the spear into the œsophagus and thence into the alimentary canal. Now turning the eye upon the large part of the body the first thing to attract attention is the presence of two long cylindrical objects coiled within. Usually at this age of the cyst the development of numerous fat globules on the interior of the body renders it so opaque that the terminations of these tubes and their connection with the body wall cannot be seen. Figs. 34 and 35, Plate VI., represent such opaque cysts. In some parts of the tube, however, can be seen polygonal cells, the faces where they meet making a zigzag line along the tube. Towards the posterior end of the cyst there can usually be seen oblong bodies lying within the tube or free in the body cavity. If these bodies are lying on their side they resemble a bean in shape. They are the *eggs*, and the long objects coiled within the body are the *genital tubes*.

By examining a number of mature female cysts from the galls of plants with soft tissues there will be found occasionally one which is not very opaque, as the fat globules are less numerous. Having found such a cyst we can see that the two tubes unite near the posterior part of the body and form a common passage, of a greater diameter, but quite short, which extends to an opening, the *vulva*. Then by following with the eye the sinuous course of the tubes in the other direction the anterior ends will be found

*Mittheilungen über unseren Kulturpflanzen schädliche, das Geschlecht Heterodera bildenden Würmer, 1884.

lying free within the body near the anterior portion. From the part where the tubes fork for nearly half their length is the *uterus*. The anterior free ends are the *ovaries*; the middle part functions as the *oviduct* and *receptaculum seminis*. Fig. 27, Plate IV., represents a cyst not very opaque, *d* is the vulva, *e* the uterus, and the free ends in the anterior portion the ovaries. The anal opening in the mature female cyst becomes displaced; it is represented in fig. 27 at *f*. Fig. 28, Plate IV., represents the uterus and ovaries very highly magnified.

V.

DEVELOPMENT AND METAMORHOSES.

(*See Plate IV.*)

EGGS.—The young ova are developed in great numbers in the ovaries. Fig. 28 represents them when some are full grown and the genital tubes are crowded for nearly their entire length. They are very tender and plastic, and when free are spherical. But packed and confined as they are in several rows inside the wall of the ovaries they are held in a polygonal form. Each one contains a large nucleus and a distinct nucleolus. When quite young they are nearly hyaline, and transparent. Near the anterior ends of the ovaries they are several layers, deep across its diameter. As they grow in size the increased pressure forces the elongated mass of young ova slowly toward the uterus, since they cannot escape at the anterior ends of the ovaries. Then because the diameter of the posterior ends of the ovaries and the uterus is but little greater than the anterior ends of the ovaries the ova must be arranged in a decreasing number of rows, until a single ovum is equal in diameter to the inside diameter of the uterus. If we count the number of ova which stand in a superficial transverse row across a well developed ovary, near the anterior end there will be four or five; now looking along the ovary toward the uterus, we will count three, two and finally one. With the increase in size of the ovum there is an accompanying development of yolk globules. The first change is the appearance of very fine granules. Then yolk globules are developed, a few at first, but become very numerous as the growing ovum passes into the uterus when it is quite opaque. The globules seem to be more numerous in a peripheral plane. The ova are held in polygonal form until one only occupies the diameter of the uterus, when they are at first rectanglar in outline. From this form, as they grow in size they simply elongate until their length is about two or three times their diameter. The ends of the egg are gradually rounded off, and it becomes slightly curved so that it is shaped very much like a bean. At first the ovum possesses a very delicate wall. The covering of the egg becomes stronger as it passes down the uterus. The fully developed egg possesses a double wall, a delicate inner membrane and an outer tough membrane.

Just the precise stage when the ovum is fertilized I have not determined, but I have found spermatozoa in the posterior part of the ovaries. The nucleus in the fully developed egg is quite distinct, though not so prominent as in the young ovum. It is largely hidden by the mass of yolk globules. It is of a pale violet color. An examination of fig. 28, Plate IV., will show many of these changes. A few of the eggs in one uterus have undergone various stages of segmentation preparatory to the development of the embryo. In dissecting living specimens very frequently the ovary or uterus becomes ruptured, in which case the ova in various stages of development escape from the great pressure exerted upon them by confinement, and not being entirely free from each other are held in beautiful grape-like clusters. Some of these are represented in fig. 28.

The mature egg is from .08mm to .10mm long (three to four thousandths of an inch), exceptionally I have found them .12mm long. Thus far its development has been an increase in size, a profuse development of yolk globules, and a change in form. Its development from this point is the multiplication of cells by division, beginning with the single cell enclosed within the egg membrane. (See fig. 1, Plate IV.) Complete but somewhat irregular segmentation takes place. The nucleus first divides in two parts, forming two nuclei. Each nucleus moves a short distance towards its end of the egg. A transverse constriction now appears about the middle of the cell which progresses until the cell is divided into two cells (fig. 2). The process is now repeated in each of these new cells resulting in four cells (fig. 4). Sometimes one of these cells is completely divided before the other begins so that there may be three cells (fig. 3). Occasionally the first line of fission is oblique so that the two resulting cells are shaped as in fig. 2'. The egg now divides into six, eight, ten cells and so on. Usually the first division is such that one cell is larger than the other, but sometimes they seem to be about equal in size. Occasionally the first division results in two cells one of which is only about one-third or one-fourth so large as the other. I have watched the cell division up to the stage represented in fig. 7. Up to this point there is great variation in the disposition of cells at the different stages resulting from variations in the somewhat uneqnal segmentation. From this point up to that represented in figs. 8 and 9, I have not, owing to the limited time over which my observations have as yet extended, carefully determined the progress of development. Figs. 8 and 9 probably represent the stage where the larger endoderm (internal) cells are completely surrounded by the smaller ectoderm (external) cells, just prior to the invagination (sinking in) of the head end to form the mouth and œsophagus.

According to *Strubell, in *Heterodera Schachtii*, the first two unequal cells into which the egg divides represent primary cells of two different groups of cells which result from farther division. The larger primary cell divides more rapidly and forms small cells, which grow around the more slowly formed larger cells which result from the division of the other smaller primary cell. The growing over proceeds first down the convex side of the egg and the ectoderm cells fold over the opposite end of the embryo, the mass of endoderm cells. Thus the "prostom" (the open space between the converging edges of the enveloping ectoderm cells) is on the concave side of the egg, and because the ectoderm cells on the concave side of the head end have grown but little it (the prostom) occupies the entire concave (ventral) side of the young embryo. At this stage if we turn the egg so that we are looking directly at the concave side the ectoderm cells will be in a boat-shaped mass, and in this boat-shaped mass of ectoderm cells will be the larger endoderm cells. The "prostom" (open part of the boat-shaped mass of ectoderm cells) now begins to close by the growth and increase of the cells at the margin. This closure takes place more rapidly at the posterior end and advances toward the head end so that after awhile there is only a small opening through the ectoderm cells near the head end of the concave side. This is finally closed so that the endoderm cells are completely enveloped by the smaller ectoderm cells.

This is probably the stage which I have figured in figs. 8 and 9, Plate IV. The larger, endoderm, cells can be seen in the center:

Untersuchungen über den Bau und die Entwickelung des Rübennematoden, Heterodera Schachtii Schmidt. Bibliotheca zoologica, Heft 2, 1888.

the smaller, ectoderm, cells on the out side. Invagination of the ectoderm cells now takes place at the head end, that is, the cells sink inward as if pushed in by some outside force. This is represented in figs. 9x and 10. By this process the mouth and œsophagus are developed. I have only studied the external changes in the embryonic development. From this point up to the fully developed larva the changes are represented in figs. 11 to 15. Beginning with figs. 10 and 11 the head end appears hyaline and finely granular and is larger in diameter than the rest of the young embryo, which at this stage is of equal length and diameter with the inside ot the egg membrane. It next begins to elongate and become more slender. This forces it to double up inside the egg membrane. It does so by turning its tail end by degrees around to its ventral side (fig. 11, 12). In some cases the tail end for a time does not move. This causes the embryo to double up midway, and sometimes to be coiled in a spiral manner for awhile. It now continues to elongate until it is coiled twice (fig. 13), then three times (fig. 14), and finally four times (fig. 15) within the egg membrane.

I have watched the egg and embryo under the microscope pass through all these changes. Sometimes the embryo would double its length in eight or ten hours. When it has reached this stage it remains a day or so still within the egg membrane while the cuticle, the tough transparent body wall is being perfected, and the slender pointed end of the tail is formed. Now by its writhing and twisting it ruptures the tough egg membrane and is set at liberty. At this stage the larva passes through its first moult, either just as it is coming from the egg membrane or very soon afterward. Fig. 16 Plate IV. represents the larva in the act of coming from the egg membrane. It is moulting at the same time. The thin larval skin can be seen slipping off its head and tail.

As the female remains in a cystic state and the cyst is surrounded by the tissues of the plant the eggs when crowded in the uterus rupture it and finally the numbers of them completely fill the body cavity of the cyst. In a few cases after freeing a cyst I have observed eggs pass out at the vulva.

Segmentation of the egg begins before it leaves the uterus, and e find in the body cavity of live female cysts eggs in all stages f development, and free larvæ, so that the female may be said to be oviviparous.

Larval Stage.—The larval stage begins with the hatching from the egg. The moult which takes place at the same time is the first moult of the larva. The young thread-like worm is from .3mm to .4mm (12 to 16 thousandths of an inch) long; it tapers gently to the blunt head end, and gradually into a slender pointed tail (fig. 17). In this form it resembles what are called "vinegar eels". In the head end we notice the exsertile spear, with its tri-lobed base, the long, slender tortuous channel of the anterior part of the œsophagus, and the ellipsoidal muscular bulb, the middle part. The lumen of the alimentary canal can also be seen, and it opens at the beginning of the hyaline space near the tail end. (See fig. 17, Plate IV.) The embryo and for a time the young larva possesses a cellular matrix inside the body wall, except at the head and tail ends. This soon develops numerous fat globules which are clustered around the alimentary canal.

The young worms, when ushered into life, find themselves imprisoned by walls of plant tissue which formed at once the prison house and tomb of their parent. (See fig. 37, Plate VI.) How to escape these bars is their first concern. Perchance fortune may favor them if the cyst is near the surface of the gall so that a crack, or partial decay of the tissues may liberate them. When not thus favored there are sometimes two courses open to them, more often only one. If the cyst opens into any of the large channels of the vascular tissue of the root, which is frequently the case, the larvæ may make their exit through these to other parts of the same root. In a majority of instances the worm must face the only alternative of starvation, and actually *batter* a hole in the wall through which it may escape. Taking position with the head end against a cell wall it thrusts forward the exsertile spear which strikes the cellulose wall forcibly, when it is drawn back and thrust out again. This process is repeated until a hole is made through the wall large enough to admit the body of the worm, into which it passes and by successively battering down the cell walls of the surrounding tissues it makes its way to freedom on the outside of the gall or to a fresh portion of the same root.

Having escaped from its confinement by one of these three courses it immediately selects another part of the root or a fresh young rootlet for attack and places itself in position for the siege. Bringing into play its exsertile ram it forcibly gains entrance to the healthy tissues of the root. The plant not able to expel the invader bends its energies in a vain endeavor to repair the injury to the roots. Increased development of cells takes place, and normal ones are turned from their proper position and function and also very much enlarged. The result is the formation of a gall, an increase of tissue in the root which supplies food and protection for hundreds of the worms, all which lessens the energies of the plant normally directed to the production of leaf and fruit.

The larvæ wander for a time through the tissues and finally come to rest. Plate VI., fig. 39, represents a larva as it is wandering through the tissues of a potato tuber. It now moults the second time and passes into a truly parasitic condition.

CYSTIC STATE.—The larvæ locate at various depths in the tissues. The body now begins to enlarge except at the two ends. Speaking vulgarly it would be said to "swell up". Almost before any increase in size of this part of the body is noticed the worm becomes rigid and could not move if it would. Its body may be turned or twisted in very curious shapes when this rigidity or fixedness comes upon it. (See Plate IV., fig. 17x.). The enlargement begins close behind the muscular bulb of the œsophagus, and for a little time this part of the body is larger than the posterior part. Very soon the enlarging takes place all along the body to the hyaline space near the tail end, and this portion of the cyst becomes generally of a greater diameter than the anterior part. The cyst is at first rudely spindle-shaped, then clavate (or club-shaped) with a very small sharply pointed process, the tail, at the larger end. Fig. 18 represents the spindle form, 19 the clavate form. Up to this point it is difficult to distinguish the sexes, but from this point they sharply diverge. The female cyst continues to enlarge, while the male undergoes a wonderful transformation and returns to the thread-like, or *anguillula* form.

TRANSFORMATION OF THE MALE.—The body of the male at this point is the same size as the interior of the cyst, very stout in proportion to its length. The first sign of a transformation is the slipping of the head from the wall of the head end of the cyst. At the same time the thick body of the male begins to elongate and double up inside the cyst while the tail end, stout and blunt, begins to curve around. This makes the third moult. (See fig. 21, Plate IV.) While the male is elongating and coiling up in the cyst it begins to moult again making four moults. The very thin skin can be seen partly slipped off the worm while yet within the cyst (fig. 21). The male continues to elongate and become more slender until it is coiled three, four, or more times, dependent on the length of the cyst, within the walls of the cyst, which still retain perfectly the shape of the cyst when the transformation began. Even the exsertile spear moults for its "mould" is left in the head end of the cyst, while the skin of the larval tail still projects as a slender process. The male coiled within this perfect wall of the cyst is a very beautiful object. Figs. 21x and 22 represent these. During this transformation the sexual organs of the male have become matured. It now breaks through the wall of the cyst and the surrounding tissue and travels blindly through the maze of cells until it comes to its mate when it pairs and then dies. Fig. 23 represents a male coming from its cyst. Fig. 21z a male of *H. radicicola* removed from a cyst.

STRUCTURE OF THE MALE.—It may be well now to note some things about the structure of the male which were not described in the Section upon the "General Characters of the Female Cyst". It is from 1mm to 1.5mm (one twenty-fifth to one seventeenth of and inch) long and about .043mm (seventeen one-thousandths of an inch) broad near the middle. Its body a little less in diameter at the posterior end; the anterior half of the body gradually tapers to the head end which is about half the diameter of the middle. The body wall is beautifully marked by prominent transverse striæ broader and much more distinct than in the larval stage. The head, exsertile spear and œsophagus have been described. The excretory canal on the ventral side opens a little posteriorly to the muscular bulb. The caudal end (tail end) is slightly curved, and very near the end are the two curved *spicules*.

The *generative organ* is paired, the long slender *testes* lying on either side of the alimentary canal reach by their free anterior ends to about the middle of the body. See fig. 21z, Plate IV. Some little distance from the caudal end of the body they unite into a *common canal* which itself near the spicules unites with the alimentary canal forming the cloaca. The *spermatozoa* are spherical. The cellular structure of the testes resembles that of the ovaries to some extent. The cells are polyhedral, and in side view the lines separating them are zigzag. See fig. 21z, Plate IV. In live males the spherical spermatozoa are easily seen at and near the common passage, but they are developed in the anterior ends of the testes. By boiling infested potatoes to soften them so that I could remove the cysts and mature males without cutting or mashing them, I found that it toughened the tissues of the animals, and made the cellular structure very distinct. I possess several microscopic mounts of the males and one with the male in the act of coming from its cyst.

Development of the Female.—About the time the cysts have reached the stage when the male begins its transformations it is quite easy to distinguish the female cyst. The alimentary canal is very large and up to this time in both sexes has occupied nearly the entire cavity of the cyst. Now it begins to deteriorate and the ovaries begin to come to maturity while the cyst continues to enlarge. While the female cyst still possesses the slender tail process*, the irregular, slender hyaline cornua of the generative organs may be seen one on either side of the large intestine which is covered with fat globules and is quite opaque, or more so than the genital tubes. See figs. 19 and 19z, Plate IV. The vulva, the opening for the uterus, is at the point in these figures where the tail process joins the cyst. The cyst continues to enlarge, or "swell", until the tail part is cast and thrust aside. The vulva is now at the posterior end, and in some cases the body is so much enlarged that a depression is formed at this point (see fig. 27, Plate IV.). The ovaries continue to elongate; and fertilization takes place long before the cyst has ceased enlarging. The ova begin to develop

*Probably the remains of the second moult.

while the cyst is comparatively small. Before the ovaries are fully developed they are capable of a slight independent motion. Frequently in examining those dissected from living cysts I have noticed a marked twisting and tortuous motion probably due to a contraction of muscles in the walls. The body wall of the female is marked by irregular transverse striæ, but not so prominent as in the male.

Length of Life Cycle.—This completes a life cycle of our *Heterodera radicicola.* It passes through all these changes, from the development of eggs, successively through the larval and cystic state until eggs are again developed in about one month. This I was able to determine by watching the development of the worms in the roots of "volunteer" potatoes which sprouted about the first of October and were infected from the soil and the "seed" potatoes. Thus in favorable seasons there would be at this latitude seven or eight successive generations in a year. Farther south where the season is longer probably the number of generations is increased. When we consider the number of eggs one female is capable of producing, from one hundred to two hundred or more, it will be seen that the worms multiply with startling rapidity. The periods of transformation of different individuals do not altogether co-inside so that at almost any season we may find worms in every stage of development.

Brief Recapitulation of the Life History.—*Egg*—The oblong, bean-shaped egg, .08mm to .10mm long, developed in the anterior part of the ovaries, after fertilization, enclosed in a double-walled membrane, undergoes partial or complete segmentation while yet within the uterus. From the beginning of segmentation to the fully developed larva 5 to 7 days are required. The thread-like larva is coiled three or four times within the egg membrane. *Larva*—At the time of hatching or soon thereafter it moults for the first time. It is "thread-like", blunt at the head end and narrowly pointed at the tail end, .3mm to .4mm long. In the head end can be easily noted the exsertile spear and the long tortuous channel of the anterior part of the œsophagus extending to a prominent ovoid or ellipsoid muscular bulb, the middle part of the œsophagus. From this point the lumen of the alimentary canal can be seen extending down through the middle of the body, in which is a matrix that develops many fat globules, the anus is situated at the beginning of the hyaline portion of the tail end. The larva now leaves the cyst cavity and enters a fresh root or different place in the same root. It wanders for a time when it comes to rest, moults a second time and then being fixed enlarges, or "swells up" into a cyst with a flask-like body, the head projecting at one end and the slender pointed tail at the other. At this time prominent sexual transformations take place. *Male*—The male moults again (3rd time) leaving the outer wall of the cyst intact, while the body of the male elongates, narrows and becomes coiled three or four times within the cyst. While this change is going on the male moults again (4th time). It is now from 1mm to 1.5mm long, anguillula like, blunt at each end, slightly curved at the caudal end where are two curved spicules: In the middle line of the body runs the alimentary canal, in the posterior half of the body are the paired testes, which are united into a common duct near the caudal end and at the cloaca this unites with the intestine. On each side within the body is a muscular cord extending the entire length of the worm. *Female*—The female does not moult again, but continues to enlarge enormously until it is gourd-shaped, and the paired generative organs, opening by a common passage at the vulva in the posterior part of the body, form long tubes which lie coiled in the body of the cyst, free at their anterior end. As the embryos are developing the body of the cyst breaks up into an amorphic gelatinous mass in which the young larvæ and eggs are found floating within the cyst cavity. Length of life cycle, one month.

METAMORPHISM OF HETERODERA.—One of the features of the greatest morphological interest in *Heterodera* is its singular metamorphic character. This metamorphism finds its completest analogy in some forms of the *Coccidæ** where the larvæ, after pursu-

*Strubell, Ad. Untersuchungen über den Bau und die Entwickelung des Rübennematoden, Heterodera Schachtii Schmidt. (Bibliotheca Zoologica. Originalabhandlungen aus dem Gesammtgebiete der Zoologie, hrsg, von R. Leuckart u. C. Chun. Heft 2.) 4°. 50 pg. 2 Taf. Cassel (Th. Fischer) 1888.

Centralblatt für Bakteriologie und Parasitenkunde. Bd. VI., No. 15, pp. 423-429, Jena, 1889.

Müller, Mittheilungen über unseren Kulturpflanzen schädliche, das Geschlecht Heterodera bildenden Würmer. Landwirthschaftliche Jahrbücher, ing for a time a wandering life undergo a metamorphosis†, accompanied by what appears to be a retrogression, so that the creatures lack the power of locomotion. At the third moult of the male it is transformed again into a more highly organized being, possessing wings and capable of seeking its mate. On the other hand the female remains fixed and incapable of locomotion and after impregnation by the male becomes enormously distended with eggs. It must be borne in mind, however, that this analogy is only superficial. *Heterodera* des not lose its power of locomotion through any retrogression of form like the loss of organs which occurs in the *Coccidæ*, though according to Strubell some parts of the head undergo retrogression. It is because of the rigidity and distention of the body of both male and female so that it cannot perform the undulatory movements of the body by which locomotion in the larval state and in the adult male is accomplished. The fact that the cyst is surrounded by the tissues of the plant does not interfere with its independent locomotion.

The cyst‡ differs morphologically from that of *Nematodes* like *Trichina* where the larva becomes encysted in the muscles of its host and does not undergo any remarkable change of form in the formation of the cyst, the walls of which are formed from extraneous and excreted matter. It somewhat resembles in its origin and earlier stages the earlier stages of certain of the *Cestodes* like *Tænia*§ where the embryo after it is located in the tissues of its host develops by distension into a vesicular body. Here, however, the resemblance ceases, and the walls of the *Tænia* cyst by invagination or evagination produce the head of the worm, or scolex, or in some cases the brood capsules, from which several heads are produced. In *Heterodera* the vesicular distension of the larva

Bd. XIII., Heft I., 1884.

Sorauer, Pflanzenkrankheiten, Zweite Auflage, Erster Band, pp. 852-854, 1886.

Strubell, Ad. Ueber den Bau und die Entwickelung von Heterodera Schachtii Schmidt. Zoolog. Anzeiger, No. 242, 17, Januar 1887. pg. 42-46, und no. 243, 31, Januar 1887, pg. 62-66.

Centralblatt für Bakteriologie und Parasitenkunde. Band I., pp. 603-604, Jena, 1887.

†Comstock. An Introduction to Entomoloy, Ithaca, N. Y., 1888.

Ann. Rept. U. S. Dept. Agr. 1880.

‡My use of the term cyst is mainly for convenience.

§Text Book of Zoology, Claus and Sedgwick.

begins after a period of wandering through the tissues of its host. Instead of invagination the wall of the male vesicle is cast, and retains the cystic form while the worm elongates and coils within it. In its "pupa" condition the male more nearly resembles *Echinorhynchus* where the embryo after a wandering state comes to rest in the tissue of its host, develops a small elongated larva which is surrounded by its firm external skin as a cyst.* The female vesicle continues to distend until in age its body is filled with eggs and young larvæ. This condition of the female has been termed by some† a "brood capsule" but it of course bears no morphological semblance to the brood capsules of certain *Cestoda*. I regret that I find it necessary here to call attention to some serious errors on the part of some of our American investigators.

One of these errors is that into which Dr. Neal‡ has fallen in his treatment of the life history of this parasite. He speaks of the eggs as "cysts." This may have been due to the fact that he regarded the numerous yolk globules in the ovaries as cells, for he speaks of the cysts (loc. cit.) which were at first without any "epidermis", being formed by "an agglomeration of cells". What he represents in Plates IX. and X. as segmentation of the "cysts" is only a representation of the first stages of segmentation of the egg.

It appears that Prof. Scribner made a similar mistake in speaking of the "cysts" and "eggs" of the nematode which causes the new disease of the §Irish potato described by him. What he speaks of as the "cysts" are the egg membranes still containing the young larvæ. What he figures as the mature worm is a young one and the round granules which he speaks of as eggs are probably fat globules. I have found potatoes here affected with a similar disease while also attacked by *Heterodera radicicola*. I have found the worms representing all stages of development. It appears that they do not form cysts in the proper sense of the word. Fig. 46, Plate VI., represents a mature female of this worm. At *a* is

*Text Book of Zoölogy. Claus and Sedgwick Vol. I., p. 362.

†Strubell, Ad. Untersuchungen über den Bau und die Entwickelung des Rübennematoden, *Heterodera Schachtii* Schmidt. Bibliotheca zoologica. Heft 2, 1888.

Centralblatt für Bakteriologie und Parasitenkunde. Band VI., No. 15, pp. 423-429, Jena, 1889.

‡Bulletin 20. U. S. Dept. of Agr. Division of Entomology, Washington, 1889.

§Bulletin of the Agr. Exp. Station, Tenn. Vol. II., No. 2. 1889.

a fully developed egg yet within the uterus, while *b* represents young ova not fully developed. In the body of the worm as well as in the eggs can be seen the round globules. Figs. 42 and 43 represent eggs, 43 an egg having undergone fission. Other eggs were observed in different stages of development up to the fully formed larva represented still within the egg membrane at fig. 44. Fig. 45 represents young worms of this species.

Fig. 47 represents a different species occasionally found accompanying these worms, but whether they are parasitic or not I have not yet had the time to determine.

Several of the worms which Dr. Neal has figured do not belong to *Heterodera*. Especially in decaying tissues one is apt to find species which are not parasitic. However, wherever they were found it is very clear that some belong to other genera than the worm in question. For example his figure 2, Plate XIII. (loc. cit.), is a mature female of another genus. An egg is represented in the uterus near the letter B, and the numerous yolk globules he speaks of as a peculiar arrangement of cells.

COMPARISON WITH HETERODERA SCHACHTII SCHMIDT.—There are many points of very close resemblance between *H. radicicola* and *H. Schachtii*. Both of these are European species, and each is known to attack widely different plants, so that the selection of a particular plant or family of plants, as a specific peculiarity is not their habit. Notwithstanding the points of resemblance there are a number of differentiating characters heretofore used the value of which can only be determined after careful study and experimentation, and even now some of these are known to be variants possessed by both species. The female of *H. Schachtii* is said to be ectoparasitic; the posterior part of its body being nearly or quite exposed. This results from the larva locating very near the surface so that its distended vesicular body breaks the surface and becomes exposed. This does not seem to be a character of very much value since many of the female cysts of *H. radicicola* are exposed.

The chief morphological differentiating characters which have been employed are as follows. The posterior part of the body of the female is rounded in *H. radicicola.* In *H. Schachtii** the posterior part of the body of the female projects into a short stout process in which is the vulva. According to Strubell (l. c.) the exsertile spear is somewhat differently constructed in the females of the two species. I have only found one female which possessed the stout process at the posterior part of the body. One of the most prominent differentiating characters used in the case of the males is the presence of the slender tail process in the cyst in *H. radicicola* and its absence in *H. Schachtii.* Dr. E. L. Mark, of the Museum of Comparative Zoölogy, Cambridge, Mass., who, before my copy of Strubell arrived, kindly compared for me some copies of my drawings, with those of *H. Schachtii* by Strubell, and aided me in the interpretation of some of the phases of egg segmentation, has made the suggestion that possibly the slender tail process in *H. radicicola* may be the result of the retention of the first larval skin which is lost in *H. Schachtii.* After this suggestion it has occurred to me that the first larval skin (at second moult) in those I have observed is cast at the time the larva comes to rest preparatory to passing into the cystic stage. In such moults I have only observed the skin as it was loosened from the anterior part of the body. Strubell says in the case of *H. Schachtii* (l. c. p. 44) that frequently the old larval skin remains attached to the hinder part of the larval envelope ("cyst") so that it has the appearance of being pointed. He is also inclined to think that the grounds for considering the two species distinct are questionable. In a foot note p. 11 he states that he is strengthened in his belief by the recent researches of Ritzema Bos in Wageningen (Biolog. Centralblatt, Bd. VII) who finds that such species as *Tylenchus devastatrix, allii, Havensteinii et Askenasyi* must be united into a single species.

That these two species of *Heterodera* are identical has been suggested by others†.

*Strubell, Untersuchungen über den Bau und die Entwickelung des Rübennematoden, Heterodera Schachtii Schmidt. Bibliotheca zoologica. Heft 2, 1888.

Müller, C. Mittheilungen über unseren Kulturpflanzen schädliche, das Geschlecht Heterodera bildenden Würmer. Landwirthschaftliche Jahrbücher. Bd. XIII., Heft I. 1884.

†Sorauer, Pflanzenkrankheiten, Zweite Auflage, Erster Band. Foot note pp. 854–855.

During my study of *H. radicicola* I have been strongly inclined to consider it identical with *H. Schachtii* since many of the variations of the two species tend to reconcile the above mentioned differences. However, since my copy of Strubell's work has arrived and I have had an opportunity to compare it carefully with my own researches I find there exists a difference in the structure of the males of very great morphological importance. Strubell states that the genital apparatus of the male is an unpaired tube,* the single tube occupies the ventral side of the body cavity for half its length, the posterior end unites with a short efferent duct which itself unites with the intestine to form the cloaca. As I have stated in a former paragraph the genital apparatus in the males I have studied is paired, the two tubes unite near the posterior end of the body to form the efferent duct. It is difficult to see how Strubell could have overlooked a second tube, if it existed, since his work was done under the ægis of Leuckart. This character possessed by comparatively a few Nematodes seems of too great importance for specific variation. To reassure myself I referred again to my microscopic mounts of the male. Müller's (loc. cit.) imperfect study of the male leaves us no clue as to the structure of the genital apparatus in *H. radicicola*. Until the European species is studied it will be impossible to say whether mine is a distinct species.

My figures 21, 23, 25, and 26, Plate IV., represent a male which differed from *H. radicicola* mainly in the presence of a short curved caudal process represented at *a*, fig. 26. At first I thought this might possibly be a different species from *H. radicicola*, but as I only found one specimen I have concluded it may possibly be an accidental variation.

All of the males which I have studied were found in potatoes. My impressions are that the species in all the different galls found here are identical. More than this at the present time could not be said. As this report is only preliminary, and it has been impossible for me during the very short period of my observations to find and carefully study the males where we must probably

*"Bei unserer Heterodera präsentiert sich derselbe als ein einfacher Schlauch,' etc., p. 22. See also his fig. 1, Taf. I.

look for the most satisfactory specific characters, in the different galls, I hope to continue these investigations during the coming year. This will also afford me an opportunity to study more fully some structural features necessarily passed over in the present work.

DISTRIBUTION OF HETERODERA.—The genus *Heterodera* is world wide in its distribution. It has been long known in central Europe where *H. Schachtii* was discovered by Schacht* in 1859 and named by Schmidt† in 1871. *H. radicicola* was first recorded in 1872 and named as *Anguillula radicicola* by Greeff‡, and transferred to this genus by Müller§ in 1884. It has been found in Java in the roots of sugar cane by Treub|| who named the species *H. Javanica*, the characters being based on some differences in size of the females from *H. radicicola*. Beijerinck¶ doubts if it is distinct from *H. radicicola*.

It was known in Brazil in the year 1878§§ in the roots of the coffee tree, and has since been studied and published under the generic name *Meloidogyne* by Golbi||||. Leuckart is of the opinion that this is a species of *Heterodera* (see foot note in Centralblatt für Bak-

*Ueber einige Feinde der Rübenfelder. Zeitschrft. d. Ver. d. Rübenzuckerindustrie, Bd. IX., S. 175-179, 1859.

†Ueber den Rüben-Nematoden (Heterodera Schachtii A. S.). Zeitschr. d. Ver. f. d. Rübenzuckerindustrie im Zollverein. Bd. XXI., S. 1-19, 1871. (Both cited by Müller, Mittheilungen über unseren Kulturpflazen schädliche Würmer.)

‡Sitzungsbericht. d. Marburger Gesellschaft z. Beförd. d. Naturwiss. S. 169, 1872. (Cited by Müller, Mittheilungen, etc.)

§Mittheilungen über unseren Kulterpflanzen schädliche, das Geschlecht Heterodera bildenden Würmer. Landwirthschaftliche Jahrbücher, Bd. XIII., Heft I. 1884.

||Quelques mots sur les effets du parasitisme de l' Heterodera Javanica dans les racines de la canne à sucre. Ann. d. jardin bot. d. Buitenzorg. Vol. VI., Part I., pp. 93-96, Leide, 1886. Abstract in Bot. Centralblatt, Bd. XXVIII., p. 269, 1886.

¶The Gardenia-root diease. Gard's. Chron. ser. III., Vol. I., p. 488-489, 1887 Abstract in Bot. Centrabllatt. Bd. XXXV. p. 92, 1888.

§§Sur une maladia du Cafeièr observée au Brésil. Compt. rend. hebd. acad. sc. Paris, 1878, T. LXXXVII., No. 24, S. 941-943. Abstract in Bot. Jahresbericht (Just) p. 173, 1878.

||||Relatorio sobre a molestia do cafeeiro do Rio de Janeiro. Bd. VIII., Archivos do Museo nacional do Rio de Janeiro.

Biologische Miscellen aus Brasilien, VII. Der Kaffeenematode Brasiliens, Meloidogyne exigua G. Zoolog. Jahrbücher, abth. f. System., Geogr. u. Biol. d. Thiere, Bd. IV. Hft. I., pp. 262-267, Jena 1889.

Abstract in Centralblatt für Bakteriologie und Parasitenkunde, Bd. V., pp. 839-840. 1889.

teriologie und Parasitenkunde. Bd. V. p. 840, 1889). It is also known in Scotland according to W. G. Smith*.

Dr. Neal† states that it cannot survive the cold of severe winters in America north of about the January isotherm of 50° as shown in the No. 2 Isothermal Lines of the U. S. Signal Service, 1881. I do not know that any experiments have been conducted to demonstrate this. If it can survive the winters in Scotland it can endure the winters of all our Gulf and South Atlantic States. The January isotherm of 50° strikes the Atlantic coast just below Savannah, includes the southeastern corner of Georgia, the very southern limits of Alabama, and a corner of Louisiana. The isotherm of the same month and year which passes near this place is 45°. It starts above Charleston, cuts Georgia through the center and passes a little south of Montgomery. The isotherm of 40° starts near the boundary corner of Virginia and North Carolina, passes north of Atlanta, and includes the major part of Alabama, Mississippi, Louisiana and Texas. The average temperature of Edinburgh, Scot., during the month of January is about 39°, so that we might fully expect the root-gall nematode, if once introduced, to thrive as far north as the January isotherm of 35°, or even farther. This isothermal line starts in at the coast north of Norfolk and runs through middle Tennessee. Indeed I am inclined to think if a favorable opportunity should occur for its introduction into our States even so far north as New York and Ohio that from its habit it might easily pass the winter in sufficient numbers to become a terrible pest. On long rooted plants like the parsnip I have found them in great numbers fifteen inches below the surface of the ground. On tomato roots, which were placed in the soil very deep to get them if possible out of the way of the attacks of the worms, I have found them so low as eighteen inches below the surface. This depth would protect them from the frost in the very severe winters of some of our northern States.

*Disease of Oats. Heterodera radicicola Müller. Gardeners' Chronicle. New Ser. Vol. XXI., p. 172, 1886. Abstract in Bot. Centralblatt, Bd. XXXI., p. 247, 1878.

†The Root-knot Disease of the Peach, Orange, and other Plants in Florida, due to the work of Anguillula. Bulletin No. 20, Division of Entomology, U. S. Dept. Agr. Washington, 1889.

There is to some extent a natural barrier to the spread of the root-gall nematode from the southern to the northern States, which is explained by the fact that very few, if any, perennials grown in the south are transported north for cultivation. However, the subject is of sufficient importance to the northern States to justify an inquiry into the possibility of its being successfully carried through the winter under the conditions I have stated.

VI.

STRUCTURAL CHARACTERISTICS OF THE DISEASED ROOTS.

NOMENCLATURE.—The abnormal growths on the roots, caused by *Heterodera radicicola* have long been termed popularly, in this country "root-knot". In Scotland they are known as *"root-ill", "thick-root", "tulip-root", "segging"; while in Germany they have long been known under the name "Wurzelgallen". The tubercular swellings on the roots of Leguminous plants (see comparison of root galls with the tubercles of the *Leguminoseæ*, at close of this Section) have long been known and published in Germany as "Wurzelknöllchen" (root-knot). In order to avoid a confusion of the tubercle with the abnormal growths dealt with here I shall use the term nematode root-gall, or root-gall. There is a tendency with some writers to use the term "gall" only for those abnormal growths which have their origin through the irritating presence of animals†. These nematode root-galls would belong to the same class of abnormal growths sometimes denominated *Helminthocecidien*. The writer does not mean by the use of the term root-gall, that it has priority to the use of the term root-knot, but in view of the appropriateness of the word, teratologically, and for the reason stated above he would recommend its adoption.

EXTERNAL CHARACTERS.—For the purpose of preparing the reader for a study of the life history and transformations of the parasite, Section II. was introduced in which attention was called to the general external morphological characters of the galls in a few plants. It is now in order to discuss more at length

*Smith, G. W. Disease of Oats. Heterodera radicicola Müller. Gardeners' Chron. New Ser. Vol. XXVI., p. 172, 1886. Abstract in Bot. Centralblatt, Bd. XXXI., p. 247, 1887.

†Sorauer, Pflanzenkrankheiten. Zweite Auflage. Heft I.

the variations in form of the galls, and then to point out the special histological changes induced.

The external form of the gall is to a great extent dependent upon the number of worms and their distribution in the tissues of the roots, as well as upon some specific peculiarities in the growth of the roots or habit of branching. If the worms are numerous and the attack is made pretty regularly in a peripheral plane at a particular point in the root the gall will be symmetrical, and either short and ovoid or elongate and fusiform according to the extent of their distribution along the axis of the root at that point. If fewer worms attack at a given point the gall is more likely to be lateral, owing to the less certainty of an even peripheral infection. Often, however, lateral galls may be so near as to unite into one, when the appearance is that of a very irregular and knotty gall, the enlargements passing by abrupt changes on different sides of the root.

For the forms of the galls in the roots of the tomato, potato and peach the reader is referred to Section II.

The galls found in the "poke-weed" (*Phytolacca decandra*) were very large, lateral and ovoid. In a species of the plant called coffee weed (*Cassia obtusifolia*) lateral galls were found on the tap root near the surface of the ground. On the grape the fibrous roots usually possessed small ovoid lateral galls, while the galls on the larger roots were irregularly fusiform and not very prominent. The galls on the cow pea (*Dolichos catiang*) are quite peculiar. They are usually irregularly pyriform and mostly lateral, with the larger end of the gall below. When a root is attacked it appears in many cases to die just below the point of attack so that the gall is abrupt at this end while there is an opportunity for the worms to distribute themselves in a diminishing ratio a short distance above the gall which makes the sloping narrowed portion of the pyriform body. The size and irregularity of the larger end of the gall is increased by one or more lateral roots which develop very near the lower end of the gall, and continue the direction of growth of the main root which died. This in turn may be attacked, develop a gall, die below the gall and produce a branch, and so on successively until several pyriform galls are formed on successive branches appearing like a string of pyriform beads, the string of which runs obliquely through them. In badly infected specimens this is more marked and presents a very singular appearance. The galls on bird's foot clover (*Lotus corniculatus*) are short and ovoid, or more usually by the very close proximity of several, elongated and very irregular in outline. This irregularity is increased by the numerous small rootlets put out by the diseased root into the bases of which worms distribute themselves and form small convex elevations on the larger gall.

In the roots of *Amarantus retroflexus* the worms were quite abundant but the galls were not prominent. On the larger roots they were irregularly fusiform, slightly twisted, and while in some cases one half inch, one inch or more in length, the diameter of the root was not greatly increased. In places the surface possessed small brownish or dirty white pustules in which were cysts located very near or quite in the surface of the gall, while in the same gall other cysts were imbedded in the central cylinder.

It is unnecessary to detail farther in this preliminary report the forms of the galls on the other diseased plants. Enough has been said to show that great variation prevails and to give the typical forms about which all may be easily grouped. A list of the diseased plants which have thus far been found in this section will be given in Section VIII. while a comparison of the disease with some other characters and diseases of plants with which it might be confounded upon external examination, will be made after the discussion of the microscopic details of the diseased tissues.

HISTOLOGICAL CHARACTERS (*See also references below**).—The worms locate preparatory to passing into the cystic state at various depths in the tissues of the root. They are not confined to any par-

*Goodale, Physiological Botany. Vol. II., Gray's Botanical Text Books.
Van Tieghem, Traité de Botanique, Deuxieme Edition, Fascicule 5.
Müller, Mitthleiungen über die unseren Kulturpflanzen schädliche, das Geschlecht *Heterodera* bildenden Würmer. Landwirthschaftliche Jahrbücher, Bd. XIII., Heft I. 1884.
Jahresbericht für Wiss. Bot. (Just) 1876, p. 1235.
Idem, 1877, pp. 516–517.
Idem, 1878, p. 174.
Idem, 1878, p. 169.
Sorauer, Pflanzenkrankheiten, Zweite Auflage, Vol. I.
Frank, Krankheiten der Pflanzen, and others.

ticular tissue element or system but locate in the vascular tissue of the central cylinder, the cambium, parenchyma or even in the bark so that the body of the mature female cyst is frequently only protected by a thin layer of the dead peripheral tissue, or sometimes is even exposed. They seem to flourish better, however in or near the softer tissues of the root. It is a very common thing to find dead undeveloped female cysts, the majority of which I have always found in the woody tissue of the central cylinder. Possibly surrounded as they are by the harder, more compact tissue there is less certainty of the male reaching them for fertilization. This, however, is only a suggestion. I have not demonstrated it. All of the tissue elements in the diseased roots undergo hypertrophy, while some of them are subject to special changes in form as well as direction of growth.

The parenchyma cells which normally have their tangential diameter greater than the radial are so changed that the radial diameter is the greater. This change in form of the parenchyma cells seems to obtain in nearly all of the parenchyma in the gall whether very near a cyst or distant from it. The increase in number of the wood and vascular cells of the central cylinder takes place though the cyst may not be located in or very near it. In such cases the fibres and ducts have their normal longitudinal direction. But if a cyst is located in or very near the central cylinder the ducts are turned in their direction of growth perpendicular to the axis of the root, bent around the cyst and then converge on the peripheral side, when, left without any controlling influence over their direction of growth they often perform very curious evolutions through the parenchymatous tissue in all directions.

A glance at figures 29 and 30, Plate V., will show at once a great difference in the arrangement of the tissue elements and the form of the cells of diseased roots compared with the same in a healthy root. These figures represent sections of roots of the cotton plant. Fig. 29 is from a section through a gall on a small lateral root, while fig. 30 is from a healthy lateral root of the same size as the non infected portions of the root from which fig. 29 was taken. Both are drawn to the same scale and the natural size of the lateral root from which fig. 29 was made is represented in fig.

31. In the healthy lateral root (fig. 30) it will be noticed that the differentiation of the woody tissue, which contains the large tracheal vessels, with the parenchyma is not so marked as in most roots so that the stellate appearance is not well represented. One of the most marked of the deformities is the displacement of the liber fascicles. In fig. 30 they are shown in normal position at *e*. In fig. 29 only one group is in what would be the normal position if the root were not diseased and of its normal size; this group is shown at *e*, fig. 29. *e'*, *e'*, *e'*, *e'*, represent displaced groups; that is in the rapid and abnormal increase of wood cells from the central cylinder they have been pushed far out of their normal position while cells of the parenchyma on the one side, and wood cells on the other have grown around the group *e*. *e''* represents one group not displaced but turned to grow in a tangential and radial direction, while *e'''* represents one group not only displaced but turned also in a tangential direction. *c* represents cells of vascular tissue which are turned in a tangential direction around the cavity of a cyst which is just below and was removed in making the section. *d* also reprsents cells of vascular tissue turned out of their normal course by the near presence of a cyst. At *a* is a cyst located in the edge of the vascular tissue of the central cylinder bordering on parenchymatous tissue; behind the cyst the cells of the vascular tissue are turned tangentially and this part of the bundle reaches over outside of the parenchymatous tissue bordering the liber fascicle *e*. The parenchyma cells between the cyst and the liber fascicle *e* are elongated radially instead of having their tangential diameter the longer.

In plate VI. figs. 36 and 37 represent the structural characters of the galls on tomato roots. The cysts *a* and *b* are seated in the parenchyma, the cells of which have long radial diameters and converge around the cyst. The parenchyma cells in this section in a peripheral plane are longer radially than tangentially. At *c* is represented a dead cyst, probably not impregnated, which lies in the woody tissue of the central cylinder. The pitted ducts can be seen to lie radially or perpendicular to the axis, turned from their normal longitudinal direction. Behind the cyst by turning in a tangential direction they converge from either side and meet.

Fig. 37 represents a section through a mature cyst lying in the vascular tissue, the cavity of the cyst at *a* is filled with eggs and young larvæ. At *b* are represented the vascular cells which lie in a normal direction cut transversely. On either radial side the ducts curve around closely following the contour of the sides of the cavity. At *c* the outer tangential side of the cyst cavity the ducts from both sides and from below converge and meet.

Fig. 36 represents a section from a moderately sized young gall. In older ones where the cysts are numerous there is often presented an intricate maze of these pitted ducts coursing in all directions.

In potato tubers the parenchyma cells are elongated so that their longer diameter is perpendicular to the surface at that point (see fig. 38, plate VI.). When the potatoes remain in the ground for some time, or have been infested for some time during their growing condition large warty growths are sometimes formed as represented in the upper right hand figure in Plate I. Again the tubers which have lain in the ground after maturity and sprouted ("volunteers"), being badly infested the young sprouts are attacked and large galls produced on them close to the surface of the tuber. In these cases pitted ducts are developed to a very great extent and a large majority of the mature female cysts are surrounded by an intricate net work of these ducts. In making sections of such galls many of these cysts are cut through and by removing the remains of the cyst, there is the appearance of a beautiful microscopic basket woven from the ducts and imbedded in the looser parenchymatous tissue close by. In the galls of the peach root beside the special structural derangements which could be classed under the head of the foregoing characters there appears in many of the nearly mature, or old female cysts a secondary growth of pseudoparenchymatous tissue from the inner periphery of the cavity which in some cases nearly fills the cavity with tender loosely compacted cells, so that the cyst is often deformed by the pressure of these ingrowing cells, and in very old ones the larvæ lie in different places in the tissue. It requires in some cases very careful search to find a female cyst which can be removed and recognized as the female of *Heterodera.*

COMPARISON OF THE EXTERNAL APPEARANCE OF THE ROOT-GALL DISEASE OF THE POTATO WITH "POTATO SCAB".—In some of the peculiarities of the disease in the potato tubers caused by *Heterodera radicicola* there is a striking resemblance, especially in the earlier stages, to the effects of the disease called "potato scab" and attributed by Brunchorst* to the action of a parasitic organism of very simple structure which he calls *Spongospora Solani*, and considers to be closely allied to the organism called by Woronin† *Plasmodiophora Brassicæ* which causes the disease of cabbages and turnips vulgarly known as "club-foot". The surface of a healthy potato is quite smooth with here and there minute rounded elevations which are usually of a little lighter color than the ground color of the surface and slightly roughened or granular. These are known as the "lenticels", the cork cells of which being loose and rounded have many intercellular spaces and permit an easy interchange of gasses between the cells of the potato and the outside. It is supposed that the potato scab disease begins in the vicinity of these lenticels. An increase in the tissue of the potato takes place here so that a low convex elevation is formed the surface of which becomes "scurfy" by the pealing off of the outer coats. From this the tissues break down and decay sets in and unless the disease is arrested the whole surface of the potato is affected. It appears that the larvæ of *Heterodera radicicola* mainly attack a potato in the vicinity of these lenticels for the first external sign of the presence of the parasite is the enlargement of these lenticels until elevations of considerable size are formed which are scurfy on the surface. Finally the elevation cracks, decay sets in and in many cases the external appearance strongly resembles a "scabby" potato. Usually, however, when the disease is arrested, the tissues being softened gradually shrivel and the potato has a wrinkled and shriveled appearance which I never saw in a potato affected by what is called the "scab". Usually also the roots will present the irregularly fusiform or ovoid galls. For the purpose

*Ueber eine sehr verbreitete Krankheit der Kartoffelknollen. In Bergens Museums Aarsberetning for 1886, p. 219.

See also "Potato scab". J. E. Humphrey, Mass. State Exp. Station, 6th Annual Report 1888.

†Pringsheim's Jahrbücher für wissenschaftliche Botanik, Vol. XI., p. 548.

of comparing "scabby" potatoes with those infested by the *Heterodera* requests were made of several gentlemen in Alabama and in some of the Northern States for "scabby" potatoes from their respective sections. Specimens were received from *Peter Collier, Director of the New York Agr. Exp. Station at Geneva, N. Y.; from Prof. E. S. Goff, Horticulturist of the Wisconsin Agr. Exp. Station at Madison, Wis.; from Mr. Clarence M. Weed, Entomologist of the Ohio Agr. Exp. Station at Columbus, Ohio; from Mr. Wilson Newman, Asst. Director of the Canebrake Station, Uniontown, Ala.; and from Prof. T. M. Watlington, Abbeville, Ala.

From the last named place the specimens received were very badly infested with the *Heterodera radicicola*, and with a few of the nematodes which cause the disease described by Prof. Scribner†. I did not find the *Heterodera* present in the potatoes from any of the other localities. When the potatoes remain in the ground for a long time the fissures in the elevations become so deep and in some places the corky growths are so large and prominent as to be easily distinguished from the appearance of "scab" in any of the potatoes the writer has seen. In Plate I. the upper left hand figure represents the very early stages of the disease caused by *Heterodera radicicola*, while the upper right hand figure represents one which has long been infected.

COMPARISON OF ROOT-GALLS WITH "CLUB-FOOT" OF CABBAGE.—It will be of great interest to compare the diseased condition of the cabbage roots caused by *Heterodera radicicola* with the disease of the roots vulgarly known as "*club-foot*" of cabbage, since in many respects the external characters are very similar while the two diseases are caused by very widely different organisms. The one which causes root-gall, *Heterodera radicicola*, is, when compared with organisms of a lower grade, an animal of quite a complex and high organization. The one which causes "club-foot" is one of the slime moulds, a plant of the very lowest organization, called by Woronin‡, who first discovered it to be the cause, *Plasmodiophora Brassicæ*. This parasite when in its ma-

*The author wishes to express his obligation to these gentlemen for their kindness.

†Bulletin Agr. Expt. Station, Tenn. Vol. II. No. 2, 1886.

‡Pringsheim's Jahrbücher für wissenschaftliche Botanik, Vol. XI., p. 548.

ture state consists of numerous very minute rounded bits of protoplasm, each independent and protected by a thin covering or wall. These remain in a resting condition through the winter in the diseased roots or in the soil. In the spring by decay of the roots these spores are freed. Under proper conditions of temperature and moisture they absorb water until the wall cracks and the bit of protoplasm is set free as a swarm cell, that is, a microscopic bit of plastic protoplasm with a very slender cilium, or hair-like process. After a time it loses this cilium and then the plastic bit of protoplasm moves slowly about in the damp soil by a streaming movement in various directions. It is capable of streaming out in such very fine threads as to enter the roots of the cabbage along with watery solutions of nutriment. Once within the root it locates in a cell and commences to appropriate the living matter of the root to itself. In this way it grows in size still remaining a very plastic body of simple protoplasm. Thousands of these enter the roots of a single cabbage. Not only do they appropriate to themselves the living matter of the root but they cause the root of the cabbage to produce an increased number of cells, so that oval or fusiform enlargements are formed. The cells of the root in which these parasitic masses of protoplasm are seated increase greatly in size compared with those which do not contain the parasite. The plasmodium, for so this mass of protoplasm is called, is yellowish in color. Late in the season it divides up into countless minute bits of protoplasm each of which secretes a protective wall about itself, and its life cycle is completed. The diseased cabbages become sickly, turn yellowish and either die or do not head.

Now in external appearance these enlargements of the roots which are called "club-foot" very much resemble the enlargements called root-galls which are produced by the nematode. Unless one was pretty certain of the locality from which the diseased specimens came, and knew the history of the disease in that locality it would be venturesome to undertake to say whether it was root-gall or "club-foot" until after a microscopic examination of the parasite, or of the structural characteristics of the diseased root.

I have some very fine specimens of "club-foot" before me which I obtained from Eastern North Carolina nearly a year ago. Having been placed in strong alcohol the enlargements are a little wrinkled and shriveled. But so closely do they resemble, especially in a fresh condition, the root-galls that when I collected specimens of cabbages here this autumn with enlargements on the roots I expected to find *Plasmodiophora Brassicæ* until after I had made the microscopic examination and found the cause to be a worm. Perhaps the enlargements of "club-foot," before they begin to crack, are a little more even in contour than those of root-galls and in the specimens I have seen those of "club-foot" are larger, especially on the tap root where very large lateral growths are formed. But if we take a thin transverse section of an enlarged root of each and compare them all resemblance vanishes. In a cross section of "club-foot" the first thing to attract attention is the great number of yellowish plasmodia, or else the spore masses within large cells, distributed all through the tissues. If the section is from an enlargement of a lateral root, unless very large, there will be little else to attract the attention when compared with a healthy root unless it be a slight enlargement of some of the other cells. The general character of the root structure is but little changed. The tracheal tissue of the axis cylinder, but little attacked is arranged in the same stellate form which we find it in a healthy root. The ducts, even when immediately in contact with cells containing plasmodia, are not turned from their longitudinal direction, or if so only slightly. The cells are not elongated and curved around the enlarged cells containing the plasmodium, but resemble the normal arrangement of small cells around a large one. Nor is the radial diameter of the parenchymatous cells proportionately increased, but if the cells are enlarged it is usually a proportionate or nearly symmetrical enlargement. In the section from the root-gall here and there is a cyst, or the amorphic remains of one containing eggs and larvæ. The color is not so yellowish as that of the plasmodia nor are the cysts so numerous. Indeed the most striking feature in the appearance of the cross section is the twisted, curved and distorted condition of the cells, especially of the tracheal vessels. In some places these are beautifully wreathed about a cyst, and by their side run very much elongated parenchyma cells, while in another place a labyrinth of vessels is woven with the parenchymatous tissue, giving to the section as a whole, viewed with the compound microscope, the appearance in miniature of a heavy field of grain after a driving storm, when the stalks of grain are twirled in all directions and matted in inconceivable ways.

When very large lateral "clubs" are formed, as on the tap root the tracheal tissue is turned in an outward direction and curved in various ways. But even then it is confined to more or less recognizable bundles, is rarely sharply curved, and never is wreathed around the plasmodia as around the cyst in the root-gall.

COMPARISON OF THE ROOT-GALLS WITH THE "TUBERCLES" OR "WURZELKNÖLLCHEN" OF LEGUMINOUS PLANTS.—To remove all possibility of a confusion of the root-galls with the tubercles (or Wurzelknöllchen) of the *Leguminoseæ*, which has probably sometimes occurred, this comparison is introduced.

These tubercles, which recent experiments* seem to show play an important rôle in the acquisition of atmospheric nitrogen by Leguminous plants, are irregularly oval enlargements of the roots, from the size of a pin head to a large pea, or sometimes elongate, or clavate and very much branched and convoluted. The root-galls will usually not be mistaken for the tubercles by one familiar with these bodies. The tubercles are formed only on the very youngest roots, so that they are connected with the root from which the diseased one branched by a very slender attachment. Sometimes, however, the attachment is very stout. Usually the surface of the tubercle, though it may be greatly convoluted or lobulated, is smoother and does not present the scurfy or cracked appearance so common, especially in age, on the surface of the root-galls. The

*Atwater, W. O. Atmospheric Nitrogen as Plant Food, Bulletin No. 5, Storrs' School Agr. Exp. Station Conn. Oct. 1889.

Bertholet, M. Expériences Nouvelles sur la fixation de l' azote par certaines Terres Végétales et par certaines plantes. Ann. de Chim. et de Phys. 6me série, T. XVI. Avril, 1889.

Hellriegel und Wilfarth, Unterschungen über die Stickstoffnahrung der Gramineen und Leguminosen. Beilagehaft z. d. Zeitsch. d. Ver. f. d. Rübenzucker-Ind d. D. R. Berlin, 1888.

Abstract in Bot. Centralblatt, Bd. XXXIX, pp. 138-143, 1889.

root-galls may occur on proportionately large roots, and in a majority of cases the attack is made some distance from the end of the root, so that the root continues to grow beyond the gall and several galls may be formed on the same root in succession. The root also continues to enlarge so that few of the galls are attached by such slender pedicels as the attachments are in the case of tubercles I have seen. Since the tubercles vary greatly on the roots of different species* there are probably cases in which it would be difficult from an external examination to say whether the enlargements were root-galls or "tubercles". The structural characters are, however, so very different that it will not be out of place here to note briefly the chief structural characters of the tubercles, and give a short résumé of the leading opinions regarding their function.

Very different views have been entertained from time to time as to the nature and significance of these tubercular swellings. The interior of these tubercles is composed of a loose parenchymatous tissue. In the younger parts of this tissue all observers agree as to the presence of strands, or threads of a very plastic nature, with no cross partitions, which course between and through the cells, often sending short flask-like branches into the cells. These possessing a resemblance to the strands of *plasmodia* or threads of certain fungi, were so regarded by Ericksson†, Kny‡, Frank§, Lundström‖. In the older parenchymatus tissue all agree in observing in the plasmic contents of the cells bacteria-like bodies of variously branched forms, forked, or Y and X forms. These were regarded by Woronin¶ and others as bacteria. Brunchorst** be-

*Sorauer. Pflanzenkrankheiten. Zweite Auflage. Erster Band. p. 743.

†Studier öfver Leguminosernas rotknölar, Lund, 1874; Bot. Zeitung, S. 381, 1874; cited by Sorauer, Pflanzenkrankheiten, Zweite Auflage, Erster Band, p. 744; and by Frank, Krankheiten der Pflanzen, Zweite Hälfte, p. 650, 1881.

‡Sitzungsber. d. bot. Ver. d. Prov. Brandenburg. 28 April, 1878; cited by Sorauer (l. c.).

§Krankheiten der Pflanzen (l. c.).

‖Ueber Mykodomatien in den Wurzel der Papilionaceen. Bot. Centralblatt, Bd. XXXIII., pp. 159-160 and 185-188, 1888.

¶Mem. Acad. imp. de Scienc. d. St. Petersbourg, X., 1866. Cited in Sorauer, Pflanzenkrankheiten (l.c.).

**Ueber die Knöllchen an den Leguminosenwurzeln. Bericht. d. Deutschen bot. Gesellschaft, Bd. III., pp. 241-257, 1885. Abstract in Bot. Centralblatt, Bd. XXIV., pp. 333-334, 1885.

lieved the tubercles (Knöllchen) were normal structures, and that the bodies which Woronin and others assumed to be bacteria were formed by a differentiation of the plasmic, protein contents of the cells into these forms, since they were found to be very rich in protein matter, and not accepting them as bacteria he called them "*bakteroids*". He regarded the "bakteroids" as reserve material which at fruiting time was absorbed by the plant. Supporters of this view were found in Schindler*, Tschirch†, and others. Many observers have noticed in these plasmic "strands", or fungal hyphæ (hyphenpilzen) minute rod-like bodies very closely resembling bacteria. These were first called bacteria by Beijerink‡, who regarded the plasmic strands in which they were found as the remains of nuclear division in the cells of the tubercle. Ward§ regarded these "strands" or "hyphæ" with their contained rod-like bodies as fungi in some respects resembling the smuts, or *Ustilagineæ*. Vuillemin|| also believed the tubercles to be caused by a fungus, but classed it with the *Chytridiaceæ*, with affinities for the genus Cladochytrium and he named it *Cl. tuberculosum*. He claims to have studied the sporangia and zoöspores. Prazmowski¶ first considered the tubercles to be caused be a parasitic fungus in some stages resembling *Plasmodiophora Brassicæ* Wor., but after later researches|||| he comes to the conclusion that the organisms in question are bacteria.

One of the most interesting of recent views, and that held by Prazmowski, Ward, Vuillemin (l. c.) and others, supported also

*Ueber die biologische Bedeutung der Wurzelknöllchen bei den Papilionaceen. Jour. f. Landwirth. Henneberg, XXXIII., pp. 325-336.

Abstract in Bot. Centralblatt, Bd. XXVII., pp. 108-109, 1886.

†Beiträge zur Kenntniss der Wurzelknöllchen der Papilionaceen. Bericht. d. Deutschen bot. Gesellschaft. Bd. V. 1887. Cited by Sorauer, Bot. Centralblatt. Bd. XXXI., p. 308.

‡Die Papilionaceenknöllchen. Bot. Zeit. p. 726, 1888. Abstract in Bot. Centralblatt, Bd. XXXVIII., No. I., pp. 458-459, 1889.

§On the tubercular swellings on the roots of Vicia Faba. Philosophical transactions, Roy. Soc. London, Vol. 178, B. pp. 539-562, 1887. Abstract in Bot. Centralblatt, Bd. XXXIV., p. 305, 1888.

||Les tubercles radicaux des Légumineuses. Ann. des. Sc. agron. franc. et étrang. 8°, p. 96, 1888. Abstract in Bot. Centralblatt, Bd. XL., pp. 123-125, 1889.

¶Ueber die Wurzelknöllchen der Leguminosen. Bot. Centralblatt, Bd. XXXVI. pp. 215-219, 248-255, 280-285; 1888.

||||O istocie i znaczeuiu biologicnem brodawek Korzeniowych grochu. Bericht aus den Sitzungen der k. k. Akademie der Wissenschaften in Krakau. Juni, 1889. Das Wesen und biologische Bedeutung der Wurzelknöllchen der Erbse, Bot. Centralblatt, Bd. XXXIX., pp. 356-362, 1889.

by the best experimental evidence is that certain microörganisms, either fungi of a very simple organization or bacteria, by an endoparasitism produce the abnormal growths, and for a time live at the expense of the host plant, but being locked within the peculiar structure of the tubercle, dissolution of their bodies takes place followed by an absorption of their protein contents by the plant, so that not only nearly all of the substance which the plant yielded to the parasitic organism is thus finally restored, but in addition a more costly element, atmospheric nitrogen, which the organisms have assimilated and prepared for their host.

The chemical and physiological researches of Hellriegel and Wilfarth*, Bertholet†, and Atwater‡ show that the plants with tubercles on their roots grown in a soil with very little nitrogenous substance gain more nitrogen than the soil contains, but when grown in a sterilized soil no such gain is made. The experimental researches of Prazmowski (loc. cit.) were directed to the biological nature of the parasitic organism as well as to proving that they were the specific cause of the tubercles. The plants experimented with were peas, but he draws the inference that the rest of the "Papilionaceen" are not essentially different in the character of their tubercles.

In brief the results of his later researches§ are as follows. The root-knots (Wurzelknöllchen) of peas are not normal structures, for in sterilized media protected from accidental infection they are never formed, but they always result from infection.

The infecting knot-organisms are bacteria identical with them in form and characters. The bacteria were taken from young knots and increased through many generations by culture in nutrient media. The causal connection between the bacteria thus isolated and the root-knots was proven by a long series of careful

*Untersuchungen über die Stikstoffnahrung der Gramineen und Leguminosen. Beilagehaft z. d. Zeitsch. d. Ver. f. d. Rübenzucker–Ind. d. D. R Berlin, 1888. Abstract in Bot. Centralblatt, Bd. XXXIX., pp. 138-143, 1889.

†Expériences Nouvelles sur la fixation de l'azote par certaines Terres végétale et par certaines plantes. Ann. de Chim. et de phys. 6 me série, T. XVI., Avril, 1889.

‡Atmospheric Nitrogen as Plant Food. Bull. No. 5, Storrs School Exp. Sta. Conn., Oct. 1889.

§Berichte aus den Sitzungen der k. k. Akademie der Wissenschaften in Krakau, Juni, 1889.

Bot. Centralblatt, Bd. XXXIX., pp. 356-362, 1889.

experiments wherein infection was produced through the inoculation of cultivated plants with bacteria, originally taken directly from the knots, and cultivated through many generations. The formation of the knots occurs only on the youngest roots and their branches.

The knot-bacteria make their way through young cell-membranes into the root hairs and epidermal cells of the root and multiply there at the expense of the plasmic contents of the cells. After the bacteria have increased to a considerable extent in the root-hair they unite near the point into grape-like clusters of colonies which lie very close together, become enveloped in a tough, glistening membrane by means of which they are united with the cell membrane of the root-hair. There arises now near the point of the root-hair, on the inside of its wall, a glistening knob-like projection. Around this bacteria knob curls the end of the root-hair in the form of a shepherd's crook, or of a screw. Out of this enveloping screw at the base of the root-hair grows the bacteria-knob as a hypha-like, or thread-like tube, which is surrounded by a glistening membrane and filled with bacteria. From this time on until the formation of the knot and the differentiation of its tissue the bacteria-tube resembles a real non-septate fungus filament; it grows at the apex and produces branches.

After growing out of the enveloping root-hair the bacteria-tube enters the epidermis of the root, pierces the rind and grows sometimes so deep as the endodermis of the central cylinder. In its growth and branching it passes between the cells splitting the membrane between two cells and crowding the two lamellæ apart, forming more or less prominent distended places in the tube, the outside of which is bounded by the two lamellæ and the inside filled with bacteria. The bacteria tubes also send short branches through the cell membranes into the cells which grow towards the nucleus, were formerly considered to be haustoria, and in unstained preparations are very difficult to distinguish from the cell contents. These Beijerinck* took to be the remains of nuclear division. In the early stages of the development of the knot no

*Die Papilionaceenknöllchen. Bot. Zeit. p. 726, 1888. Abstract in Bot. Centralblatt, Bd. XXXVIII., pp. 458-459, 1889.

bacteria are found free in the contents of the cells, they are all enclosed in the bacteria-tube.

In consequence of the presence of the bacteria-tube in the deep layers of the rind the cells lying near begin to increase in number by division, slowly at first, but soon in rapid succession. At the same time the bacteria-tube grows into this newly formed tissue and branches profusely. Following this division of cells there arises at this point a meristematic, or growing, tissue which through rapid increase becomes of considerable size, in which now the characteristic tissue of the knot is differentiated. In the midst of this meristematic tissue there arises a parenchymatous tissue, of large cells, into which the bacteria-tube grows and branches profusely in all directions. Later through the dissolution of the tube the bacteria are set free in the parenchymatous tissue which now becomes the so called "bacteroid tissue." The outside of the knot is differentiated into the rind, a few layers of cells with little plasmic contents disposed radially, the outside layer of which becomes corky. Between the bacteroid tissue and the rind is a zone of small-celled tissue capable of division and growth and free from bacteria, the meristem or growing point of the knot. On the inner periphery of the meristem a zone of fibrovascular bundles is formed which originates as branches from the central cylinder of the root. Between the fibrovascular zone and the bacteroid tissue a layer of starch containing cells exists. As the knot, or tubercle, enlarges the meristematic zone by growth advances in a peripheral plane. The peripheral part of the parenchymatous, or bacteroid, tissue also continues to advance by growth, and the peripheral part being younger contains the bacteria-tubes with their rod-like bacteria contents, and these bacteria-tubes continue to grow and follow up the advancing peripheral portion of newly formed parenchymatous tissue while behind follows up the process of dissolution of the membrane of the tube and the liberation of the bacteria into the plasmic contents of the cells making the bacteroid tissue.

From several series of experiments conducted with every precautionary measure he reaches the conclusive proof that by means of infection with knot-bacteria the plants (peas) even when grown in a soil deprived of all nutriment and providing for the exclusion of all other organisms, could provide the necessary nutriment from the store of nitrogen in the atmosphere. But whether from nitrogen in combination, or as Hellriegel (l. c.) claims from the elementary nitrogen of the atmosphere the researches have not yet been carried far enough to say.

If bacteria taken out of the knots in peas are cultivated in suitable nutrient media they increase for an unlimited time by fission retaining a rod-like form. In the knots under the influence of the plant they increase in the same way and possess the same form until the time when dissolution of the membrane of the bacteria-tube takes place and they are set free in the bacteroid tissue. In the plasmic contents of the cells of the bacteroid tissue they increase for a time but change their form and branch in a forked manner forming X and Y forms. At last their bodies become hyaline and dissolution takes place. The plant begins to empty the older cells of the bacteroid tissue by appropriation of their contents for its own use. The time when this absorption of the contents of the bacteroid tissue begins and the energy with which it proceeds bears a distinct relation to the amount of nitrogenous matter in the soil at the command of the plant. When the soil is well supplied with it the knots grow to considerable size, the bacteroid tissue is filled with bacteria and bacteria-tubes and presents a flesh-red color, and remains in this condition until the maturity of the plant. The dissolution of the bacteroids and the emptying of the bacteroid tissue proceeds very slowly and irregularly. On the other hand when there is a scarcity of nitrogenous matter in the soil at the command of the plant the dissolution of the bacteroids and the emptying of the bacteroid tissue begins early and proceeds rapidly while the bacteroid tissue has a greenish color.

In both cases the emptying begins in the oldest part of the bacteroid tissue and advances towards the meristematic zone. Even in the oldest part of the bacteroid tissue remain numerous living bacteria and tubes containing bacteria which with those in the peripheral zone of the parenchymatous tissue escape into the ground upon the decay of the knot and there increase and perpetuate the infectious character of the soil.

In knots partly eaten by insects, which is quite common, the masses of bacteroids become surrounded anew by a membrane and the bacteria-tube thus formed, by sprouting divides into successively smaller colonies surrounded by membranes, which Prazmowski first took to be a kind of spore formation when the real nature of the organisms were unknown to him.

The structure of the knot is adapted to favor the symbiotic relation which exists between the host plant and its parasite. The corky layer of the rind prevents not only the ingress of foreign organisms but prevents the escape of the bacteroids, while the fibrovascular tissue which surrounds the bacteroid tissue provides the channel of communication between the plant and the contents of the knot. The plant being the master imprisons the bacteroids within the tissues of the knot, for a time nourishes them with the material which is the product of carbon assimilation in the leaf and the willing bacteroid slave assimilates atmospheric nitrogen producing protein matter, when finally the plant completely overpowers them, dissolves their bodies and carries off their protein contents for its own use.

VII.

TREATMENT.

The following discussion of the treatment of the root-gall nematode is mainly suggestive, and anything farther must be preceded by careful experimentation.

DIFFICULTY OF REMEDIAL APPLICATIONS TO PLANTS ALREADY DISEASED.—It is evident from the endoparasitic habit of the worms that direct applications of vermicides to the roots will not destroy them without fatally injuring the plants themselves. When the worms first enter the tissues of the roots they are so minute that no channel is left large enough for the entrance of any poisonous fumes which might be applied in the soil. Also the hypertrophy of the tissue of the roots incident upon the presence of the parasites would effectually close up any aperture made. Dr. Neal* in some experiments conducted by him under the direction of Dr. Riley has shown that the application of bisulphide

*Bulletin 20, U. S. Dept. Agr. Division of Entomology.

of carbon, kerosene emulsion and various arsenical solutions, in quantities sufficient for the destruction of the worms was generally fatal to the plants themselves, while the use of alkaline fertilizers, like hard wood ashes, muriate and sulphate of potash, kainite, etc., produced a hard growth less susceptible to attack.

STERILIZATION OF THE SOIL BY STARVATION.—The cheapest and probably at the same time the most effectual mode of sterilizing the soil will be to starve out the worms by a rotating system applied to the selection of fields, or plats of ground, upon which are grown only such plants as are positively known to be insusceptible to attack. A real difficulty arises even here for so many plants in widely different families are known to be susceptible to the disease, and plants that are absolutely insusceptible can in some cases only be determined after a series of trials. Dr. Neal reports (loc. cit.) that according to his experience *Amarantus spinosus* is the "most dreaded and destructive agent in the spread of the root knot." In this section, even in the immediate neighborhood of other plants badly diseased I have found this species free so far as examined, while *Amarantus retroflexus*, growing side by side with it, is diseased. Similar cases in the habit of a related species of *Heterodera* (*H. Schachtii* Schmidt) are reported from Europe. This species is very destructive to sugar beets and many other plants. Among a number of plants which were supposed to be insusceptible was barley*. Upon a piece of land very badly infected by the "Rübennematode" barley was sown for three years successively. The first two years no injury was noticed, but in the third year the crop was destroyed a short time before harvest by severe attacks of the worms. Dr. Neal (loc. cit.) also speaks of the Japan Clover (*Lespedeza striata*) as a substitute for the Cow pea (*Dolichos catiang*) as a forage plant and fertilizer. In this vicinity *Lespedeza striata* ranks as one of the species slightly affected, while "birds foot clover" (*Lotus corniculatus*) is very badly affected. It is evident that thorough investigations must be made to determine the useful plants which are very nearly, or quite, insusceptible to the attacks of the worms. By growing such crops upon selected ground for a period of a few

*Quoted from Sorauer, Pflanzenkrankheiten, Zweite Auflage, Vol. II., p. 853.

years, exercising at the same time great caution in not allowing any weeds or grasses, which may be susceptible, to grow, the area selected could be sterilized. Now by taking up successively different areas and treating them in the same manner a persevering farmer could practically rid his land of the worms. So far as observed here buckwheat and alfalfa are among the insusceptible plants which could be experimented with.

Rotation of Crops.—Here we find occasion again to emphasize the oft repeated necessity of a judicious rotation of crops, but with special reference to a wise alternation of insusceptible with susceptible plants. It is evident that if we start with a sterilized soil and grow for one year an annual which is liable to the disease there is little danger of infection of the ground. If the following year this is followed up by the cultivation of another nearly or quite free from attack the soil will with greater safety bear another crop of the plant grown the previous year.

Clean Cultivation.—The absence of clean cultivation is one of the most fruitful sources of the thorough impregnation of the soil with the worms. It was of course impossible to make an application of this principle to the enemy in question before that enemy was known, and especially before the time required for its complete development from the egg had been determined. Now that these facts are known and since we know many of the plants subject to the disease it is to be hoped this method will be employed by those desirous of subduing the worms. Not only should an effort be made to prevent the growth on arable land of all plants growing wild which are liable to serious infection, but so soon as a crop has been gathered, or it is found that the crop will not be worth gathering, from any cultivated plant liable to serious infection the farther growth of the plants should be stopped, or what is better the roots of the plants should be gathered and burned when possible. In gardens this would not be a serious task compared with the benefit to be derived. I have noticed cabbages, tomatoes and potatoes, all which are seriously susceptible to the disease, growing in an abandoned condition for two months in the latter part of the season, all the while providing for the rapid development and multiplication of the parasites. During this time two successive generations of the worms are developed. Each female egg would on the average, making no allowance for fatalities, produce in the first generation 200 young. Allowing 50 per cent of these for males there would be 100 to start the second generation for every one at the beginning of the first. These would then on the basis of a similar computation produce 20,000 young or 10,000 females to be the producers of the third generation. Then during the time of the abandoned growth of these diseased plants every productive parasite has produced 10,000 productive parasites.

TREATMENT OF PERENNIALS.—The greatest care should be exercised in the cultivation of perennials like the grape, peach, fig, etc. The young plants should be obtained from sources where it is known they have been grown in non-infected soil. The orchard or grapery should be selected and by a system of cultivation of insusceptible plants be rendered sterile by starving out the worms. Then the practice of cultivating either for forage or as a fertilizer plants liable to the disease in the orchard should be discontinued. Where orchards or graperies are so seriously injured as to interfere with the productiveness of the trees or vines, they might be preserved for a few years while the orchard is renewed in soil freed from the worms, when they should be destroyed.

The peach trees and grape vines which I have examined in the vicinity of Auburn, while slightly affected do not appear yet to suffer any serious consequences. Young trees and seedlings are more seriously affected. The most badly diseased grape cuttings I have seen were those grown very near diseased cabbages and tomatoes. Care should also be used in the cultivation of seed potatoes which are not infected.

TRAPPING THE WORMS.—In Germany cultivators of the sugar beet have resorted with a degree of success to trapping the worms of a related species (*H. Schachtii*)* from badly infected soils by the cultivation of plants very susceptible to the disease, and then gathering the roots before the worms are fully developed and destroying them. Such plants they call "catch plants" ("Fangpflanzen").

*Sorauer, Pflanzenkrankheiten, Vol. II., p. 854.

COMPOSTS.—If roots are ever used in the making of composts great caution should be used since there is danger of infecting soil hitherto free from the worms by fertilizing such land with compost material containing diseased roots. ...nn* has shown that such infection does take place in the case of related species, *Heterodera Schachtii* Schmidt, and also states that the material may be rendered innocuous by placing unslacked lime in layers with the infected refuse of plants which may be used in compost. For distribution see close of Section V.

VIII

PLANTS AFFECTED.

The following list of plants affected with the Nematode root galls is by no means complete. It comprises only such as with limited time I have been able to determine thus far in the vicinity of Auburn. From the foregoing study and comparison of the root-galls with externally similar teratological root-growths it will be seen that two essential characters must be determined before in all cases we can say the abnormal growth is a nematode root-gall: a microscopic examination to detect the presence of the worm and the histological changes accompanying its parasitism. Both of these tests have been applied in making up this partial list. Those marked with a * are badly affected.

1 Amygdalus Persica (peach).
2 Ficus Carica (fig).
3 Vitis vinifera (grape, several varieties).
4 *Solanum tuberosum (potato).
5 Solanum esculentum (egg plant).
6 *Lycopersicum esculentum (tomato).
7 Physalis sp.
8 *Abutilon sp.
9 Gossypium herbaceum (cotton).
10 Hibiscus esculentus (okra).
11 Sida spinosa.
12 Modiola multifida.
13 Cassia obtusifolia (coffee weed).
14 *Dolichos catiang (cow pea).
15 Phaseolus.
16 Lespedeza striata (Japan clover).
17 *Lotus corniculatus† (bird's foot clover).
18 Melilotus alba.
19 Ipomœa tamnifolia.

*Die Rüben Nematode. Zeitschrift des landwirthschaftlichen Central-Vereins der Provinz Sachsen. No. 12, pp. 332-335, 1870.

† Determined by Dr. G. W. Vasey.

20 Ipomœa lacunosa.
21 Clematis sp.
22 Phytolacca decandra.
23 *Helianthus annuus (sunflower).
24 *Citrullus vulgaris (watermellon).
25 *Cucumis melo ("nutmeg melon," "citron").
26 Beta vulgaris (beet).
27 Amarantus retroflexus (spineless careless weed).
28 Chenopodium Anthelminticum (worm seed).
29 Zea mays (corn).
30 *Brassica oleracea (cabbage).
31 Brassica Rapa (turnip).
32 *Brassica campestris rutabaga (rutabaga).
33 Marrubium vulgare (horehound).
34 *Pastinaca sativa (parsnip).
35 Lactuca sativa (lettuce).
36 *Tragopogon porrifolius (salsify).

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The following ist of works is not intended as a complete bibliography upon the subject, but is a list of those which have been consulted by the author during the preparation of this report. Those marked by a * were not seen in the original, but abstracts in either the Bot. Jahresbericht (Just's), the Bot. Centralblatt, or the Centralblatt für Bakteriologie und Parasitenkunde.

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EXPLANATION OF PLATES.

[All the Plates are original, and except the first two, which are from photographs, were drawn by the author from nature. In Plates IV, V and VI, all the figures are magnified except 31 and 32].

PLATE I. IRISH POTATOES (*Solanum tuberosum*).—The cracks in the large potato (seed potato), result from the increased growth of cells at the points where the Heterodera exists. The upper left hand figure is a small young potato taken from this same plant, the elevations and projections caused by presence of the Heterodera. The enlargements on the roots of the potato are the galls. (Natural size, from photograph.)

PLATE II. Tomato root showing root-galls two-thirds (natural size, from photograph.)

PLATE III. Parsnip and Salsify, showing root-galls, natural size.

PLATE IV. Development and transformations of Heterodera radicicola (Greeff.) Müll.

Figs. 1-9 different stages in segmentation of mature eggs; 10 invagination at anterior pole; 11, young embryo of the length of the egg, beginning to elongate and coil inside of the egg membrane, the caudal end, which is below in the figure, turning toward the ventral side, the cephalic end, above, granular and nearly hyaline; 12, 13, 14 farther elongation of embryo, 15 mature larva coiled five times within the egg membrane.

Fig. 16. Larva coming from egg membrane, and moulting at same time, the partially cast skin can be seen slipped from the head and tail. At the boundary between the hyaline and strongly granular portion near the tail end can be seen the anal opening.

Fig. 17. Sexually immature worm, larva; 17x same not so greatly magnified in one of the various forms sometimes found prior to the cystic state; 18, 19, 19z various degrees of distention of the larva; 20 young female cyst, showing ovaries; 21 male undergoing metamorphosis; 21x and 22 same with metamorphosis complete, in pupa state; 23 emergence of sexually mature male from cyst; 24 front view of head of male showing the position of the lamellæ around the spear; 25 anterior end of female, *a* exsertile spear, *b* anterior part of the œsophagus: 26 posterior end of a male (see page 25), *a* caudal appendage (probably an accidental variation), *b* spicules; 21z sexually mature male very greatly magnified, showing the paired testes.

Fig. 27, Mature female cyst, *a* middle part of œsophagus (suctorial bulb), *b* anterior part of œsophogus, *c* exsertile spear, *d* vulva, *e* genital tubes, the anterior ends of which form the ovaries.

Fig. 28. Genital tubes of female cyst with mature eggs still farther enlarged; *a* vagina; the uterus extends from the vagina a little more than one-third the length of the tube, near the middle is the *receptaculum seminis*, the oviducts and ovaries occupy a little more than one-half of the free ends. The small ova are very tender and flexible, but by pressure of the mass are held in a polygonal form within the ovaries. If the ovary is broken at a point as at *b* or *c* the young ova escape and assume a spherical form, and not yet being free cells are held together in a beautiful cluster as represented in the figures. As the young ova increase in size by growth, the pressure causes them to move toward the oviducts, they gradually develop numerous yolk globules which darken their appearance, passing through the receptaculum seminis are fertilized, and entering the uterus segmentation begins, finally the mass of developing eggs in the genital tubes ruptures them and the eggs and embryos are set free within the body of the cyst.

PLATE V. Structural effects of the disease in roots of cotton and peach.

Fig. 29. Cross section of gall on lateral root of cotton plant; *a* female cyst showing ovaries, etc., *b* old female cyst showing eggs and young larvæ in the amorphic remains of the parent, *c* deformed vascular tissue by the side of a

cyst, *d* deformed vascular tissue, the tubes turned in a radial and tangenital direction to the axis of the root, *e* liber fascicle in normal position of healthy root, e′ liber fascicle displaced, and, by increased growth of parenchyma and vascular tissue, carried far out from normal position, e′′ liber fascicle deformed and growing in a radial direction, e′′′ liber fascicle displaced and growing in a tangential direction.

Fig. 30. Cross section of healthy lateral root of cotton plant, magnified but in proportion with Fig. 29.

Fig. 31. Galls on lateral root of cotton plant (natural size).

Fig. 32. Root-gall of Peach, natural size, but small specimens.

Fig. 33. Section through female cyst in root of Peach, showing the ultimate growth of soft, pseudo-parenchymatous tissue which sometimes entirely fills the cavity before the larvæ have all escaped, *a* amorphic remains of female cyst showing eggs and part of genital tubes, *b* original outline of cyst, *c* hypertrophied tissue from surface of cavity of cyst.

PLATE VI. Female cysts and structural effects of the disease in roots of the Tomato, and the tubers of the potato (excepting Figs. 42-47). All magnified.

Fig. 34. Mature female cyst, *a* exsertile spear, *b* middle part of œsophogus, *c* ovary, *d* eggs escaped from the uterus,

Fig. 34. Mature female cyst of a different form.

Fig. 36. Cross section of diseased root of Tomato, *a* and *b* female cysts, *c* dead cysts which probably failed to be fertilized.

Fig. 37. Section still more magnified, *a* cyst cavity of female showing eggs and larvæ in amorphic remains of the parent, *b* normal vascular tissue in cross section, *c* deformed vascular tissue turned in a radial and tangential direction around the cyst.

Fig. 38. Section of outer portion of potato tuber showing *a*, female cyst external, with head end only in the tissues; *b* radial elongation of cells.

Fig. 39. Sexually immature larva making its way through cells of the potato tuber.

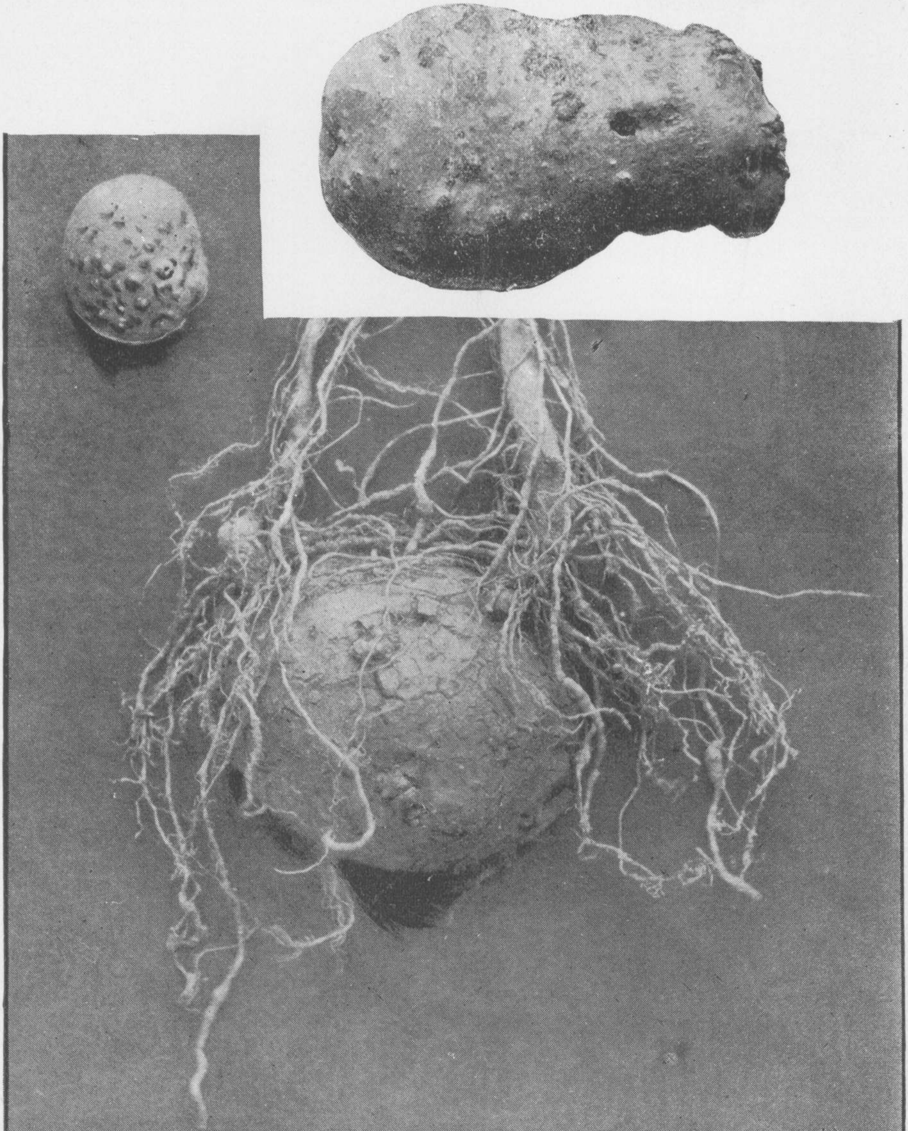
Fig. 40. Section of outer portion of potato, *a* young cyst in situ, *b* cork cells of lenticel (the section was through the side of a lenticel).

Fig. 41. Section of outer portion of potato tuber where decay of the tissues has begun, *a* female cyst in situ, *b* cyst cavity containing amorphic remains of parent, and young larvæ and eggs.

Fig. 42. Egg of 46; 43, cell division of same in process of development; 44 young larva in egg membrane; 45 young larva after hatching; 46 mature gravid female, *a* mature egg, *b* young ovum (Figs. 42-46 illustrate the egg, larva and mature female of the nematode which produces the disease of the Irish potato characterized by Prof. Scribner).

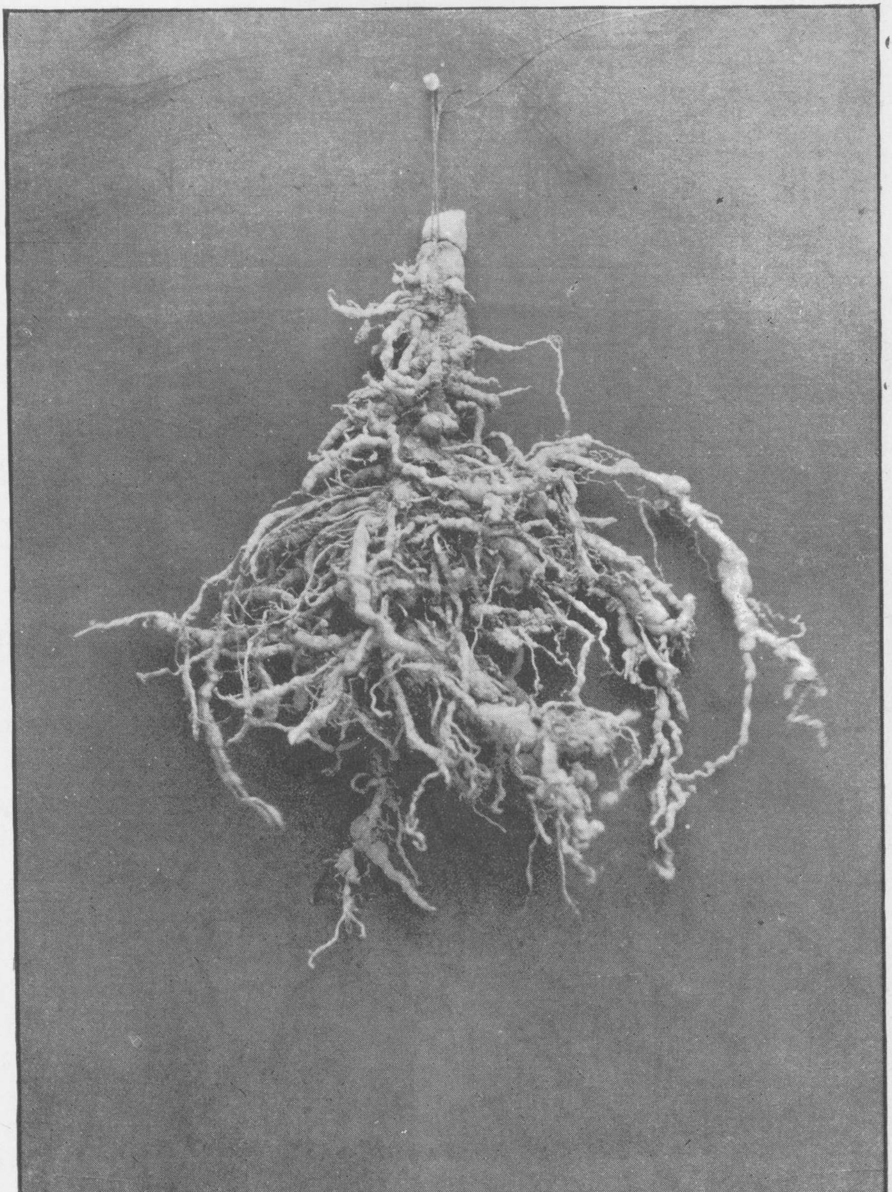
Fig. 47. Mature female of a different genus found sometimes associated with the former.

PLATE I.—NEMATODE ROOT-GALLS.



IRISH POTATO.

PLATE II.—NEMATODE ROOT-GALLS.



TOMATO.

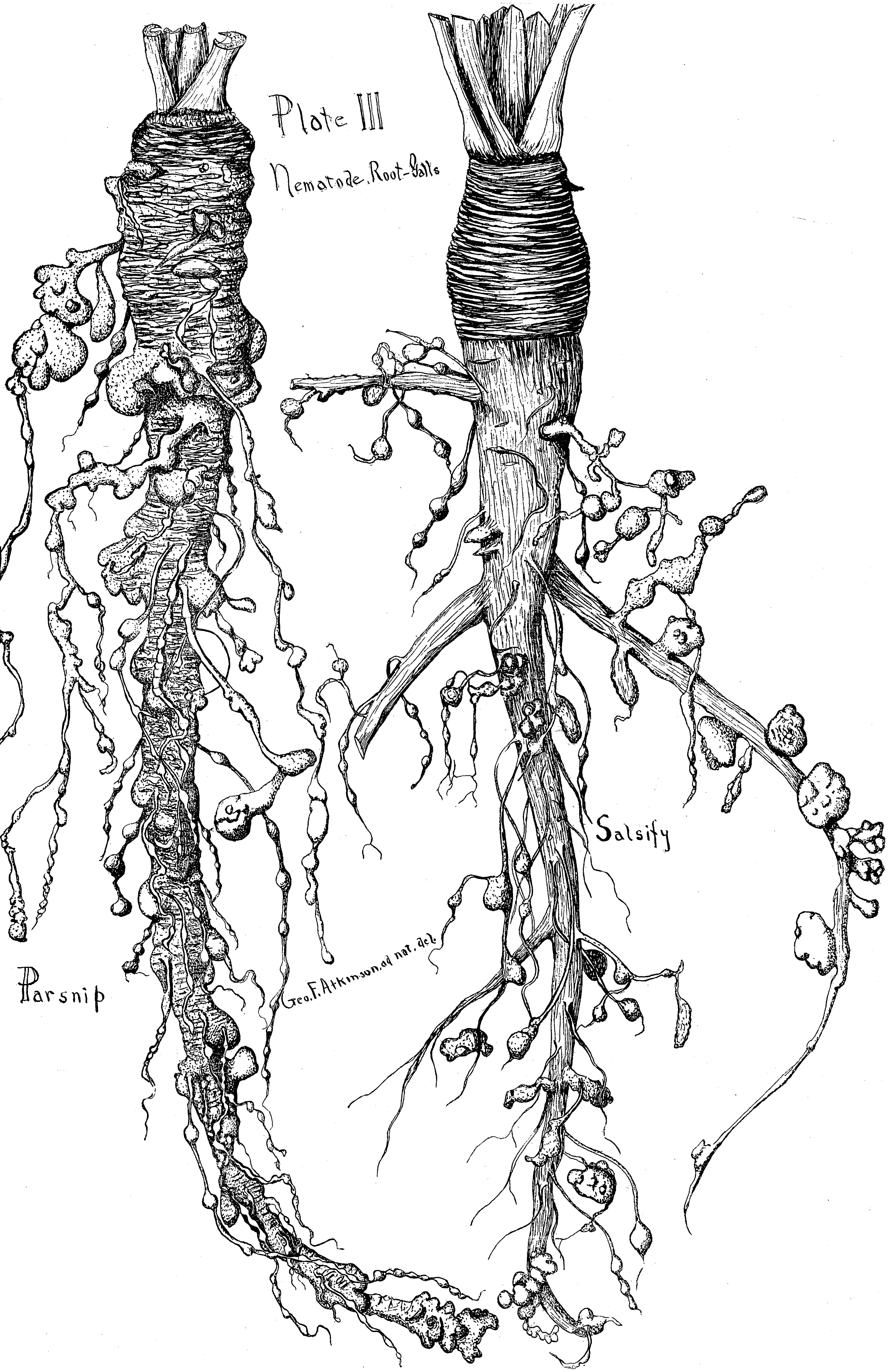
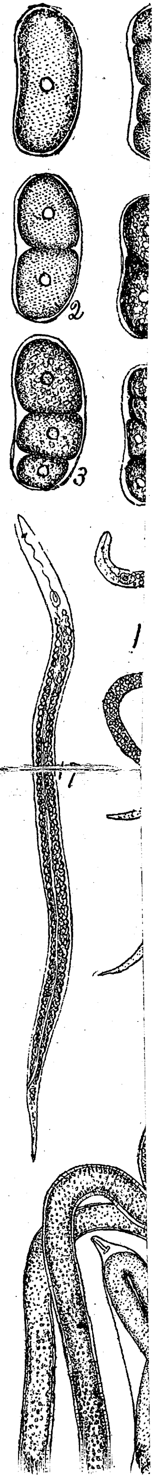


Plate III
Nematode Root-Galls
Parsnip
Salsify
Geo. F. Atkinson, ad nat. del.


2
3
1
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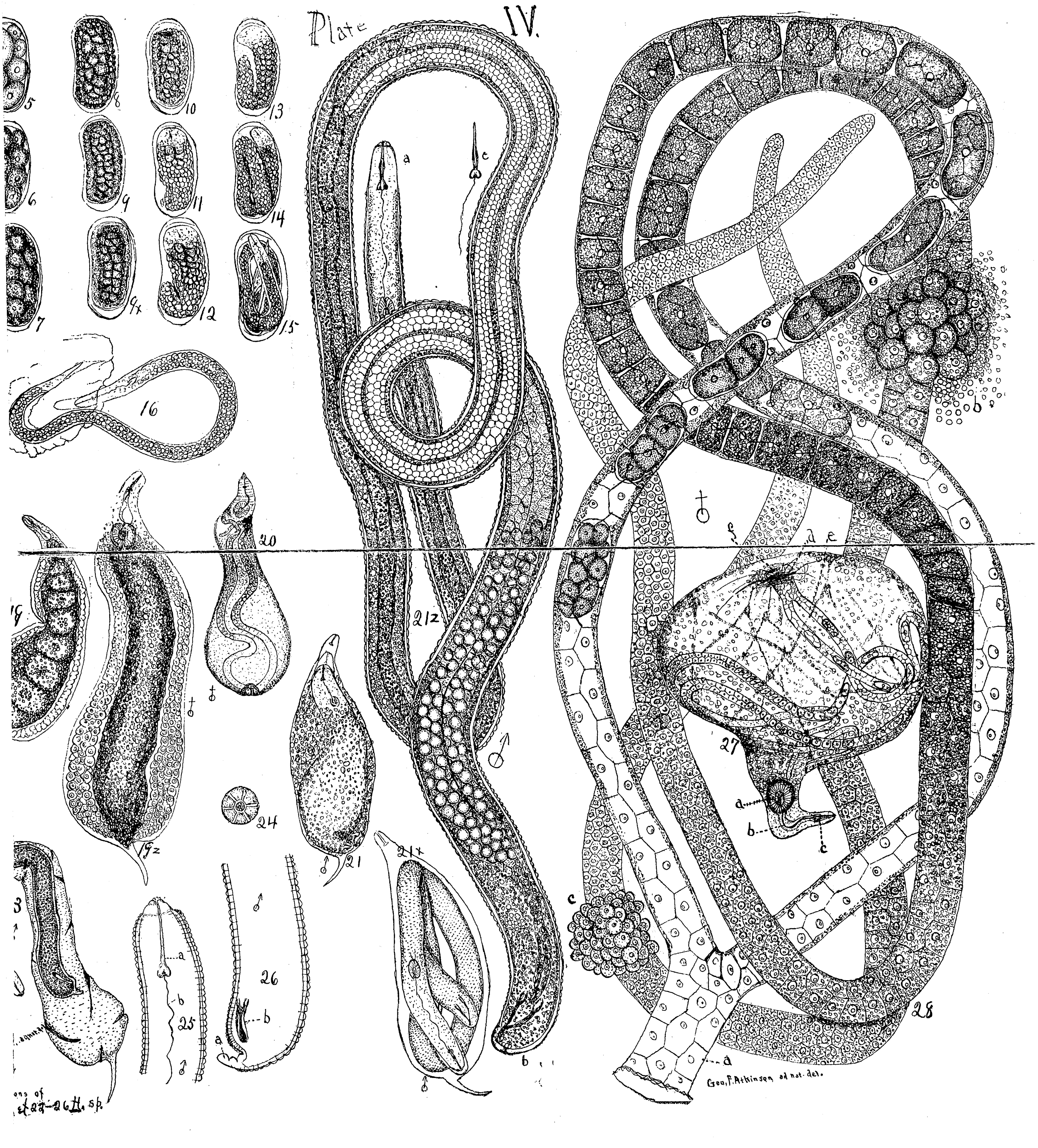
Plate IV.
5
6
7
8
9
9x
10
11
12
13
14
15
16
19z
20
21
21x
21z
24
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26
27
28
Geo. F. Atkinson ad nat. del.

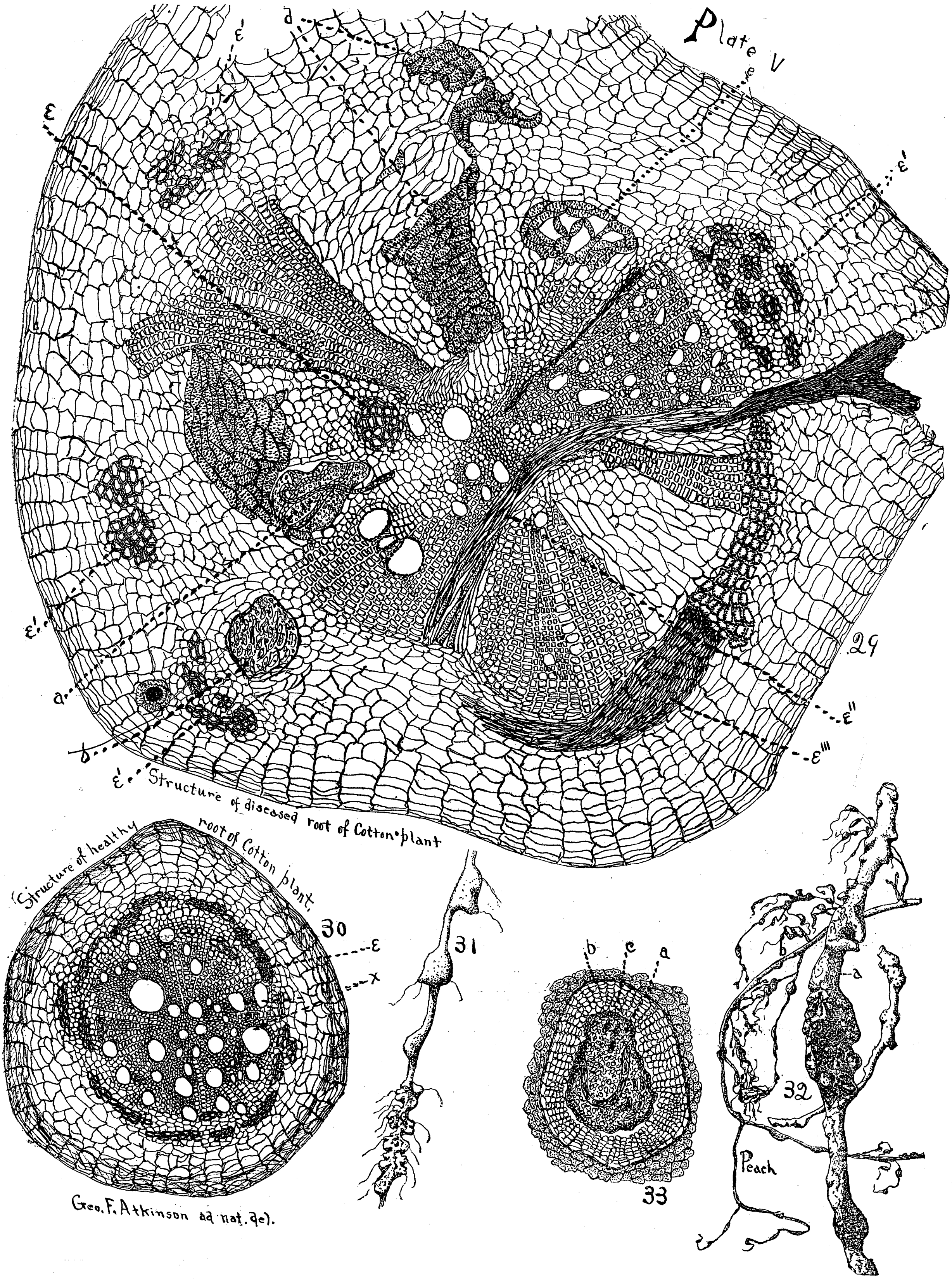
Plate V
Structure of diseased root of Cotton-plant
29
Structure of healthy root of Cotton plant.
30
31
32
33
Peach
Geo. F. Atkinson ad nat. del.

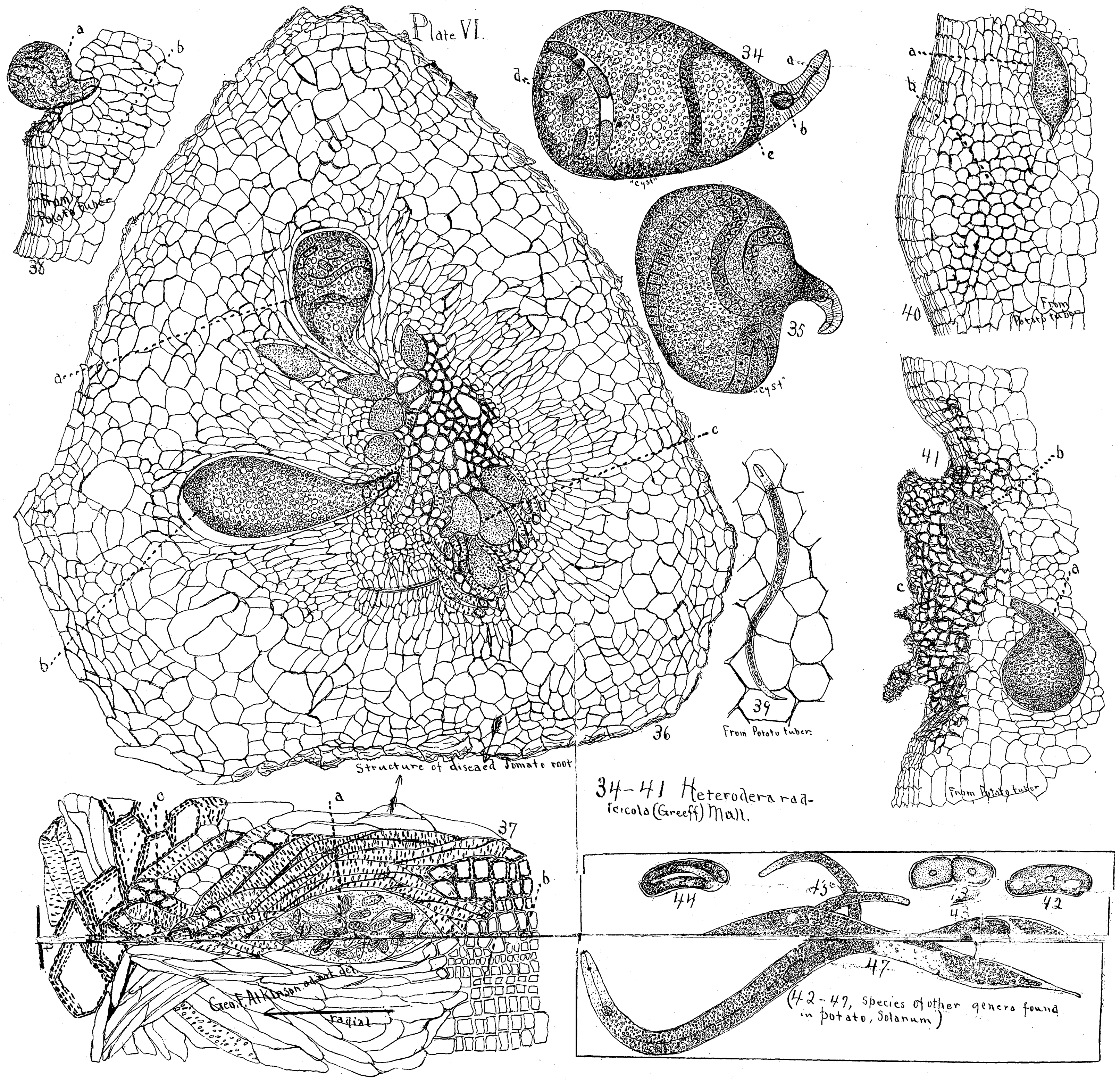
Plate VI.
34
"cyst"
35
"cyst"
From Potato tuber
38
40
From Potato tuber
36
39
From Potato tuber
41
From Potato tuber
Structure of diseased Tomato root
37
radial
Geo. F. Atkinson ad nat. del.
34-41 Heterodera radicicola (Greeff) Mull.
44
43
42
47
(42-47, species of other genera found in potato, Solanum)

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