IREE CEDAR RUST FUNGI, THEIR LIFE HISTORIES AND THE DISEASES WHICH THEY PRODUCE

A THESIS

PRESENTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF CORNELL UNIVERSITY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

BY
JAMES LEROY WEIMER

Reprint from Cornell University Agricultural Experiment Station Bulletin 390,
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CONTENTS

THREE CEDAR RUST FUNGI

THEIR LIFE HISTORIES AND THE DISEASES THEY PRODUCE[1]

JAMES LEROY WEIMER

The three fungi considered in these investigations are *Gymnosporangium Juniperi-virginianae* Schw., *Gymnosporangium globosum* Farlow, and *Gymnosporangium clavipes* C. & P. Except for a discussion of the hosts concerned, the fungi, together with the diseases that they produce, are treated separately.

HOSTS

Certain species of the genus Juniperus on the one hand and various species of the family Rosaceae on the other, serve as hosts for the alternate stages in the life cycles of the fungi named above. In the telial stage all three species occur on *Juniperus virginiana* L. Kern (1911)[2] reports *G. Juniperi-virginianae* and *G. globosum* also on *J. barbadensis* L., and *G. clavipes* on *J. communis* L. Several horticultural varieties of *J. virginiana* are also known to be hosts. In this discussion, however, only *J. virginiana* will be considered as the telial host since it is the only species common in central New York State, in which locality the investigations were made.

In their aecial stage these fungi occur on certain closely related members of the family Rosaceae. Among these are the cultivated and the wild varieties of apple (*Pyrus malus* L.) and crab apple (*Pyrus coronaria* L.), quince (*Cydonia vulgaris* Pers.), pear (*Pyrus communis* L.), June berry (*Amelanchier* spp.), mountain ash (*Sorbus* spp.), and numerous species of Crataegus.[3]

[1] Also presented to the Faculty of the Graduate School of Cornell University, May, 1916, as a major thesis in partial fulfillment of the requirements for the degree of doctor of philosophy.

AUTHOR'S ACKNOWLEDGMENTS. Grateful acknowledgment for assistance and suggestions is made to Professor H. H. Whetzel; to Dr. V. B. Stewart for help and criticism in preparation of the manuscript; and especially to Dr. Donald Reddick, under whose immediate direction the work was performed.

[2] Dates in parenthesis refer to *Literature cited*, page 548.

[3] For a more complete list of hosts see Kern (1911).

THE DISEASE CAUSED BY GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE

The disease caused by the fungus *Gymnosporangium Juniperi-virginianae* is generally known as *cedar rust*, although the galls are referred to as *cedar apples* or, more rarely, as *cedar flowers*. The term *apple rust* is most commonly applied to the aecial stage. Other names, such as *leaf rust*, *stem rust*, *fruit rust*, and *orchard rust*, are sometimes used to designate this disease.

HISTORY AND GEOGRAPHICAL DISTRIBUTION

The fungus is native to North America and has never been reported elsewhere so far as the writer has knowledge. Although it had already been known for a long time, it received but little attention prior to the work of Farlow in 1880. During the last decade, numerous investigations have been conducted bearing on the life history of the organism and on methods of control of the disease on the apple.

The apple rust stage is widely distributed throughout the eastern half of the United States wherever cedar and apple occur together.[4]

ECONOMIC IMPORTANCE

Owing to the fact that cedar trees occur in considerable numbers in but few States, apple rust has become of great economic importance only in certain localities. In some of the Southern States, where cedars grow in close proximity to the orchards, the disease causes an annual loss aggregating several thousand dollars, and there is considerable evidence that it is becoming more destructive each year. Pammel (1905) had never observed this rust on cultivated apples in Iowa prior to 1905. Emerson (1905), speaking of conditions in Nebraska, G. E. Stone (1911) in Massachusetts, and Giddings and Neal (1912) in West Virginia, state that the disease is becoming more serious each year. Stewart (1910) records several outbreaks in New York State, but says that the disease is rarely of much economic importance. R. E. Stone (1908) in Alabama, and Reed and Crabill (1915) in Virginia, list this as the most serious disease of apples in their respective States. In central New York the disease is very common on wild species of apple but is seldom found on cultivated varieties. The writer had two orchards under observation during the seasons of 1914 and 1915, one of which contained numerous cedar trees that were affected with *G. Juniperi-virginianae*, *G. globosum*, and *G. clavipes*, while the other was only about a half mile distant from a cedar grove that was severely

[4] For limits of geographical distribution see Kern (1911).

infested with these three species of rust fungi. No affected apple leaves or fruit were found in either orchard. A few affected leaves and two affected apples were found in the Cornell University orchard in 1914.

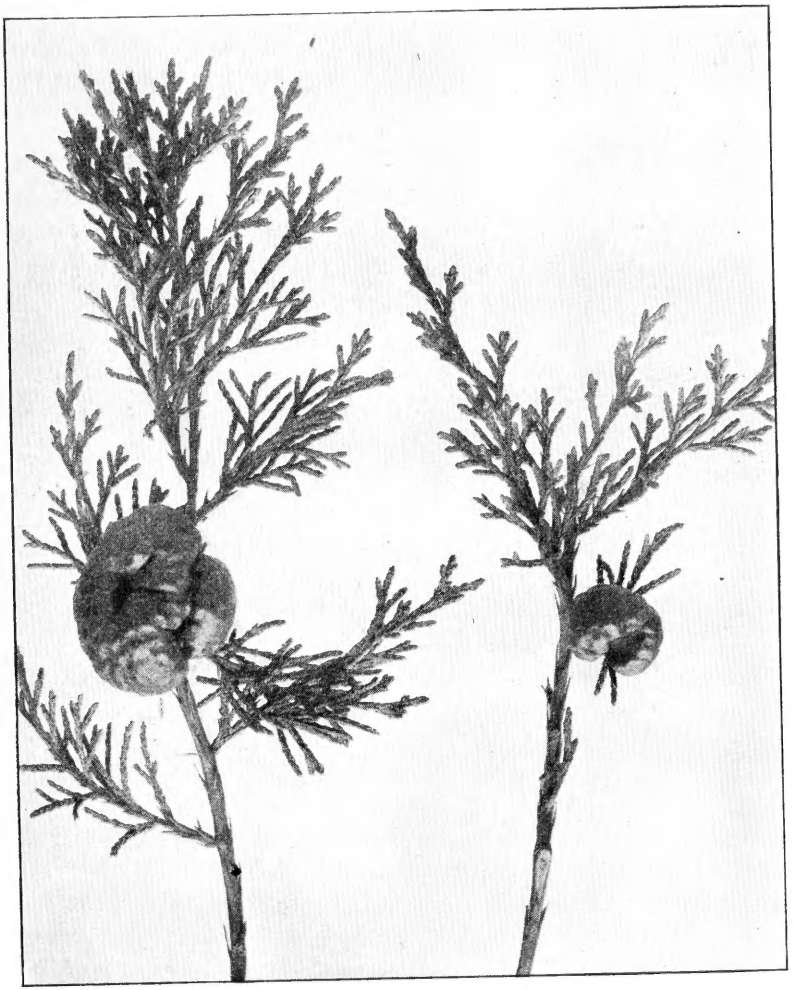

FIG. 136. GALLS OF GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE
The galls are in the winter condition and show the depressions from which the telial horns protrude in the following spring

NATURE OF LOSSES

Although the greatest loss from this rust occurs on the apple, cedar trees also may be materially injured. The injury to apple trees caused by the disease is largely due to premature defoliation and to a reduction

in the vital activities of the less seriously affected leaves. Premature defoliation year after year greatly reduces the vigor of the trees and death may finally result. Reed, Cooley, and Crabill (1914) state that

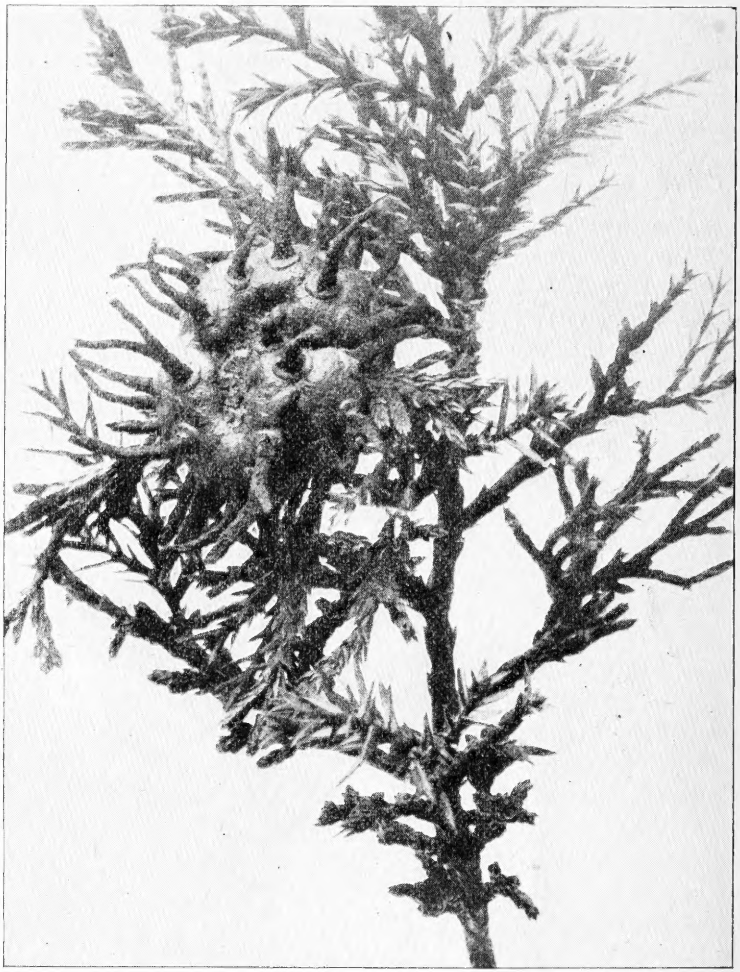

FIG. 137. TELIAL HORNS OF GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE
The telial horns are shown as they appear after one gelatinization period

where the disease is severe for several years in succession the trees make but little growth, become much weakened, and are more subject to attacks of insects and of other fungi. Another source of loss is due to the deformation of the affected fruit, such fruit in most cases being unsatisfactory for

market. The young twigs may also become affected[5] and die; in many such cases death of a tree may ensue before it reaches bearing age.

SYMPTOMS

On cedar

On the cedar tree the first evidence of the disease caused by *G. Juniperi-virginianae* is a minute greenish swelling on the leaf, usually noticeable first on its upper, or inner, surface. The affected part of the leaf enlarges rapidly and becomes gradually darker in color, and by the last of September a nearly full-grown cedar apple is formed. At this time the gall is greenish brown in color, from globose to reniform in shape, and of a diameter varying from two millimeters to five centimeters. In New York State the slight pit-like depressions in the outer surface of the gall appear about October 1 (fig. 136). In the following spring the telial horns protrude from the depressions. These horns are golden brown in color and cylindric-acuminate in shape (fig. 137). During warm spring rains they gelatinize and enlarge about two to three times (fig. 138). Later the galls die, but often they remain attached to the cedar tree for a year or more.

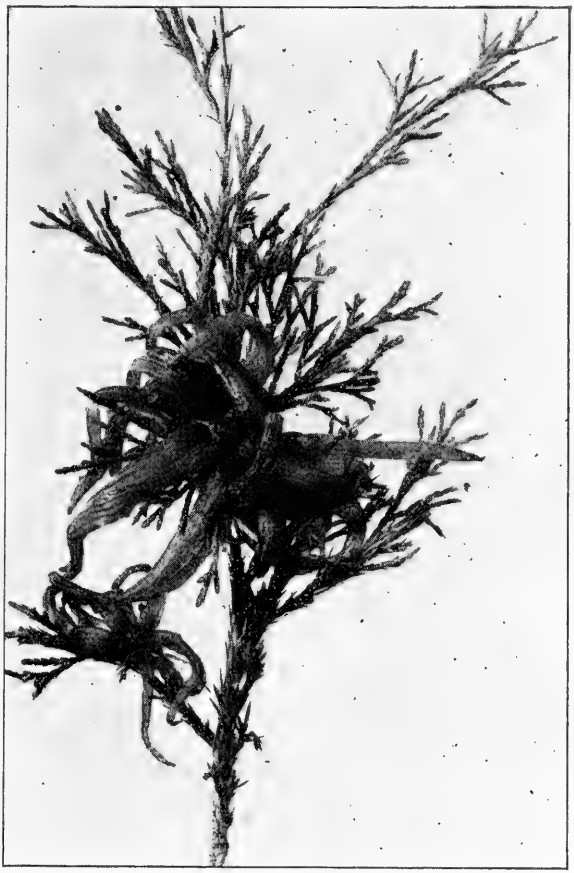

FIG. 138. GALL OF GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE
The telial horns are shown as fully gelatinized

[5] Twig infections of a wild variety of apple were very common at Ithaca, New York, during the summer of 1914.

On apple

On the leaves

The first evidence of infection by *G. Juniperi-virginianae* on the apple leaf is the appearance of very small greenish yellow spots about one-half millimeter in diameter. These spots gradually enlarge and the color changes to orange-yellow often bordered by concentric red bands (fig. 139).

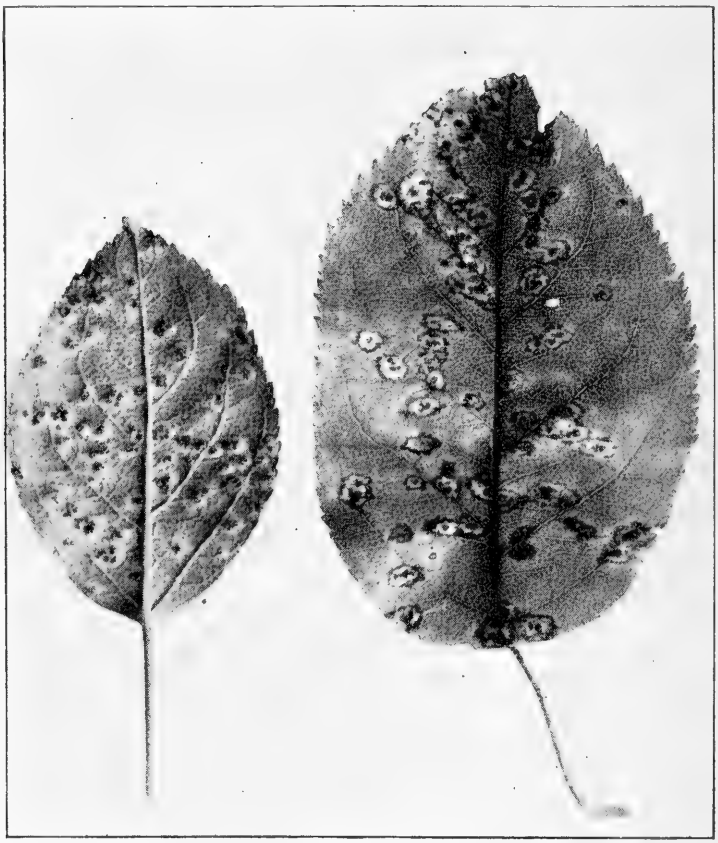

FIG. 139. APPLE LEAVES AFFECTED WITH GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE

The characteristic lesions of the rust are shown on both sides of the leaves

In these lesions minute yellow pycnia soon appear, which vary in number according to the size of the affected area. After a few days the pycnia exude droplets of a yellow, sweetish substance, and soon afterward they turn black. The underside of the lesion becomes hypertrophied about this time and the aecia soon appear. These may be arranged in a circle near the margin of the swollen area or they may be scattered over the lesion.

On the fruit

The lesions on the fruit are similar to those on the leaves except that normally they are larger and bear a larger number of aecia (fig. 140). The spots are yellow and wrinkled, and as a rule are confined to the blossom end of the fruit although they may occur on the sides or on the stem end. Affected apples may be dwarfed and deformed.

On the twigs

In apples of very susceptible varieties twigs of the current year's growth may be severely affected by the rust. Infection takes place early in the season. The twig does not elongate, but it increases in diameter, and as a result a short, thick, stubby twig is produced in which pycnia and aecia are formed in abundance. Seriously affected twigs die at the end of the season.

FIG. 140. APPLE FRUIT AFFECTED BY GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE
The apple on the right shows the aecia protruding from the surface, while the apple on the left shows only pycnia

ETIOLOGY

Nomenclature

The cedar fungus was first named *Gymnosporangium Juniperi-virginianae* by Schweinitz in 1822. In 1825 it was named *G. macropus* by Link, but *G. Juniperi-virginianae* is considered the accepted name.

Life history

Telial stage

Inoculation of cedar.— According to Kern (1911), Plowright was the first to infect cedar trees with a rust fungus. On June 25, 1884, he inoculated a small one-year-old juniper seedling, about 2.5 centimeters high, with

G. clavariaeforme (Jacq.) DC. Evidence of infection was apparent on July 1 but the tree died before any spores were formed. In another instance Plowright inoculated a tree 3 decimeters high and spores were produced one year from the following spring, showing that nearly two years are necessary for the completion of the life cycle of the fungus. Heald (1909) failed to obtain infection in cedars with *G. Juniperi-virginianae*.

Each summer for the past three years, small cedar trees growing in the greenhouse have been inoculated by the writer. The methods used in making the inoculations were for the most part those employed by Kern (1911) in infecting accial hosts. Aeciospores were scraped from an affected apple leaf into tap water, and the suspension of spores thus obtained was sprayed on a cedar tree with an atomizer. Other affected leaves were suspended over the tree so that the spores fell directly on it. After the tree was sprinkled with the infected water it was covered with a large bell glass so that the moisture would be retained. Each day the bell glass was removed and the inner surface sprayed with water, in order to maintain a moist atmosphere. After a period varying from forty to sixty hours the bell glass was removed.

In the autumn of 1914 five trees were thus inoculated. The results are recorded in table 1:

TABLE 1. INOCULATION OF CEDAR TREES WITH SPORES OF GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE IN 1914

Number of trees inoculated	Date of inoculation	Number of infections apparent	Fungus
3	July 25	1, on July 30, 1915*	*G. Juniperi-virginianae*
1	September 8	No infection	*G. Juniperi-virginianae*
1	September 27	No infection	*G. Juniperi-virginianae*

* See discussion of this case in the text, page 517.

All the inoculated trees were examined carefully on November 6, 1914, but no sign of infection was evident. In one case certain parts of several leaves were yellowish green in color, closely resembling infected leaves, but there was no further development and the leaves finally died. On July 26, 1914, two cedar trees which had been inoculated with *G. Juniperi-virginianae* the previous autumn showed certain leaves that appeared to be infected. Leaves on different stems showed yellow discolorations, while the other leaves were of the normal green color. Although the leaves with the discolored spots died without showing further evidence

of infection, it is possible that the fungus was more virulent under these conditions and killed the leaves without showing any signs of gall development. None of the foliage on the check trees showed the yellow discoloration.

On July 30, 1915, a small cedar apple was found on a cedar tree that had been inoculated on July 25, 1914, by suspending over the tree the fruit of an apple infected with *G. Juniperi-virginianae*. When first observed this gall was one millimeter in diameter, globose, and green in color. It appeared to be developing from the upper, or inner, side of a small scale leaf. This tree was brought into the greenhouse in the early spring of 1914 and all cedar apples were removed. It was carefully examined again on April 10, 1915, for any signs of cedar apples and none were found. That this gall could have been the result of natural infection before the tree was removed to the greenhouse seems impossible, since in that case it would have developed in the previous year. The gall was undoubtedly that of *G. Juniperi-virginianae*, as is evident by its method of origin, its color (at first green and later turning to the characteristic brown), and its surface character. By October 1 it had doubled in size, and spores were produced in February of 1916. Apparently the gall resulted from the inoculation. It is, however, impossible to determine this point absolutely.

Susceptibility of individual trees.— Observations made during the past three years seem to indicate that individual cedar trees show a difference in susceptibility. Some may be severely affected while others are practically free from the disease. Certain trees produce a considerable number of *G. Juniperi-virginianae* galls, while others bear almost exclusively the galls caused by *G. globosum*, and still other trees may be affected severely by *G. clavipes*. Furthermore, some of the trees may have all three species present in great abundance, but usually a tree is attacked primarily by a single species.

There is a wide variation in the number of cedar galls of *G. Juniperi-virginianae* produced from year to year. This variation usually depends on the abundance of the alternate stage in the preceding year. This is not always true, however, since favorable infection weather may not prevail at the time when infection of the cedar would naturally occur. In the summer of 1914 an abundance of the aecial stage of all three species was produced, and a corresponding increase in the number of cedar apples was apparent in the fall of 1915. There is less fluctuation in the case of *G. globosum* and *G. clavipes*, since these forms are perennial.

Infection period.— It is generally accepted that infection of the cedar may occur with the production of the first mature aeciospores, and continue throughout the season. During the seasons of 1915 and 1916 the aecio-

spores matured about August 1 in New York State. Many workers have had difficulty in germinating these spores, and for that reason Reed and Crabill (1915) have advanced the theory that a rest period is necessary and that the aeciospores do not germinate until the spring following their dispersal. It is probable that the mycelium develops within the tissue of the cedar for a period of several months after infection occurs, before any material change is noticeable. The galls first make their appearance in the latter part of July and continue to grow rapidly until late autumn, when they are practically mature.

Mycelium and haustoria.— Prior to the formation of telial horns, the mycelium is distributed throughout the gall, where it occupies the intercellular spaces. The entire leaf from which the gall originates is permeated with mycelium even before much hypertrophy or other change becomes evident. The mycelial cells vary in length and the septa are often difficult to locate. This fact undoubtedly accounts for the mistake of Sanford (1888) in thinking that no cross walls exist. The binucleated condition can readily be demonstrated. The hyphae vary in width but average about 2.5 μ.

Haustoria are present, but not abundantly in the young galls. Reed and Crabill (1915) give a detailed account of the formation of haustoria. They were able to find only the very early stages in the autumn, and believe that mature haustoria are not developed until just preceding teliospore formation in the spring.

Development of telial horns.— About the first of October or later, depending on the season, aggregates of mycelium are developed in certain areas, forming typical stromatic layers. The host cells in these regions are often completely insulated and very small. The rapidly forming mycelium inhibits the growth of the host cells in its midst, but the adjoining cells continue to multiply and enlarge so that a depression results. From these stromatic layers the teliospore stalks arise. Sections of galls collected early in December, 1915, show the spore stalks and the immature spores in abundance. The spores are cut off from the tips of the short stalk-cells by septa, and almost simultaneously become two-celled. The young spores contain two nuclei in each cell, but these fuse when the spores reach maturity.

In 1915 the more advanced galls showed the telial depressions about October 1. No further change was noticed until early in the following spring, when the telial horns pushed out from the depressions and continued to develop for some time. The telial horns consist of a vast number of spores borne on much elongated pedicels. They are first formed beneath the epidermal tissue, and when warm weather begins the pedicels elongate and carry the spores out with them. In 1914 the telial horns began to

make their appearance about the middle of April, and mature spores were present on April 25 but gelatinization did not take place until May 5. In 1915 the epidermis was broken open about April 15 and the first gelatinization took place on May 8.

An experiment was conducted to determine whether or not the telial horns are capable of gelatinization as soon as they emerge from the gall. A cedar apple with horns not more than one millimeter in length was placed in a glass beaker containing water. Within less than half an hour the horns had swollen to twice their original size. Apparently the spore stalks are capable of gelatinization as soon as they have ruptured the epidermis of the gall, but an attempt to germinate the spores at this time failed.

The telial horns may become from 2 to 20 millimeters in length by 1.5 to 3 millimeters in width before the first gelatinization takes place. At this time the telial horns are cylindric-acuminate in shape. They are golden brown in color and are evenly distributed over the surface of the gall. With the first warm spring rains after the horns are protruded, they enlarge to as much as three times their original size. The horns during this period are of a jelly-like consistency and are much lighter in color than before, due to the fact that there is less coloring matter in the gelatinous spore-stalks than in the spores. With the return of drier conditions the horns regain approximately their original size. The tips of these protrusions usually dry down more than the remainder, and are often of a hard consistency. After each succeeding rain one-half hour or more in duration, gelatinization may occur, and this may be repeated as many as fifteen or twenty times. Nevertheless, some of these periods may not be of sufficient duration to permit the spores to germinate. In 1914 the first gelatinization took place on May 5, and after the horns had dried it was noted that for nearly one-fourth of their length from the apex to the base they were lighter-colored and much firmer in consistency than before gelatinization. After the rain period of May 21 about one-half of the horn was lighter-colored, and after the rain on June 5 only a small area at the base retained its original color and its ability to gelatinize. This basal part became swollen on two subsequent occasions, a smaller part each time, until finally the horn was light in color throughout and became detached from the gall on July 1.

A microscopical examination of the part of the horns which assumed a lighter color showed that approximately fifty per cent of the spores had germinated. It has been observed also that the spore stalks of germinated spores are unable to gelatinize. They become dry and hard, so that when they are teased apart and examined the empty spore walls are generally broken from their stalks or only short pedicels remain. It would seem

from the foregoing observations that the horn becomes lighter in color and hard progressively from the apex to the base, and also that the spores at the apex are older, mature earlier, and germinate more readily than those at the base. Reed and Crabill (1915) are of the opinion that the teliospores on the outside of the tentacle germinate first and shrivel away, and then those on the interior of the tentacle come to the surface and germinate in their turn. The writer's observations show that, although the spores over the entire surface of the horn germinate, those at the apex germinate more readily. These observations agree with those of Wörnle (1894), who states that the spores at the apex are the oldest.

Teliospore germination.— The time of spore germination varies with the season. In 1914 and 1915 the spores were mature about April 25. Tests made show that the spores will not germinate as soon as the horns rupture the epidermis of the gall. Weather conditions are an important factor, and as much as two weeks may intervene before germination occurs. When cedar apples with telial horns that were just emerging were brought into the laboratory, the spores germinated after about seven days.

The teliospores are characteristically two-celled, but occasionally one-celled and three-celled spores are found (fig. 141, A). They range in width from 15 to 22 μ and in length from 33 to 65 μ.[6] The spore is narrowly ellipsoidal to rhombic oval in shape. It is slightly or not at all constricted at the septum. The wall is cinnamon brown in color and averages about 1 μ in thickness. The pedicels are thin and of equal diameter throughout, varying in width from 3 to 5 μ for different spores. There are two germ pores in each cell of the spore, one on each side of the cell near the septum. Spore germination is of the usual rust type, resulting in the formation of a promycelium bearing four basidiospores (fig. 141, B).

Heald (1909) found that under favorable conditions the promycelium and basidiospores may be produced in from twelve to twenty-four hours; Coons (1912) states that the process of developing germ tubes requires from six to fifteen hours; while Reed and Crabill (1915) found four hours to be the minimum time for germination. The writer has obtained mature basidiospores within less than three hours under optimum conditions; in fact, under such conditions from three to four hours is the usual time required.

The most satisfactory germination of teliospores was obtained from spores placed on a clean slide in a film of tap water. The slide was placed in a petri dish, which contained a small quantity of water to prevent too rapid evaporation from the slide. On one occasion a spore taken from a telial horn just brought in from the field on a clear day and germinating under the conditions described above, had formed a small bud-like process

[6] Spore measurements were made in all cases with an oil-immersion lens, using fresh spores mounted in water.

at the end of one hour; after two and one-half hours the promycelium had continued its development and the septa were visible; by the end of three and one-half hours the basidiospores were formed. Instances have been noted in which the spores germinated and the basidiospores were present within less than three hours.

One of the important factors affecting spore germination is the amount of moisture. Blackman (1903) discusses this subject in some detail. He used spores of other species of rust, placing some in hanging drops

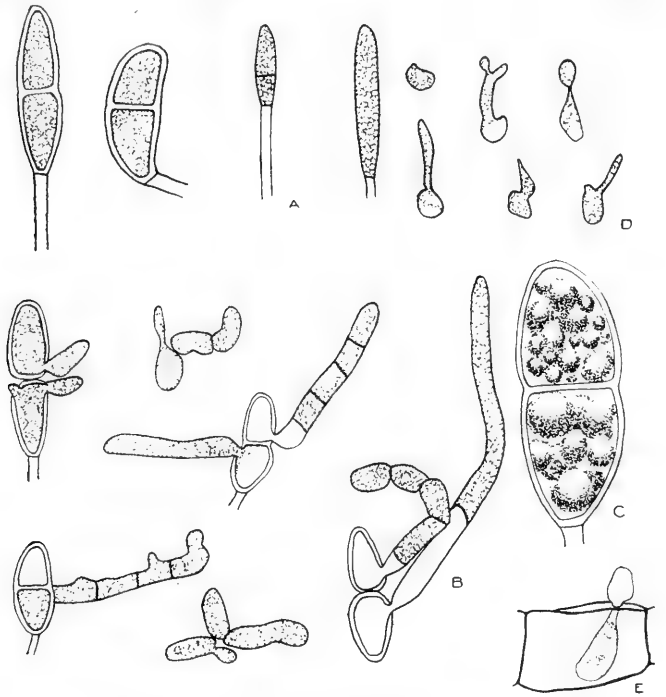

FIG. 141. SPORE FORMS OF GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE

A, Various types of teliospores of *G. Juniperi-virginianae*. × 350. B, Various stages and types of teliospore germination of *G. Juniperi-virginianae*. × 350. C, Teliospore of *G. Juniperi-virginianae*, showing the appearance of the cell contents when incubated at 30° C. for four hours. × 375. D, Various stages of basidiospore germination of *G. Juniperi-virginianae*. × 350. E, Penetration of a basidiospore of *G. Juniperi-virginianae* directly through the wall of an epidermal cell. × 350

and some on slides in petri dishes. He found that those in hanging drops developed long germ tubes and formed no basidiospores until they had grown through the drop into the air, which rarely happened. The others formed basidiospores and a characteristic promycelium at once. Blackman concludes that the presence or absence of air is the determining factor, as this varies with the water supply.

It has often been observed by the writer that teliospores germinating on a slide produce only long tubes when covered with water, but when there is only a small amount of water present the usual promycelium and basidiospores are formed. An attempt was made to germinate teliospores in a saturated atmosphere without permitting the spores to come into contact with other moisture than that in the atmosphere. This attempt failed, but in cases in which the air became supersaturated, and small droplets condensed on the slide, germination was obtained.

Temperature is another factor that plays a large part in spore germination. Reed and Crabill (1915) found that 15° C. was the optimum temperature for spore germination and 11.5° C. was the minimum. The upper thermal death point was 30° C.; the lower thermal death point was not determined, but it was much below freezing.

Considerable work has been done by the writer in an attempt to determine the most favorable temperature conditions for germination with the three rust species studied. For the first of these experiments the following method was used: Telial horns were placed in a watch glass in tap water and teased apart until several spores could be obtained in each drop of water. Suspensions of spores thus prepared were placed on slides in petri dishes and allowed to germinate at different temperatures. It was found after several trials that spores which had been broken entirely free from the horn or were isolated from all other spores did not germinate so readily as did those that remained clinging in groups. After repeated trials it was found that a better indication of spore germination could be obtained by placing a telial horn, or a part of one, on a slide. In this way more nearly normal conditions were maintained, but the larger number of spores made it impossible to estimate the percentage of germination except in a comparative way. In the case of *G. Juniperi-virginianae* an entire telial horn was placed on a slide, and often horns from the same gall were used in a series of tests. In the case of the other two species only parts of the horns were used. The quantity of basidiospores lying along the side of the horn on the slide was often used as a guide in estimating the relative amount of germination. Observations were usually made every hour, and the rate of germination for the entire period was considered in making the final comparisons.

The extremes found for all three species were practically the same as those found by Reed and Crabill (1915) for *G. Juniperi-virginianae*, the lowest temperature at which germination occurred being 7° C. and the highest 29° C., with the upper thermal death point 30° C. (fig. 142). The optimum temperature, however, as shown by these experiments, ranges from 22° to 25° C., the best germination taking place at from 23° to 24° C. These experiments were run in triplicate and were repeated on several occasions throughout the season, so that some temperatures

were tried at least twelve times. In all cases the results obtained were uniform. Reed and Crabill (1915) found that a temperature above 20° C. greatly retarded the development of basidiospores and that no spores were produced when the temperature was above 24° C. In the writer's experiments an abundance of basidiospores were obtained at a temperature ranging from 22° to 25° C., and there were some at 26° C. After incubating at 30° C. no spores germinated, even when placed under optimum conditions. The oily contents of the spores coalesced into large drops, giving the appearance shown in figure 141, C (page 521). The normal variation is relatively great in tests of this kind, but the experiments were repeated a sufficient number of times to make the observations comparatively conclusive.

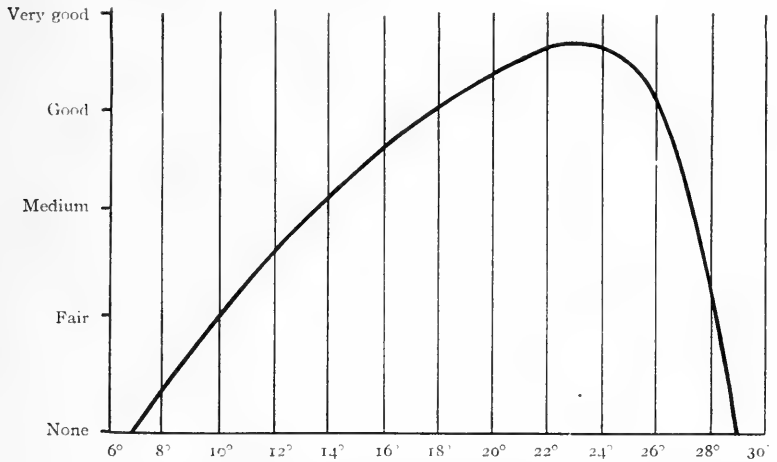

FIG. 142. INFLUENCE OF TEMPERATURE ON GERMINATION OF RUST SPORES
The curve shows that the best germination of teliospores occurred at a temperature between 22° and 24° C.

When conditions are unfavorable for germination a long germ tube may be formed or a bud-like process may take the place of a promycelium. Again, the promycelium may break up into four parts, each of which may then form a basidiospore or may germinate by a germ tube. The cells of the promycelium may germinate by germ tubes without breaking apart, or other uncommon methods of germination may occur. These abnormal conditions of germination are usually found where an overabundance of moisture is present or where the temperature is somewhat lower than the optimum.

Dissemination of basidiospores.— When the basidiospores reach maturity they are forcibly discharged from their sterigmata. With the beam-of-light method the falling of basidiospores was observed by the writer in the same manner as is described by Buller (1909) and later by Coons

(1912). An experiment was set up in which the discharge of basidiospores began at half past six o'clock in the evening of one day and continued until after ten o'clock the next forenoon — although at that time the rate of discharge was much slower. Evidently the dispersal of basidiospores can continue for some time after a period of rainfall if slow-drying conditions prevail. In observing the process under the microscope an abrupt sidewise movement of the basidiospore was always noticed several seconds previous to its discharge, and almost simultaneously a bubble appeared at its base.

The basidiospore farthest from the spore is the first to be formed, followed by the others in their respective order. The outermost spore is discharged first, followed by the next in order. Only about one minute elapses between the disappearance of the apical basidiospore and the one nearest it, but a much longer period elapses before the last two are discharged. Often the terminal basidiospore is mature before the sterigma of the basidiospore nearest the spore is even formed. This method of discharge readily accounts for the wide dissemination of basidiospores by air currents.

Germination of basidiospores.— Farlow (1886), Crabill (1913), and Reed and Crabill (1915), have contributed to the knowledge of secondary basidiospore formation. The basidiospore normally germinates by the development of one or more, rarely two, germ tubes from the side of the spore. Under certain conditions, instead of a germ tube a sterigma similar to those formed on the promycelium is put forth, and on the end of this a secondary basidiospore is produced. This secondary spore is identical in appearance with its parent except that it is somewhat smaller. Various stages of basidiospore germination are seen in figure 141, D (page 521). The chief factor influencing the production of the secondary spore is an excess of moisture.

Two cedar apples, one caused by *G. Juniperi-virginianae* and the other by *G. globosum*, with horns protruded, were subjected for twelve hours to a fine mist from a spray nozzle attached to a water tap. The temperature of the room was 23° C. and that of the water about 8° C. When the material was examined it was found that a large number of the spores had germinated abnormally, and that the basidiospores which were formed had already germinated by means of secondary spores. It is impossible to determine whether or not the excess moisture was the only cause of this abnormal germination, since the temperature factor may also have been of importance.

Aecial stage

Inoculation and infection of apple.— The first basidiospores are usually disseminated in the spring about the time when the buds of the aecial hosts open, though some may be formed previous to this time. Infection

usually occurs on the dorsal surface of apple leaves. The germ tube penetrates the epidermis and the pathogene becomes established within the tissues of the host.

In these inoculation experiments a suspension of basidiospores in tap water was placed on various parts of both the upper and the lower surface of Wealthy apple leaves. After seven, fourteen, and twenty-one hours, respectively, parts of the leaves thus inoculated were removed, fixed, and embedded in paraffin. Several of these were later sectioned and examined. In one case, after a period of seven hours a germ tube of a basidiospore was found to have penetrated the lower epidermis directly and passed about two-thirds of the distance through the epidermal cell (fig. 141, E, page 521).

Several leaves from a small apple tree were inoculated by placing basidiospores in suspension on the foliage, with a camel's-hair brush. Some leaves were inoculated on the upper surface and others on the under surface. Infection was apparent after ten days on all the inoculated leaves. This demonstrates that infection can take place on either the upper or the lower surface of the leaf. In all cases, however, pycnia were produced only on the upper surface. Apparently, therefore, the production of pycnia on the upper surface of infected leaves is due, not to the fact that infection occurs there, but to some other factor. Pycnia have never been seen on the lower surface of leaves, although many aecia have been observed arising vertically from the upper surface.

In 1914, and also in 1915, the first evidence of infection in nature was found about June 1. The mycelium is similar to that found in the telial hosts except that it is uninucleate and only a limited area of the host tissue is invaded.

Effect of environmental factors.— It is evident that the amount of rust present in a given season will depend largely on weather conditions. Moisture is necessary for teliospore germination and for infection of the aecial host, and therefore the number of infection periods depends primarily on the number of rain periods.

An attempt was made in these experiments to determine the approximate amount of moisture necessary for infection of the aecial host. Cedar apples were immersed in tap water for a few minutes and were then placed under a bell glass. After about four hours, when an abundance of basidiospores were being discharged, the gall was suspended over a small apple seedling. A lamp chimney inclosed both the seedling and the gall. The seedling was not moistened. The cedar apple retained its moisture for a long time in this position, and the basidiospores formed a yellow coating over the surface of the leaves of the seedling within a few hours. After eighteen hours the chimney was removed, and ten days after inoculation abundant infection was evident on nearly all the leaves. This

experiment was repeated several times and in each case the same results were obtained. Apparently sufficient moisture collected on the leaves from the water transpired and from that which evaporated from the telial horns to permit basidiospore germination and infection. A careful inspection failed to disclose any drops of water collected on the leaves inside the chimney.

Other experiments were attempted in which the lamp chimney containing the cedar apple was suspended over the apple tree so that the basidiospores fell on the tree but no opportunity was offered for the condensation of water on the leaves. No infection occurred under these conditions. This experiment was repeated on a large tree in the open. The basidiospores were allowed to fall on a few young leaves which were not inclosed within the chimney. On the night when the experiment was set up there was a heavy dew followed by forty-eight hours of precipitation. Abundant infection occurred and aecia were developed within the usual period of time.

From these experiments it is evident that but little moisture is necessary for infection. There must be sufficient moisture to cause the telial horns to gelatinize and to keep them in that condition for a period of from four to five hours, followed by conditions of high humidity to furnish the necessary moisture for infection. This is contrary to the opinion of Reed and Crabill (1915), who state that infection takes place only in the presence of abundant moisture. It is not clear whether they mean to include the whole process of basidiospore formation and infection or only the latter, since they also make the statement that infections followed short periods of rainfall.

Strains of the fungus.— Since this disease is so destructive in West Virginia and Nebraska, specimens of cedar apples from each of these States were procured for the purpose of making comparative inoculation tests with the strain of the fungus found in the vicinity of Ithaca, New York. These specimens, obtained through the kindness of N. J. Giddings and E. M. Wilcox, were used to inoculate Wealthy apple trees in the open and apple seedlings in the greenhouse. Young leaves on different branches of each tree were inoculated with the three strains of fungi and their development was observed closely. Infection was apparent at exactly the same time in all cases and the development of the disease was identical in all particulars. In no case was there any evidence to show that one strain was more virulent than the others. The apples of West Virginia and of Nebraska may be more susceptible than those of central New York, which probably accounts for the fact that this disease is so destructive in the former States.

Varietal susceptibility of apple.— Numerous lists of susceptible and of resistant varieties of apples have been recorded by various writers. The

most important of these are by Emerson (1905) in Nebraska, Chester (1896) in Delaware, R. E. Stone (1908) in Alabama, Smith and Stevens (1910) in North Carolina, Reed, Cooley, and Crabill (1914) in Virginia, and Giddings and Berg (1915) in West Virginia. Stewart (1910) says that in New York State the varieties Wealthy, Boiken, and Rome are very susceptible, Hubbardston and Sutton are slightly susceptible, and McIntosh, Yellow Transparent, Gravenstein, Red Astrachan, Oldenburg, and Baldwin are resistant. The writer has had no opportunity to make observations on the susceptibility of different varieties of apples, but the following have been artificially infected several times: Wealthy, Wagener, Twenty Ounce, Tompkins King, Alexander, Baldwin, Rome Beauty, Bietigheimer, Baxter, Boiken, Banana, Black Gilliflower, Dartmouth.

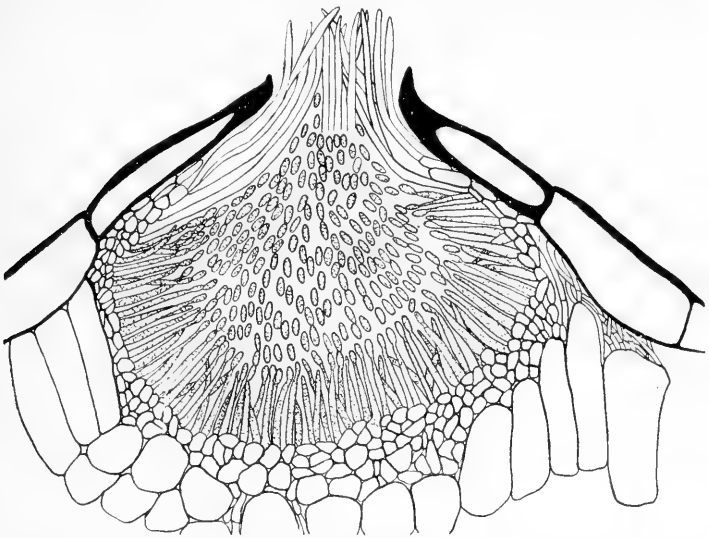

FIG. 143. PYCNIUM OF GYMNOSPORANGIUM GLOBOSUM IN CRATAEGUS LEAF. × 350

The variety Wealthy is considered especially susceptible, although Stewart and Carver (1896) state that it proved to be resistant in Iowa. Seedling apples are very susceptible when artificially inoculated.

Several specimens of Salome apples were received in the autumn of 1913 and a large rust lesion was present on the blossom end of each. This variety should probably be included with those listed as susceptible in New York State.

Pycnia.— The pycnia are the first fruiting bodies to appear in apple tissue attacked by the rust fungus. Masses of short-celled mycelium collect at certain points under the epidermis and form the flask-shaped pycnia of the usual rust type. Hyphal branches extend into the pycnial cavity and from the ends of these the pycnospores are abstricted (fig. 143).

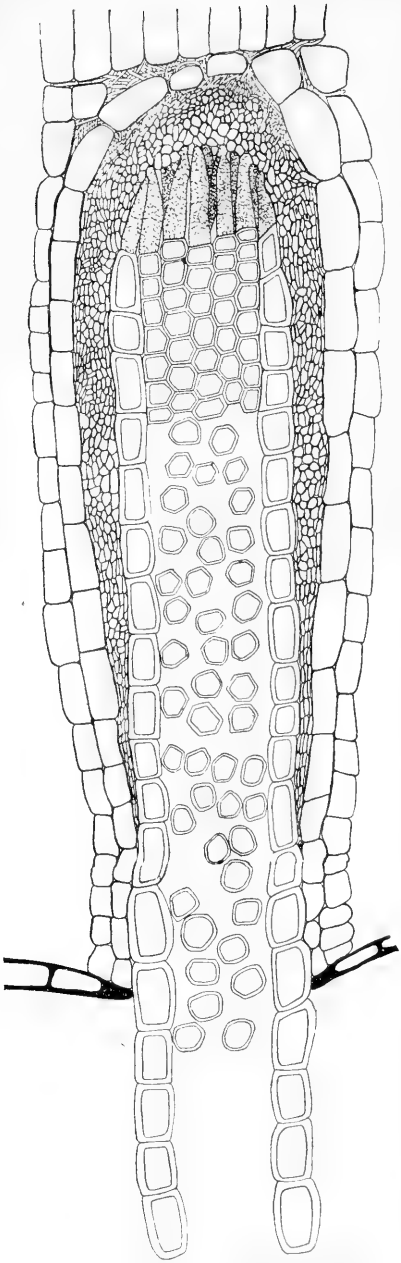

FIG. 144. AECIUM OF GYMNOSPORANGIUM GLOBOSUM IN CRATAEGUS LEAF

Aecia.— From two to four weeks after the pycnia become visible, depending largely on weather conditions, the aecia begin to break out on the lower surface of the leaves or from among the pycnia on stems or fruit. In New York State the aecia usually begin to break open about the first of August.

The tissues from which these fruiting bodies arise may be considerably hypertrophied, the spongy parenchyma especially being modified. Many septate strands of mycelium collect beneath the surface in the diseased area and from these the aecia are finally developed. The aecia are formed entirely within the host, but as they mature they break through the inclosing tissue, the peridium soon dehisces, and the spores are then scattered.

The aecia in all cases are composed of the inclosing pseudoparenchyma, the fertile spore-bearing stalks, and the aeciospores surrounded by the single layer of peridial cells (fig. 144). The aecia spores are binucleate and measure 16 to 24 μ by 21 to 31 μ. The spore wall varies in color from yellow to brown. When dehiscence occurs the peridium splits longitudinally between practically each row of cells. The ends of the cells remain attached, forming long strands which are one or more cells wide by several cells long. The individual cells are comparatively long and narrow, measuring 10 to 16 μ by 65 to 100 μ; they become much recurved when moist. The side walls are sparsely rugose with ridges extending the entire distance across. The aeciospores drop out of the aecia as they mature, and are carried by the wind to cedar trees where they initiate the telial stage.

Germination of aeciospores.— Many investigators have experienced great difficulty in germinating aeciospores. Heald (1909) states that he succeeded in germinating them previous to the first of October, after which time only one or two per cent germinated. Reed and Crabill (1915) found it impossible to germinate them except for an occasional germ tube, which seemed to be in a very weakened condition. Numerous trials made by the writer indicate that only a small proportion of these spores are capable of germination.

TABLE 2. RESULTS OF AECIOSPORE GERMINATION TESTS OF GYMNOSPORANGIUM JUNIPERI-VIRGINIANAE IN 1915

Number of slides	Date	Cultural solution	Temperature	Method	Percentage of germination
5	August 5	0.2 per cent cane sugar and cedar leaf	24° C.	Spores on dry slide, culture solution added	1
1	August 5	0.2 per cent cane sugar	24° C.	Spores on dry slide, culture solution added	75
1	August 5	0.2 per cent cane sugar	24° C.	Spores on dry slide, culture solution added	25
3	August 5	0.2 per cent cane sugar	24° C.	Spores on dry slide, culture solution added	0
5	August 5	Tap water	24° C.	Spores on dry slide, culture solution added	1
2	August 5	0.2 per cent cane sugar	24° C.	Spores shaken on slide, culture solution sprayed in fine droplets on slide	0
5	August 5	0.2 per cent cane sugar	24° C.	Spores shaken on slide, small drop of solution added	0
5	August 5	0.2 per cent cane sugar	24° C.	Large drop of solution placed on slide, spores allowed to fall on solution	2 spores on each slide
2	September 29	Tap water	22° C.	Suspension of spores	0
1	September 29	Tap water	23° C.	Suspension of spores	0
1	September 29	Tap water	26° C.	Suspension of spores	0
4	September 29	Tap water	15° C.	Suspension of spores	0
2	August 28	Tap water	23° C.	Spores shaken on dry slide, then placed in moist chamber	0

The method used in this work was practically the same as that recorded for the germination of teliospores. Water and a cane-sugar solution were used as culture media, to which, on various occasions, cedar leaves were added. In some cases the spores were shaken directly on the slide in order to obtain only mature spores, while in other preparations the aecia were placed on the slide and crushed, thus liberating all the spores present. The quantity of culture solution was varied, and in some cases the spores were first placed on the slide and the culture media was then added, while in other cases the spores were allowed to fall onto the surface of the culture solution.

The results of these experiments are recorded in table 2. Apparently a small proportion of aeciospores germinate under artificial conditions. Some of the spores used in the experiments were obtained from naturally infected and others from artificially infected leaves. The presence of cedar leaves in the culture media did not influence the germination of the spores.

Other germination tests were made with spores used for inoculating cedar trees, but only a few spores germinated. Hanging-drop mounts were employed in some cases not recorded, but these yielded no better results.

THE DISEASE CAUSED BY GYMNOSPORANGIUM GLOBOSUM

The disease caused by the fungus *Gymnosporangium globosum* is commonly known as *cedar rust*, *Crataegus rust*, or *pear rust*, depending on the stage referred to. The pathogene is native to North America and was first studied carefully by Farlow (1880). It is widely distributed throughout the eastern section of the United States, where it causes a rust of various species of Crataegus. The disease is of little economic importance, although on rare occasions the fungus attacks pears and quinces (Stewart, 1910).

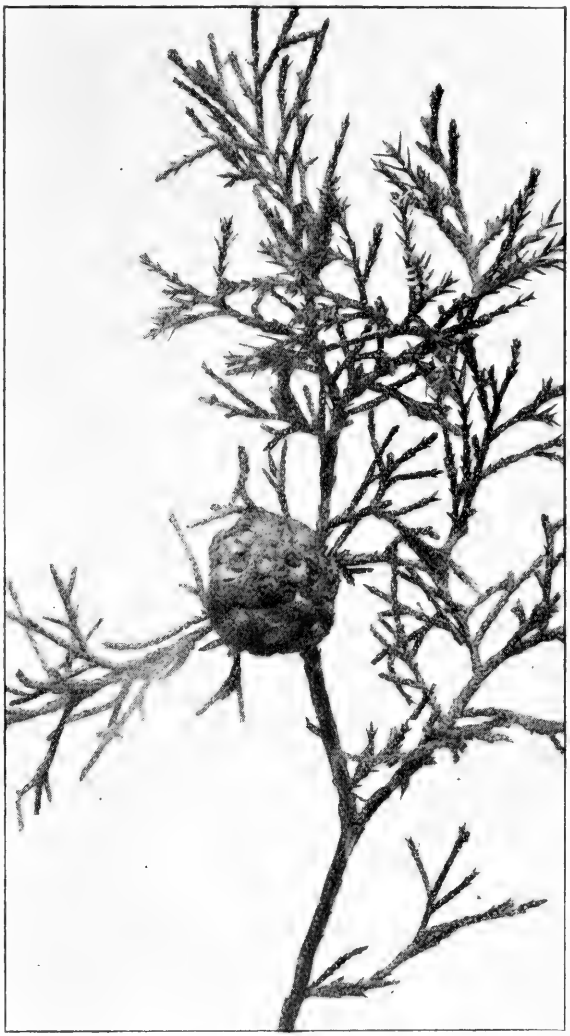

FIG. 145. CEDAR APPLE CAUSED BY GYMNOSPORANGIUM GLOBOSUM. WINTER CONDITION

SYMPTOMS

On cedar

The galls produced by this species are similar in appearance to those caused by *G. Juniperi-virginianae*. The gall produced by *G. globosum*, as the name would indicate, is usually globose in shape and is not so large as the gall caused by *G. Juniperi-virginianae*. The surface of the young gall in early autumn is smooth except for the shreds of the old leaf which cling to it. It approaches mahogany red in color, in contrast to the greenish brown of the *G. Juniperi-virginianae* gall. Instead of the pit-like depressions on the surface, the galls pro-

duced by *G. globosum* have small elevated areas, or mounds (fig. 145). From these raised areas the telial horns appear in the following spring.

The telial horns are wedged-shaped and are chestnut brown in color (fig. 146). Scars of the horns of former seasons are often apparent between the horns on old galls. When the warm spring rains occur, the protrusions gelatinize and enlarge to about double their normal size (fig. 147). These horns dry and drop off at the end of the fruiting season, but the galls may continue to live and bear spores for several seasons. The old galls turn brown and become roughened on the surface due to the scars of the telial horns.

FIG. 146. GALL CAUSED BY GYMNOSPORANGIUM GLOBOSUM
The typical telial horns are shown prior to gelatinization

On quince

A yellow spot, such as characterizes the lesions caused by *G. Juniperi-virginianae* on the apple leaf, is formed by *G. globosum* on quince foliage. The pycnia and the aecia are likewise formed on the upper and the lower surface of the leaf, respectively. To all external appearances the symptoms are the same as those described for *G. Juniperi-virginianae* on apple foliage.

On pear

Stewart (1910) states that infected spots on the upper surface of pear leaves are dark brown or nearly black in color, with a conspicuous red

border. Spots on the under surface are of the same dark color but have no red border. Aecia are produced in the largest lesions and also on the infected leaf petioles. In many cases the rust spots are arranged in

FIG. 147. TELIAL HORNS OF GYMNOSPORANGIUM GLOBOSUM FULLY GELATINIZED

two irregular rows, one on each side of the midrib, giving the appearance of infection having occurred before the leaves were unfolded. In 1910 Stewart observed that infected fruits were still clinging to the trees on June 15, although they were usually less than half the normal size. The

fruit is often deformed and bears a circular, flattened, black lesion devoid of aecia near its base. Aecia are produced rarely.

On Crataegus

The lesion produced by *G. globosum* on Crataegus leaves is almost identical with the rust lesions on apple foliage. The red border about the margin of the spot is not so common, however, and the aecia are rarely arranged in the form of a circle (fig. 148).

The twigs of Crataegus are not commonly affected by this rust, but an occasional twig infection has been observed. The lesion is yellow,

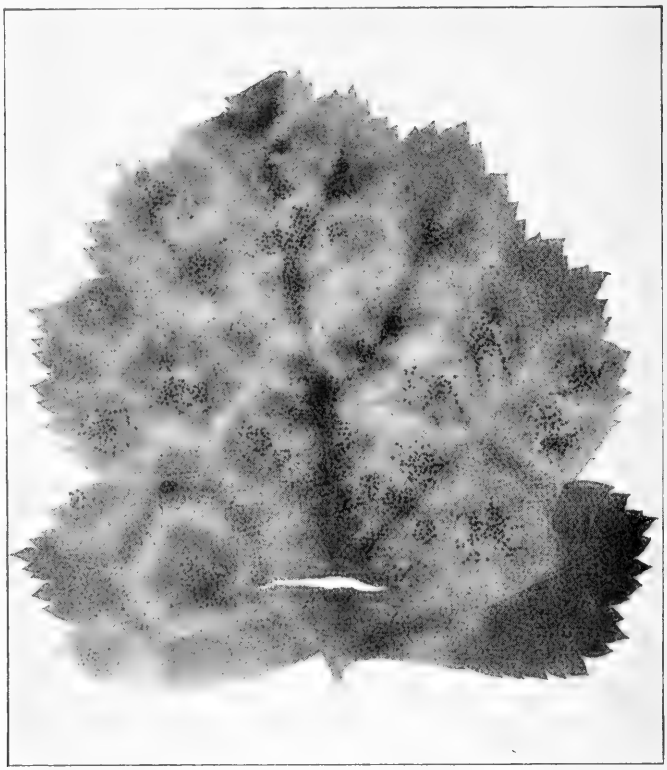

FIG. 148. CRATAEGUS LEAF ARTIFICIALLY INOCULATED WITH GYMNOSPORANGIUM GLOBOSUM
The groups of pycnia are apparent in the lesions

similar to that on the leaf, but practically no swelling of the twig is apparent. Pycnia are produced in this discolored area, followed later by aecia (fig. 149).

Infected fruits have been found, but these are not common. Here again a yellow spot is formed but little or no hypertrophy results. The pycnia and the aecia follow in the same lesion.

FIG. 149. AECIA OF GYMNOSPORANGIUM GLOBOSUM
The aecia are developing from the under surface of Crataegus leaves. The stem and the leaf petiole are also affected

ETIOLOGY

Nomenclature

The fungus now known as *G. globosum* was first named by Farlow in 1880. He gave it the name *G. fuscum* var. *globosum*, but later (Farlow, 1880) changed the name to *G. globosum*.

Life history

The details of the life cycle of this species are almost identical with those of *G. Juniperi-virginianae*. The aeciospores of the two species mature at approximately the same time. The time of infection of the cedar has not been determined, but it is presumably during the period when the aeciospores are being dispersed.

Rust-infected Crataegus leaves were collected on September 26, 1914, and exposed to the weather in a wire screen. At this time aeciospores taken from these leaves failed to germinate. Subsequent tests were made and germination was obtained until December 15, but all attempts to germinate these spores after this date failed.

Since aeciospores will germinate during and even later than the time of their dispersal, the writer sees no reason for assuming that infection does not take place until the following spring, as Reed and Crabill assume for *G. Juniperi-virginianae*. Although the penetration of the germ tube has never been observed, there is but little doubt that it enters the stomata. The mycelium develops within the cedar leaf for a period of from ten to twelve months before any sign of infection becomes apparent.

Telial stage

Development of telial horns.— The mycelium of this species is practically identical with that of *G. Juniperi-virginianae* and there is almost a complete absence of haustoria in the young galls. The telial horns are developed from a stromatic layer in the same manner as are those of *G. Juniperi-virginianae*. They begin to develop in the autumn but it is not until early the next spring that they become far enough advanced to penetrate the surface of the gall.

In the spring of 1915 the epidermis over the papillae had begun to break open on March 29, while at that time no evidence of this breaking could be found on the galls of *G. Juniperi-virginianae*. The telial horns were apparent on April 10. No growth in plant life was evident at that time and there was still considerable ice and snow on the ground. Spores capable of germination were present in these tentacles on April 15.

The telial horns continue to increase in size so that when gelatinization first takes place they may be from 1.5 to 3 millimeters thick by from 2 to 5 millimeters broad at the base and from 6 to 12 millimeters high. The number of horns on a gall varies from one to one hundred or more. They are distributed on the gall unevenly and are chestnut brown in color. Instead of standing singly they may coalesce and form a continuous band around the gall. The horns of *G. Juniperi-virginianae* have never been seen to fuse in this way.

The first gelatinization period usually coincides with the first warm rain period after the horns are protruded, and the number of times this process may occur during a season varies greatly. In 1914 the horns gelatinized four times and fell off on May 20, while in 1915 twelve such periods were recorded before the horns became dry on June 2.

The telial horns of this species may be more than double in size when swollen, and are then thinner in consistency than the jelly-like horns of

G. Juniperi-virginianae under similar conditions. After each protrusion the horns of the latter species dry down to their normal form with the exception of the tips. In the case of *G. globosum* drying occurs until the last gelatinization takes place, at which time the horns form a solid mass of thin, jelly-like substance over nearly the entire surface of the gall, and this substance intermingles with the adjoining leaves and twigs. When drying occurs this material clings to the leaves or twigs and is pulled loose from its attachments. The galls do not die as do those of the other species, but live and fruit year after year.

The teliospores of *G. globosum* closely resemble those of *G. Juniperi-virginianae*. They are practically of the same width, from 15 to 21 μ, but are often somewhat shorter, ranging in length from 37 to 54 μ. There are also the same number of pores and these are similarly located. The spore stalks are cylindrical in form. Teliospore germination is similar to that of *G. Juniperi-virginianae* (fig. 150).

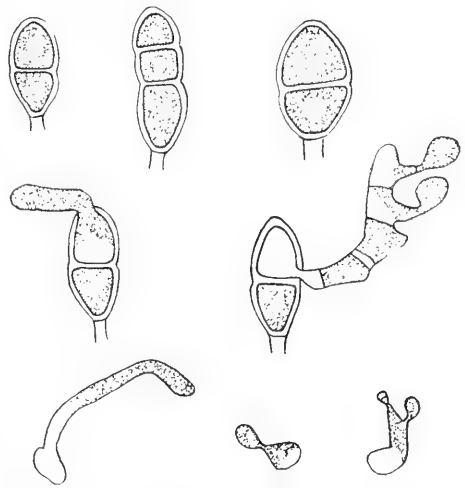

FIG. 150. VARIOUS TYPES OF TELIOSPORES OF GYMNOSPORANGIUM GLOBOSUM
Some of the teliospores and basidiospores have germinated. × 350

Accial stage

The pycnia and the aecia of *G. globosum* are similar to those of *G. Juniperi-virginianae*, the greatest difference being in their size. The size and shape of the peridial cells is somewhat different for the two species. The peridial cells of *G. globosum* are broadly lanceolate in face view and measure 15 to 23 μ by 60 to 90 μ, and are linear-rhomboid in side view, measuring from 13 to 19 μ thick. The outer wall is smooth and about 1.5 μ thick, while the inner and side walls are slightly thicker and are rugose with ridge-like papillae of varying lengths.

Acciospore germination.— Most attempts to germinate the aeciospores of *G. globosum* have yielded negative results. On two occasions slight germination was obtained, as is shown in table 3.

Inoculation of cedar trees.— Following the methods described under *G. Juniperi-virginianae*, many attempts have been made during a period of three years to obtain infection of red cedar with *G. globosum*, but thus far no positive results have been obtained.

TABLE 3. RESULTS OF AECIOSPORE GERMINATION TESTS OF GYMNOSPORANGIUM GLOBOSUM IN 1915

Number of slides	Date	Cultural solution	Temperature	Method	Percentage of germination
2	September 29	Tap water	22° C.	Suspension of spores	0
2	September 29	Tap water	23° C.	Suspension of spores	0
3	September 29	Tap water	15° C.	Suspension of spores	0
5	September 30	Tap water	24° C.	Spores in test tube immersed in an ice-and-salt bath at −4° to −6° C. for 1 hour, then allowed to incubate in tap water at 24° C.	0
5	October 2	Tap water	24° C.	Spores treated same as above but not frozen, then suspended in water and incubated at 24° C.	0
20	October 2	Tap water	−4° to +28° C.	Suspension of spores	0
2	November 8	Tap water	24° C.	Spores in suspension; taken from leaves exposed to the weather since Sept. 26, 1915	10
1	December 9	Tap water	24° C.	Spores in suspension; taken from leaves exposed to the weather since Sept. 26, 1915	2 spores germinated (only a few spores were present in this mount)

THE DISEASE CAUSED BY GYMNOSPORANGIUM CLAVIPES

The rust fungus *Gymnosporangium clavipes* causes a disease of quince, Crataegus, and cedar, which is commonly known as *quince rust*, *Crataegus rust*, or *cedar rust*. The fungus is native to North America and was first studied in some detail by Farlow (1880). It is widely distributed in eastern and central United States but is of little economic importance except on the quince. The writer observed a severe outbreak of quince rust in western New York in the summer of 1912.

The chief source of loss from quince rust is due to the misshapen or stunted condition of the diseased fruit. Twig infections also are common and these result in the death of the shoots affected.

SYMPTOMS

On cedar

On cedar the lesions of *G. clavipes* are confined to the twigs, and are less conspicuous than those of the other two species herein described. This species forms no large pendent galls, and in the early stages, as well as in many of the later ones, there is no noticeable hypertrophy of the affected twigs (fig. 151). A fusiform swelling may often occur, however, producing roughened areas on the bark (fig. 152). The affected areas may vary from 1 to 30 centimeters or more in length, but it is difficult to detect the early stages of infection of cedar until the telial sori emerge in the spring from the diseased areas. The telial sori are small, hemispheric, and orange-brown in color, and may also occur on the young shoots among the leaves. They gelatinize in early spring, and, as is true of the two preceding species, they finally dry and fall off. The fungus continues to fruit from the canker year after year.

On quince

Although quince leaves are not commonly affected by *G. clavipes* in nature, infection has been produced artificially on several occasions. The veins alone are attacked and often become swollen to double their normal size. The swelling of these veins causes the leaves to curl. The lesions are not accompanied by a change in color, as is the case with infected areas of apple or Crataegus leaves and of quince leaves affected by *G. globosum*. Pycnia are produced in longitudinal rows along the affected veins, similar to those described for *G. globosum* on pear foliage, but no aecia have ever been found. The leaves are finally killed and soon fall after the aecia are produced on the stem below.

In the spring the terminal buds of quince shoots are often attacked, the growth of affected twigs is retarded, and an increase in diameter occurs. The foliage is stunted, as in the case of the rust on apples. Pycnia and

Fig. 151 Fig. 152

FIG. 151. CANKER SHOWING TELIAL SORI OF GYMNOSPORANGIUM CLAVIPES

FIG. 152. CANKER CAUSED BY GYMNOSPORANGIUM CLAVIPES

The diseased area has a roughened appearance and is slightly enlarged as compared with the stem above and below

characteristic aecia appear later. Affected twigs die at the end of the season. On diseased quince fruit the affected part is often much enlarged, and in this area pycnia and aecia develop in abundance.

On Crataegus

The symptoms caused by *G. clavipes* on Crataegus are almost identical with those on quince. Although the leaves are rarely attacked, diseased leaves become curled and finally die without producing aecia (fig. 153).

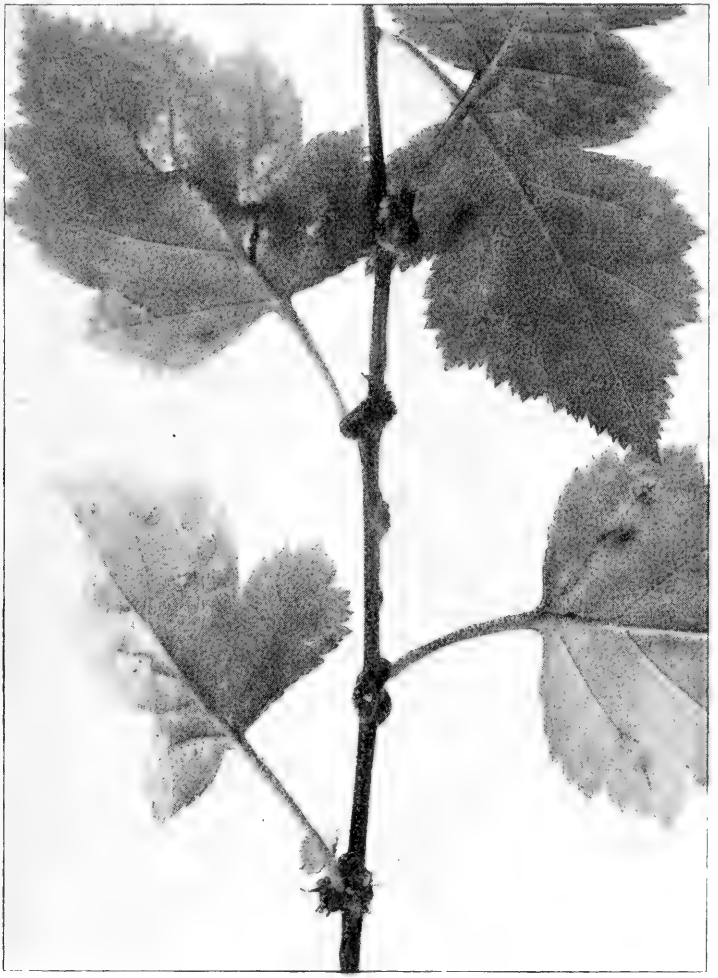

FIG. 153. GYMNOSPORANGIUM CLAVIPES AFFECTING LEAVES, PETIOLES, AND STEMS OF CRATAEGUS
These infections were produced by artificial inoculation

The stems, the leaf petioles, and the fruit are attacked commonly, and hypertrophy of the affected area occurs without change in color. Pycnia and aecia are produced in great quantities (fig. 154). The hypertrophied area is in some cases confined to only one side of the stem or the fruit.

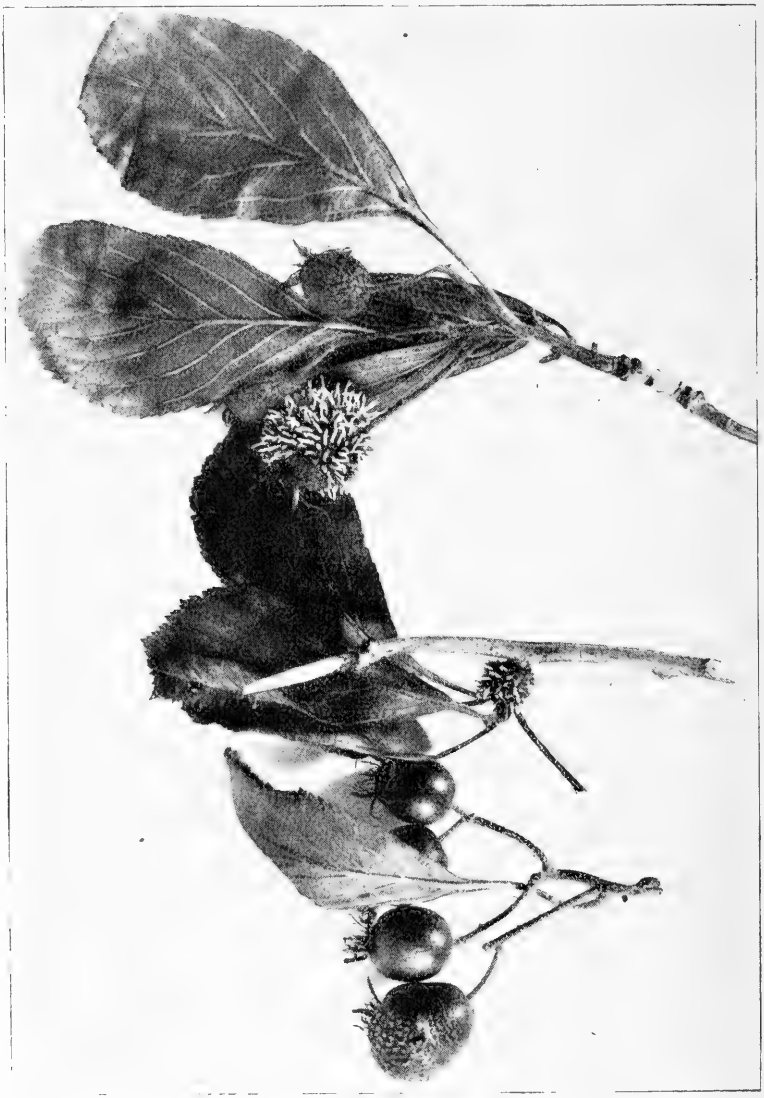

FIG. 154. FRUIT OF CRATAEGUS, SHOWING AECIA OF GYMNOSPORANGIUM CLAVIPES PROTRUDING FROM THE SURFACE

The thorns are often attacked and enlarge to double their normal size. The fungus may extend from an infected thorn into the twig at the base, and form a canker in which aecia may be produced in abundance late in the season. On October 12, 1915, a specimen was received from Romulus, New York, which bore fresh aecia in a canker that had developed at the base of a thorn.

ETIOLOGY

Nomenclature

This fungus was first named *Caeoma* (*Peridermium*) *germinale* by Schweinitz in 1832, and was given the name *G. clavipes* by Cook and Peck in 1873. Since the latter name is the first applied to the telial stage, it is the one now commonly accepted.

Life history

Only a small amount of literature has appeared which has a bearing on the origin and development of the telial stage of *G. clavipes*. This may be due, in part at least, to the fact that the disease causes little or no malformation on cedar.

Judging from analogy with other species, it is assumed that infection takes place in the late summer and autumn when the aeciospores are scattered; but no evidence of a diseased condition becomes apparent until the appearance of the telial sori. The sori develop on the two-years-old twigs and are apparently the result of infections of the previous year. This is in accordance with the process in the preceding species. The incubation period of this species is the same as that for *G. globosum* and *G. Juniperi-virginianae*; the infections that occurred during the summer and autumn of 1913 did not appear until the spring of 1915. The mycelium, which is similar to that of the other species, collects in masses beneath the corky exterior covering of the cedar twig, and from these stromata the spores arise and produce the telial horns (figs. 155 and 156).

Telial stage

Development of telial sori.— The first evidence of infection by *G. clavipes* is the appearance of the mound-like telial sori. These were first noticed in 1914 on April 22 and in 1915 on April 15. In 1914, however, the first basidiospores were formed in nature on May 5, while in 1915 some were produced on May 1. The telial sori appear on what seem to be normal and healthy twigs (fig. 157). They may be found emerging from the bark of branches of all sizes. In most cases little or no hypertrophy is noticeable, but in the older twigs slight fusiform swellings are developed.

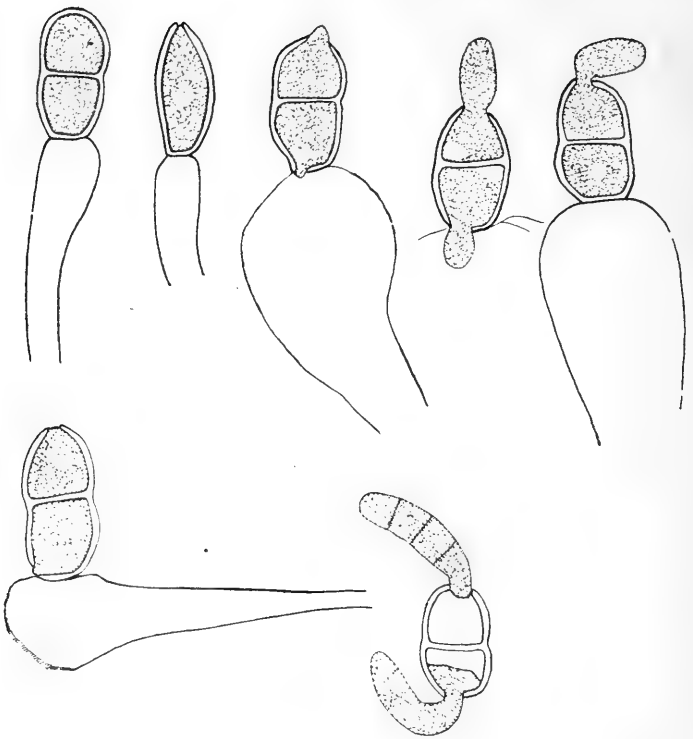

FIG. 155. TELIOSPORES AND TELIOSPORE GERMINATION OF GYMNOSPORANGIUM CLAVIPES
The spore stalk disappears at the time of germination of the lower cell. × 350

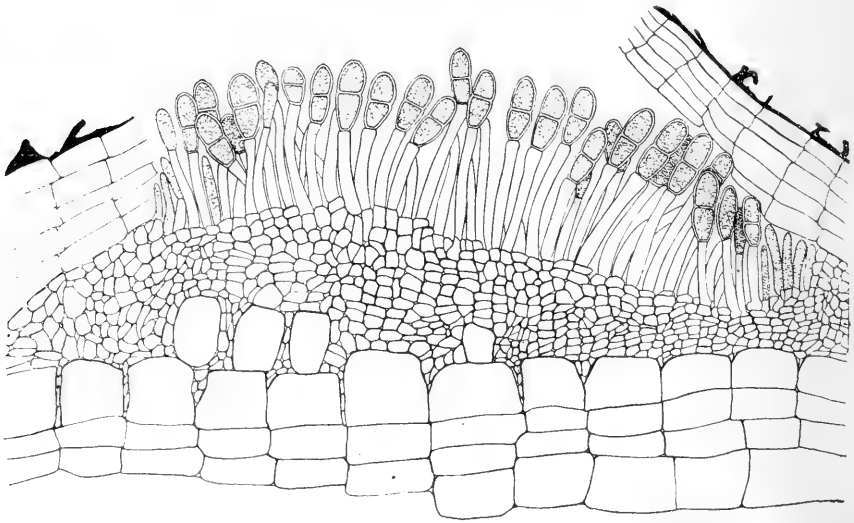

FIG. 156. A TELIAL SORUS OF GYMNOSPORANGIUM CLAVIPES
The sorus is just breaking through the cork tissue. × 220

The telial sori are decidedly different from the telial horns of *G. Juniperi-virginianae* and *G. globosum*. Instead of being long and of small diameter they are usually short and dome-shaped. These sori may be of various widths and they often coalesce and form a ring entirely around the twig. They are orange-brown when dry but become lighter-colored when gelatinized. In the latter condition they have a very soft, jelly-like consistency. After one or two gelatinizations the jelly-like substance spreads over the branches and the leaves, but later it becomes dry and drops off. The telial sori never recover their original shape. In 1914 there was a period of heavy precipitation from June 20 to June 22 and the sori did not regain their normal form after that time. In 1914 there were four gelatinization periods as compared with eleven in 1915. During several of these periods of gelatinization few or no basidiospores were formed. Numerous cankers caused by this pathogene have been under observation since the spring of 1913, and each year telial sori have

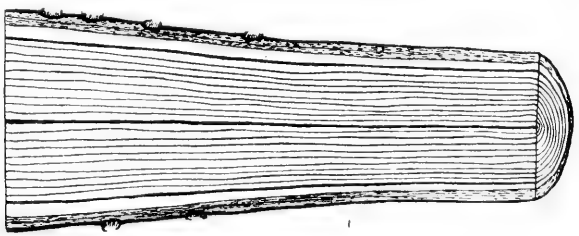

FIG. 157. DIAGRAMMATIC SECTION OF CEDAR TWIG AFFECTED WITH GYMNOSPORANGIUM CLAVIPES
The relative size and position of the telial sori are shown

developed in the cankered areas. Undoubtedly the cankers were formed several years previous to 1913.

Teliospore germination.— The teliospores of this species are capable of germinating at about the same time in the spring and under the same conditions as those of *G. globosum* and *G. Juniperi-virginianae*. The curve in figure 142 (page 523), and the discussion of methods and results on page 522, apply to this species also.

The spores of *G. clavipes* differ slightly from those of the other two species. They vary in length from 29 to 50 μ and in width from 17 to 25 μ. They may be slightly constricted at the septum, rounded or acute at the apex, and obtuse at the base. The wall is yellow and is from 1 to 2 μ thick, being slightly thickened at the apex. The pedicels may vary in diameter just below the spore from 7 to 50 μ, depending on the degree of swelling. Each cell has but one pore, the pore in the upper cell being in the apex and that in the lower cell being on one side near the base of the spore.

Spores of *G. clavipes* are peculiar in that often the germinating spores no longer have their spore stalks attached. It has been found that these stalks may be present if only the apical cell germinates, while, on the other hand, if both cells germinate the pedicels are never present or at least have not been seen. As soon as the basal cell begins to germinate, the side of the spore stalk nearest to the germ pore enlarges rapidly. The swelling continues until the wall of the stalk just below the germ pore finally disappears. Often before this stage has been reached the opposite side of the pedicel wall begins to disappear, so that soon only small remnants of the wall remain clinging to the spore. On certain slides on which spores were placed to germinate, absolute alcohol was added when the process of germination was only partially complete. The alcohol extracted the water, and the stalk returned to its normal shape and size. After the wall of the pedicel had become invisible it failed to return to view on the addition of alcohol. Apparently the lower promycelium develops at the base of the spore and thus displaces the pedicel. It is probable that the disappearance of the spore stalks when germination occurs accounts for the complete destruction of the telial sori as mentioned above. Numerous observations have been made to determine whether or not a similar phenomenon occurs in *G. globosum* and *G. Juniperi-virginianae*, but this has never been found to be the case. In these species the promycelium develops near the septum, so that it is not obstructed by the pedicel.

The disintegration of the pedicel in *G. clavipes* has been noticed also by certain other writers. Farlow (1880) states that when quickly swollen, especially by the absorption of reagents, the inner part of the pedicel expands more quickly than the outer part, so that the latter is ruptured just below the spore, leaving a hyaline ring surrounding the pedicel at the base of the spore. Farlow's explanation of this phenomenon seems logical so far as it goes, but it is not clear why this process takes place only when it accompanies the germination of the lower cell.

The methods of ejection and germination of the basidiospores of *G. clavipes* are identical with those described for *G. Juniperi-virginianae*.

Throughout a period of three years numerous attempts were made to produce infection with spores of *G. clavipes* on red cedar trees, but only negative results were obtained.

Aecial stage

The conditions influencing infection and the development of pycnia and aecia of *G. clavipes* are similar to those for the other two species. Both fruiting structures resemble closely those of *G. Juniperi-virginianae*. The pycnia, however, are about one-fourth larger. The peridium and

the peridial cells, together with the size of the aeciospores, serve as the distinguishing features. The aecia are much broader than those of *G. globosum* and the aeciospores measure from 21 to 32 μ by from 24 to 39 μ.

The peridium of *G. clavipes* is white, while those of the other two species are slightly yellowish. The peridium splits longitudinally, in some cases to the base of the cup, but the strands may be several layers of cells in width. These strands may either stand erect or become more or less recurved at their extremities. Kern (1911:455) describes the peridial cells as follows:

> Peridial cells seen in both face and side views, polygonal-ovate or polygonal oblong in face view, 19–39 x 45–95 μ, rhomboid in side view, 25–40 μ thick, outer wall moderately thick, 3–5 μ, inner wall very thick, 13–23 μ, coarsely verrucose with loosely set, large, irregularly branched papillae, side walls verrucose on inner half similar to inner wall.

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