Technical and Bibliographic Notes / Notes techniques et bibliographiques

The Institute has attempted to obtain the best original copy available for filming. Features of this copy which may be bibliographically unique, which may alter any of the images in the reproduction, or which may significantly change the usual method of filming are checked below.

- Coloured covers / Couverture de couleur
- Covers damaged / Couverture endommagée
- Covers restored and/or laminated / Couverture restaurée et/ou pelliculée
- Cover title missing / Le titre de couverture manque
- Coloured maps / Cartes géographiques en couleur
- Coloured ink (i.e. other than blue or black) / Encre de couleur (i.e. autre que bleue ou noire)
- Coloured plates and/or illustrations / Planches et/ou illustrations en couleur
- Bound with other material / Relié avec d'autres documents
- Only edition available / Seule édition disponible
- Tight binding may cause shadows or distortion along interior margin / La reliure serrée peut causer de l'ombre ou de la distorsion le long de la marge intérieure.
- Blank leaves added during restorations may appear within the text. Whenever possible, these have been omitted from filming / Il se peut que certaines pages blanches ajoutées lors d'une restauration apparaissent dans le texte, mais, lorsque cela était possible, ces pages n'ont pas été filmées.

- Additional comments / Commentaires supplémentaires:

This item is filmed at the reduction ratio checked below:
Ce document est filmé au taux de reduction indiqué ci-dessous.

<table>
<thead>
<tr>
<th>Reduction Ratio</th>
<th>10x</th>
<th>14x</th>
<th>18x</th>
<th>22x</th>
<th>26x</th>
<th>30x</th>
</tr>
</thead>
<tbody>
<tr>
<td>Checked</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
The copy filmed here has been reproduced thanks to the generosity of:

National Library of Canada

The images appearing here are the best quality possible considering the condition and legibility of the original copy and in keeping with the filming contract specifications.

Original copies in printed paper covers are filmed beginning with the front cover and ending on the last page with a printed or illustrated impression, or the back cover when appropriate. All other original copies are filmed beginning on the first page with a printed or illustrated impression, and ending on the last page with a printed or illustrated impression.

The last recorded frame on each microfiche shall contain the symbol "—" (meaning "CONTINUED"), or the symbol "▼" (meaning "END"), whichever applies.

Maps, plates, charts, etc., may be filmed at different reduction ratios. Those too large to be entirely included in one exposure are filmed beginning in the upper left hand corner, left to right and top to bottom, as many frames as required. The following diagrams illustrate the method:

1 2 3

4 5 6
On the Biology of Fomes Applanatus
(Pers.) Wallr.
On the Biology of Fomes Applanatus
(Pers.) Wallr.

By

J. H. WHITE, M.A., B.Sc.F

A Thesis submitted in conformity with the requirements of the Degree of
Doctor of Philosophy in the University of Toronto.
ON THE BIOLOGY OF FOMES APPLANATUS
ON THE BIOLOGY OF Fomes Applanatus.

BY

J. H. WHITE, M.A., B.Sc.E.

I. INTRODUCTION.

II. SPECIES INVESTIGATED.

(a) Identity.
(b) Hosts.
(c) Related species.

III. SPORE STUDIES.

(a) Spores.
(b) Sporophore.
(c) Spore production and discharge.
(d) Secondary spores.
(e) Spore germination.

IV. CULTURAL STUDIES.

(a) Historical.
(b) Tube cultures.
(c) Cultures on wood.

V. DECAY.

VI. PARASITISM.

VII. SUMMARY.

I. INTRODUCTION.

The most important agents responsible for the decay of wood substance in our forests and elsewhere are undoubtedly those plants comprising the autobasidiomycetous group of fungi, and of these the poly pores cause the most destruction. The foundation work in this field was laid by R. Hartig, and he has been followed by many investigators both in Europe and in America—von Schrenk, Spaulding, Meinecke, Hedgcock, Long, Weir, Ward, Munch, Faul, Atkinson, Buller, and others. While much of the work of these investigators would probably
be substantiated by more exacting methods than they have employed, there is one general weakness in method throughout in that the identification of causal agents has been carried out almost solely on the basis of proximity of attacking bodies; in contrast to the investigations of other plant diseases there has been very little work by the application of bacteriological methods to establish the cause and effect by cultures and inoculations. At least there is very little indication of this in the literature published on the subject.

Among the many polypores that attack our structural and standing timber there is none more common owing to the large size of its potential gregarious brackets, more frequent than the species _Elenia maculata_, more generally known as _Fomes applanatus_. It is very widely distributed, being found throughout Canada and the United States, and within this territory is of very common occurrence. In the hardwood localities where it occurs its attacking bodies are to be seen in great abundance on tree trunks, stumps, dead limbs and logs. It grows more frequently on deciduous than on coniferous species, and while it usually attacks dead wood it also found quite extensively on living trees. With its wide distribution, common occurrence and rapid growth, it is responsible for the decay of very large quantities of wood annually. Because of its frequency, many references are made to this fungus, but strangely enough, aside from Head's study [20] on its relation to a decay of cottonwood, no extensive investigation has been heretofore undertaken on the fungus. This may be accounted for by the fact that it ravages in Europe do not appear to the same extent as in America, consequently receiving little attention there, or because of the retention of statement of opinion expressed by certain pathologists that the fungus is a pure saprophyte. To this must be added the very important fact that in dealing with the question of parasitism versus saprophytism of wood destroying fungi, there have been a lack of reliable criteria for distinguishing between the two, and so there have been inconclusive grounds for combating any widely accepted view either one way or the other.

The present investigation of _Fomes applanatus_ compares three main lines of inquiry - a study of the action of the fungus, a determination by the application of cultural methods as to whether it is really responsible for the rot feature it seems to cause, and to investigate in relation to the larger subject of host relationship the possibility of finding some reliable and definite criteria by which we may distinguish parasitic action on wood from saprophytic action.
ON THE BIOLOGY OF TOMES APPLEMUSES

II. SPECIES INVESTIGATED

All Identity. Like many other plants of wide geographical range this fungus exhibits considerable variation in its morphological characters, and at times its identity with the north European Tomes applanatus has been questioned. Thus Moore (40) considers it an entirely distinct species a position based on the creation of the specific name melilotina in 1876 by Levillier (27) on material sent him from northeastern America. It is of interest to note in this connection that Levillier found specimens in the same consignment which he regarded as being identical with the European F. applanatus; that is, in one lot of American plants sent to him he regarded some as being identical with the European F. applanatus and others as belonging to a new species, restricted to America, and named by him Polyporus melilotina. The differences noted by Levillier had to do with the colour of the cap and the pores and the width of the fertile border underneath. However, American mycologists (including Moore) today consider that Levillier was wrong in so far as he recognized two species from America, and hold that all of our plants belong to the same species whatever we may call it. A study by Atkinson (12) in 1908 would appear to establish its identity with the European form, thus reducing P. melilotina to a synonym—a view contrary to that held by Moore, as already stated, who regards our form as different from the European and restricted to America. The writer has examined hundreds of hunting bodies in this region, and finds that the characters of the trimming body are fully as variable as stated by Atkinson. In particular there is much variation in the width of the fertile band, as illustrated in Fig. 4, moreover on the same plute the band is wider early in the growing season than later; it is generally wider in one wet old pile than in old ones; occasionally one finds narrow and wide banded plects growing on the same log, though this is not the rule. Further, an examination of the Sylkow European material in the herbarium of the University of Toronto has brought out no criterion for separating it from the New World form. Neuman (33) in a very recent study, also considers our species identical with the European. A careful weighing of the evidence seems to show that there is little doubt of the identity of the European and the American forms, at least as yet no constant feature has been described that would distinguish between the two, and I quite agree with Atkinson in relegating P. melilotina to the rank of synonymy and in calling our plants Tomes applanatus.

Hence various painted forms of motions are on record by different writers. Earle and Sewarum (11) and their Host Index recorded 4 or
F. applanatus on certain species belonging to some of the genera named above.

In this region, this fungus seems capable of destroying the wood of any species of deciduous tree, and a list of its hosts includes practically all the species of our local flora. To these may be added three species of conifers, viz: Tsuga canadensis—stumps and wood on the ground, in localities near Toronto; Picea Stroblos—planking supporting a lawn, Toronto; Picea (probably P. rubra)—bridge timber in Adirondacks, N.Y., collected by Professor J. H. Lamill, and dam timber in Quebec, collected by Mr. A. W. McCallum.)

While there are many references scattered throughout the literature with regard to the association of Fomes applanatus with living trees, no lists, with the exception of some inadvertent records, have been published from this distinctive point of view. Heald (26) in 1900 reported finding it on cottonwood. Numman (33) records it on apple, oak, cottonwood and willow; while Hedgecock (21) enumerated Lepidobalanus strychnifolia, Pyrus malus, Morus rubra, Populus tremuloides, P. trichocarpa, Quercus rubra, Acer saccharum.

My list of its occurrence on living trees includes the following species:

Acer saccharum.
A. saccharum.
A. saccharum.
Acer platanoides.
Betula alba var. papyrifera.
B. lutea.
Carpinus caroliniana.
Fagus grandifolia.
Gleditsia triacanthos.
Liriodendron tulipifera.
Morus alba.
Populus alba.
P. balsamifera.
P. grandidentata.
P. nigra var. italica

**15. Related Species**

The genus *Fomes* as defined by Murray (30) includes several other representatives in America, and it is interesting to
note that there is good reason for thinking that at times all of these may be parasitic. Two of them, _E. fasciata_ and _E. tormata_, are tropical or subtropical forms, appearing to replace respectively the northern _fomentaria_ and _aplanaata_. Of _E. tormata_ little is known, though said to be common on deciduous wood and widely spread throughout the tropics; Petch (37) reports that "as a rule it is merely saprophytic (in Ceylon) but several instances have been noted in which it is a wound parasite", notably on _Acacia decurrens_. A form from Nicaragua and Panama standing very close to _tormata_, if indeed distinct, has been differentiated as _E. Linnellii_. Fawcett (16) has reported that _E. fasciata_ is frequently a parasite of orange trees and water oaks in Florida; it also occurs on dead wood. _E. lobata_, a species found from New York to Iowa and south, but so far not recorded for Ontario, occurs on discoloured trunks of certain deciduous trees, especially the white oak, as well as perhaps more commonly on dead deciduous wood. Of it Murill (30) says, "Facts thus far collected indicate that _E. lobata_ is a southern form and confined to a much more restricted area than _E. megaloma_, within this area it is often abundant and quite destructive to the oak, its favorite host." _E. fomentaria_ (recently elevated to a new genus, _Klingiella_, by Murill on account of the hyaline character of its spores) very abundant in Canada and the United States, especially on birch and beech and sometimes maple and poplar, is regarded as a parasite by American pathologists. It also is native to temperate Europe, where it has long been regarded as a parasite on the hardwoods. Thus, whatever we may consider _Fomes applanatus_ to be, there is a general uniformity of opinion that the species commonly grouped with it are to be classed as wound parasites. A return will be made to this subject later on in this paper, but an account will first be given of cultural studies and of the biology of the spore.

### III. Spore Studies

My investigations on the spores have revealed many features of interest, especially in connection with their organization and their discharge. I have found no spores of any kind produced by the mycelium either in nature or in cultures, nor are there any references to such elsewhere in the literature. Some observers have claimed that there are conidia growing on the upper surface of the pileus referred to here in the section entitled "Secondary Spores," but so far as my observations go there are none but basidiospores and these are borne only on the walls of the pores where they regularly belong.
(a) Spores: The basidiospores are unicellular, 7-9 µ long by 5-6 µ wide, and dull reddish-brown in colour. They are broadly ovate with one side more convex than the opposite half and the apex broadly conical but in dried spores appearing truncated. A very large central globule is present. The spores are smooth according to some writers and echinate according to others. Atkinson (2), who was the first to investigate the nature of the spore wall, says: "The spore wall is hyaline or nearly so, with numerous perforations into which it appears that the brown or yellowish-brown content of the spore projects." According to him those who have described the spores as echinate have been misled by the appearance of the numerous dark ends of the perforations as seen in a surface view of the wall, which he holds to be thick as well as hyaline. But a study of the spores shows that Atkinson has not properly interpreted their structure. In studying their development, we find that the basidiospore starts out with a thin hyaline wall, and then that later within this original thin hyaline walled basidiospore a rough coated, thick and yellow walled endospor is formed. The spore "wall" in one sense then is accordingly double. As the endospor is more shortly elliptical than the original basidiospore, the tip of the latter is not occupied and this hyaline tip being thin walled and without supporting contents usually collapses. This gives to the mature spore the "truncated" appearance invariably noted.

Regarding the attachment of the spores, two views have been held: various mycologists have assumed that the spores were attached by their narrow pointed ends to the sterigmata, since their descriptions regularly speak of ovoid spores, "truncated at the base." This view has been taken by Patouillard (30), Bresadola (8) and others. Atkinson, however, on critically examining the shapes of the discharged spores, concludes that the older views are wrong, that the narrower end is the apex or distal end, and that the spore is "attached to the sterigma by the side of the broad end opposite the more convex side of the spore." One wonders whether any of these botanists have ever observed the spores in situ, for razor sections made through the new pore layer of an actively sporulating fruiting body reveal spores in a stages of development attached to basidia, leaving no question as to the mode of their attachment, and establishing by direct observation the correctness of Atkinson's conclusion that the so-called "truncated base" is in reality the apical end of the spore.

(b) Sporophore: The sporophores of F. apllnatus are perennial and so a new tube layer is formed during the growing season of each year of it life. In nearly all cases a tube layer is formed sometime during the
first season, the time of its formation being contingent on the organization of the contextual foundation on which it is laid. The sporophore may vary in width from an inch or two up to four or five inches before the tubes appear, and may attain a growth of eight inches in width and five inches in depth before the end of its first season. The life of the sporophore is short when compared with such a form as F. ignitae, in some fruits of which as many as 80 annual layers have been counted (3). The fruiting bodies of F. applanatus under apparently normal conditions may die at the end of the second or third year, recalling in this respect its close relative F. lobbatus which lasts but a single season, but which organizes, however, a new pilaen immediately beneath the dead sporophore of the preceding year. The average life of the sporophores of F. applanatus in this region is four or five years, though occasionally one may find fruiting bodies showing as many as eight or ten layers of pores.

The organization of the second and succeeding pore layers is almost unique in that the layer is initiated by the formation of a sterile layer which completely covers the exposed surface of the pores of the preceding season; it is on this layer that the new pores are formed. Of our native perennial polyopes Famittoria laminita is possibly the only other one that exhibits such a phenomenon. This layer begins to form with the opening of the growing season, and by the end of April the pores are indicated. In this locality a tube length of 1.40 inch is commonly found by the first or second week in May, and the fall of spores from the new hymenial surface has already commenced. In this connection it may be stated that Butler (10) found P. squamaeus discharging spores when the tubes were only 1 mm. long. The growth rate of the tube layer is at first comparatively rapid, the layer often measuring 0.8 inch in thickness by the end of July; after that growth slows down very considerably, gradually becoming imperceptible. It may be presumed, however, that some growth continues to take place throughout the rest of the season.

10. Spor Production and Discharge: As an essential part of my studies on the spore production and spore discharge of Fomes applanatus, continuous observations were made on the same fruiting body throughout the years 1915 and 1916, extending over the full twelve months of each year. From early spring until late in autumn, spore traps were set daily under this one sporophore; during the winter months the spore traps were exposed without interruption, but were collected weekly instead of daily, as it was found that daily visits were entirely superfluous. In addition to the unbroken series of observations on this one fruiting body throughout two consecutive years, collections of data relative to spore discharge were made regularly for longer or shorter periods of time during the summer months from many other specimens.
One of the most noteworthy results of this work has been the discovery that the period of spore discharge begins early in May and continues without interruption up to the first heavy frost in late October or early November, when it suddenly ceases—except for a few spores which may fall any time throughout the winter and to which further reference will be made, and in this respect establishes a new record. Spore discharge, in brief, in the case of _Fomes applanatus_ continues for approximately six months—probably a new record for all fungi. The only approach to this prolonged spore fall for a polypore under natural conditions known to the writer is the case of _Polyporus squamosus_, in which species Butler was astonished to find discharge going on for sixteen days, and estimated three weeks as the probable limit. During this period of approximately six months the liberation of spores apparently never ceases, and is remarkably uniform. When spore fall first commences, the deposit is rather scanty for a few days, but even then is quite evident to the unaided eye. Soon, however, a degree of daily deposit is reached which does not seem to vary much for the balance of the season. A marked increase that may be observed is in the months of July and August. The daily slide collections for two seasons showed invariably their usual coating. Changing slides at regular intervals throughout the day and even throughout the night likewise gave no indication of any periodicity of discharge. Day and night throughout the season the process of dispersal seems continuous. On a still day one may readily see the spores drifting away from a fruiting body in curling clouds like wreaths of very fine smoke as long as one cares to watch them. I have observed these clouds held as late as October 15. Night examinations of spore clouds were made with no other special apparatus than that of a lantern.

From these facts it is apparent that the number of spores liberated is beyond comprehension. The phenomenon of spore cloud visible to the unaided eye alone indicates their countless numbers. The many caught on a glass slide in 24 hours is ordinarily sufficient to render the aqueous solution opaque. Butler, from a count estimate in the case of _Polyporus squamosus_, a form which also exhibits spore clouds, concluded that at least 1,375,000 spores were discharged from one tube in three days. A similar calculation with _F. applanatus_ gave the incomprehensible number of 1,000,000 million spores liberated in 24 hours from a fruiting body with a reported surface of about one square foot. Now, as there may be hundreds of equally active fruiting bodies to the acre in many forest areas, especially where there is much fallen timber—the writer has counted as many as twenty recognized active fruiting bodies of _F. applanatus_ on a single cherry log in the woods—it is easy to appreciate the sum total with which some
ON THE BIOLOGY OF Fomes Applicatus.

In the discussion of the germination and continuity of spores in October or November, it was pointed out that spores which were discharged over a long period of time reached a maximum after approximately fifteen days and continued to be discharged for a period of two months. The discharge of spores, in this case, was never entirely stopped, as evidences of spore discharge were evident throughout the fall season. Any discharge that occurred in late August and early September appeared in their usual daily pattern, with the discharge day and hour remaining constant throughout the season. Discharge of spores was most severe in October, the discharge of very few spores being observed at those in November and December. Spores were never discharged in great numbers, nor were they always visible to the naked eye. The mass of spores discharged appeared to be of a more squarous form, with at least a thousand spores per square inch. Similar observations were made by a number of mycologists who, in their studies with a microscope, found the spores in hundreds of spore clouds, especially in November and December, as many as thousands of spore clouds and some

spores will drift into places where conditions are favorable for their germination and growth, and of the chance that the infection will be established itself in any susceptible tree.

But spore discharge over such a long stretch of time as six months, characterized by neither diurnal nor seasonal periodicity, means more than an enormous crop of spores; it also implies a pronounced tolerance of the sporophore to changes within wide limits in such environmental factors as light, temperature, and humidity. That the sporophores of F. applicatus develop normally in total darkness we know from Spanghel's observations on mine fungi. That spore discharge is materially affected by weather conditions in general is borne out by our own observations on identical fruiting bodies during the season of 1915 and 1916, which were markedly different climatically in this region. The year 1916 began with a rather backward spring and continued cold and wet until the end of June, but was followed by an unusually hot and dry summer; while in 1915 there was an average spring followed by a summer of average temperature but high precipitation. Yet from day to day throughout both seasons, even on successive days of contrasting weather, the density of the daily brown deposit on the glass slides set as spore traps essentially remained the same, so far as could be judged without actually counting the spores.

Also, temperature changes, except within very wide ranges, did not appear to affect spore discharge. For instance, collections made half-hourly one night in late August from 9 p.m. to 9:30 the next morning, with temperature changes from 0° C. down to 7° and up again to 12° showed a uniform copious deposit. The discharge, however, is stopped by a freezing temperature; and this appears to be an unusual phenomenon among polypores. I have not been able to find any previous record where spore fall in a polypore is abruptly terminated by frost. In this connection it may be noted that Buell (11) found that some Hymenoxycetes continued to shed their spores at the freezing point of water, though at a very diminished rate, while Overholts (33) as well as Buell states that the fruiting bodies of many Polyporaceae gathered in midwinter (January and February) throw an abundance of spores when brought into the laboratory. It is true that throughout the depths of winter, very few spores were invariably found on my slides left for a week under a fruiting body of F. applicatus, but there was good reason to believe that these were spores that had lodged and had mechanically fallen out after their exterior surfaces had lost their natural adhesiveness. This loss of adhesive power is exhibited in the case of spore deposits on slides kept in the laboratory, and lodged spores are to be seen at any time
in the winter in razor sections of the tubes. At any rate the fact remains that spore discharge is copious up to the first hard frost, and that consequently it is inconsequential no matter how mild the weather may be.

Variations in atmospheric humidity likewise were not reflected in fluctuations in spore discharge, an observation in harmony with that of Buller (11) on P. squamosa who could detect no change in spore production when the surrounding humidity was greatly changed. Spore discharge, however, is greatly affected by one factor other than frost, and that is the moisture content of the sporophore. When this is lowered below a certain minimum spore production is checked, and is not resumed until the necessary amount of water is restored. Fungi growing on bodies in unshaded positions in dry weather throw up spores sparsely, and no doubt the explanation of this is to be looked for in their low moisture content. It further happens occasionally that sporophores growing under unfavorable conditions produce few spores or none at all. It is not improbable that such sporophores are naturally sterile—a phenomenon has been observed in Coprinus, Agaricus, and other genera.

(d) Secondary Spores. Although secondary spores are produced by comparatively few Hymenomycetes, Eumaeus allawayii is stated to produce conidia on the dorsal surface of the pilus. Schultze-Mosgander (142) was the first to make this statement in 1880. Murrill in his specific description says that the upper surface of the fructifying body is conidiate-bearing and usually brownish during the growing season from the covering of conidia. This brown coating is not infrequently to be seen, but examination showed that in every case it was composed of basidiospores. These are mechanically deposited by the current of air after they fall from the hymenial tubes. This can easily be proved in such a case by covering the top with a sheet of paper which soon bears the same coating of spores. Moreover, the upper end of such an organization is not to favour spore production, because it is heavily encrusted during its first season. Young fructifying bodies in stages of development, as well as very many of other ages, have been persistently examined in the field for conidia, but without success. Likewise none of my artificial cultures produced conidia.

(e) Spore Germination. In the germination studies the usual hand drop method with Vatierghen cells was used. Various media were tried, including distilled and tap water, solutions of sugar, glucose sugar, maltose, peptone, meat extract, acids, alcohol, alcalies, etc., and graded percentage strengths. Decorations of wood and hanging drops of water containing pieces of wood were also experimented with. The greatest success was attained with two brands of domestic malt extract.
The fact remains that, although the growth is stated to have been produced in the autumn of 1828 by Schützer von Platen, it did not come to light until 1830, and its existence was not generally known until 1835.

The growing season of the fungus is indeed very long, as in the case of 
the leaf-mold, and this is probably to be attributed to the 
slow movement of the spores under 
favorable conditions. It may be 
noted that Price (38) found the spores of P. squamosus to have a 
viability of 70 days, and Miss Bayless (4) those of Polystictus 
avericolor between 11 and 17 weeks.

Every conceivable possible factor in the germination was tested out. Most of the experiments were carried out at ordinary room temperature; tests showed no acceleration or retardation by altering temperature conditions between 10° and 27° C. Tests were carried out in bright light, dull light and darkness; spores were given different lengths of time after 
spore fall to "ripen", before being tested; they were even allowed to undergo freezing outside; they were collected from natural lodgments in 
the woods at various times and tested immediately. Nor could viable 
spores be traced to those liberated at any particular period of the 
sporulating season. The Van Tieghem cells were set up without using 
water to seal them; the glassware was treated in various ways, being washed in 
alcohol, or acid, or distilled water, the results were the same. The 
hundreds of tests with reference to possible controlling factors involved 
many weeks of labour, and in the end nothing was uncovered that would 
induce a higher percentage of germination, or any germination at all from 
many slides. The seemingly erratic behaviour would appear to be ex-
plainable only on the grounds of inherent low viability of the spores.

The first signs of germination in the malt extract medium are generally 
visible in about 24 hours, seldom sooner, when a few spores put
forth their germ tubes (Text Fig. 1). A definite polarity is exhibited by the tube always issuing from the "truncated" apical end of the spore. The wall appears to be lighter in color and apparently thinner, and the apex is almost equal in diameter. In the earlier stages, in general the two habits observable: In the one the hypha grows out in the direction of the long axis of the spore for some distance, branching soon commencing, though it may be delayed till the leading hypha is some 15 times the length of the spore. In the other type, the hypha at once assumes the direction at right angles to the long axis of the spore; branching being earlier and results on the average in a more symmetrical system. Generally these types are not much mixed in the same culture, as a

appearing in separate cultures. Practically all the germination obtained in a given mount is in evidence in 48 hours, though a few belated ones are encountered; and since growth proceeds at a fairly uniform rate any particular hanging drop presents a rather orthodox picture at any given stage. The spore features and the germinating hyphal system are so characteristic that one readily notices any foreign spore or its product.
Growth is very rapid. Text Fig. 1 showing an average plant which has attained the size represented 72 hours after the spores were sown in the malt extract. Though cross walls are difficult to discern in the young plant in untreated cell cultures, branching can usually be made out to take place just below a septum. The only change observable in the spore during germination is an immediate reduction in size of the central globule and this reduction in size continues until it finally disappears. The protoplasm of the hyphae is colorless and shows minute highly refractive bodies. After four or five days vacuolation is noticeable in the older cells.

In connection with the germination tests one more fact is worthy of note. In some of the old mounts it was observed that dense fuzzy or witches' broom-like masses appeared on some of the hyphae. The same growths were encountered in some tube cultures. They proved on examination to be made up of very numerous short branches, strictly localized and of such an appearance as to lead one to expect conidia, but none were found. Their significance is unknown. Brefeld (7) noted and figured the same thing.

IV. Cultural Studies.

(a) Historical: Prior to the appearance of Hartig’s “Wichtige Krankheiten der Waldsamme” in 1874 and his “Zersetzungsscheinungen des Holzes” in 1878 but little was understood about the decay of wood; the latter thesis included accounts of seven species commonly attacking coniferous timber and six causing decay in oak. Hartig was the first to associate a specific decay with a particular fungus and in emphasizing this fact he made his most important contribution. His modus operandi involved a complete description of the fungus concerned, a minute account of the destruction of the wood, with many illustrations of the progressive microscopic and macroscopic changes. In no case was there any attempt to establish identity of the causal form by culture or inoculation.

The next contributor of importance in this field was Mayr (26) who in 1884 described in detail the action of two species of Polyporus parasitic on birch. But his methods were similar to those of Hartig and likewise included no cultural studies. This statement also applies to most subsequent work; thus in the last fifteen years, while American mycologists have given a very great deal of attention to polypores responsible for the decay of timber and of forest trees, in general the studies have had largely to do with the macroscopic and microscopic changes expressed in...
the specific rot or disease, and with preventive measures, little cultural work on the causal forms has been done.

In 1887 Ward (31) opened up a new field in connection with the study of wood-destroying fungi, by proving that such forms are capable of culture. His studies were on *Stereum hirsutum*. He first of all eliminated the spores on gelatine and agar media, using sugar or rum as a nutrient, and succeeded in obtaining an abundant growth of mycelium, the mycelium obtained in this way was then transferred to sterilized blocks of wood kept moist in containers. In the course of four months fruiting bodies made their appearance in his culturing medium, it is true, but which nevertheless sporulated. It was for the first time a basidiomycetous wood-destroying fungus was cultured on its host from spore to spore. Ward's purpose, however, was not to test the possibility of such artificial cultures. He had not in view demonstration that the activities of decay usually associated with some of these fungi were really traceable to it, but rather to show that the culturing technique employed in the study of other fungi diseases was likewise applicable in the study of the diseases of wood.

Contrary to hopes that might have been aroused by Ward's success, *Stereum hirsutum*, experience has shown that similar attempts with other fungi commonly lead to disappointment, so that, as yet, repeated successful cultures of the sporulating fruiting body as an end attained constitutes a very brief list. Little trouble is ordinarily encountered in securing spore germination and a growth of mycelium, and it is to be expected that more intensive effort will reveal the knowledge of how environmental factors conducive to fruitation. Where time and space are factors, the perplexities of technique are greatly increased, because of the difficulty of preventing drying out or of the introducing into the culture new supplies of water and nutrients without permitting at the same time the entrance of contaminating molds or bacteria. A brief review of such work that follows, only the wood-destroying forms are noted.

Biffen (5) followed Ward's studies in the following year with an account of similar work in relation to the action of *Calyptrodes* on the wood of *Aesculus*. He germinated the spores in hanging drops of sugar solution; the mycelium obtained in this way broke up into chains within nine or ten days, and these were transferred to sterilized wood blocks. Normal sporulating sporephores were produced within a month. Four of the previously Costantini and Martinelli (12) described exhibited normal fruitations of this same species obtained on wood cultures in two months.
Biffen (6) has similarly investigated *Bulgaria polymorpha*. The spores in this case were germinated in beewort gelatine, and from plate cultures sterile blocks of oak were inoculated; fruiting cups bearing ascospores appeared in three months. His paper gives the action on oak in detail, and the development of the fungus.

Falek (13) in 1902, reported culturing three agaries to the fruiting body stage, following in general, Biffen's method.

Among American mycologists excellent work on cultural investigations of xylophilous fungi has been done by Lyman, Spaulding, Buller and Zeller. Lyman's work (25) is by far the most extensive, but as his interest centred in the secondary spores of Autohiasidymycetes, the securing of fruiting bodies was rather incidental. He cultivated some 75 species of Thelephoraceae, Hydnaceae and Polyporaceae from their spores. Unfortunately the bulk of his notes was accidentally lost, but he reports that "in the majority of species studied I was able with more or less difficulty to raise basidiosporic mycelia in the laboratory." Spaulding (33) in 1905 reported culturing *Schizophyllum commune* successfully, but in later cultures of another agaric, *Lenziotes septaria*, on sterilized pieces of wood he got only abnormal sporophores which he does not mention as sporulating (44). The highly destructive *Lenziotes lepidus* was also studied in a similar manner by Buller (9) in connection with a decay of street paving blocks, and with like results. Zeller (51) cultured *Lenziotes septaria* from spore to spore. Buller (10) has given us a very interesting biological paper on *Polyergus squamosus* including a very detailed account of the structural and chemical changes brought about in maple wood by this fungus, and likewise of the responsible enzymes. Cultural studies were also made, the spores being germinated in hanging drops of malt extract and cultured on extract solidified with gelatine. In nine months, however, there were no signs of any attempt towards the formation of a fruiting body. Later, this species was cultured on blocks of wood by Price (38) who succeeded within six to ten months in getting abnormally shaped fructifications. This, though, occurred only in the case of those cultures kept in dull light, and none appeared in darkness nor in bright light. All his fructifications remained quite sterile. Miss Bayliss (4) has published a biological study of *Polystictus versicolor*, including its destructive action on wood in detail. The cultures on wood blocks produced only abnormally shaped fruiting bodies, sterile even after 17 months. Some of these were induced to sporulate later by removal from their containers and placing outside under natural conditions. So far as I can find *Polystictus versicolor* is the
first polypore to be successfully cultured to sporulation, though conditions were not wholly artificial.*

My work on *Fomes applanatus* demonstrates that it now is added to the list of wholly culturable forms, the first of the *Fomes* carrying through the cultures the procedure was first of all to grow mycelium on agar in tubes, and then to transfer portions of the mycelium to sterilized wood in large containers. It was found that the fungus never fruits on an agar medium. The mycelium was obtained from three sources: (1) spores, (2) pieces of sporophore, (3) pieces of dead wood, and thus three parallel series of cultures were carried through.

(b) *Tube Cultures.* The spores used for starting cultures were obtained from the deposits on slides set in spore traps as already described. These slides were stored in ordinary microscope slide boxes and used occasion demanded. The glassware used in the *Fomes* cultures was sterilized, the malt extract was sometimes sterilized, and sometimes it seemed to give a rather higher percentage germination when sterile, and for all practical purposes served equally well, for the sterilization of infected mounts in the many hundreds of cells employed was negligible. The hanging drops of the cells were inoculated with very few spores so that every spore in the mount could be examined as to identity. After germination, with care one plant could be picked out with a platinum loop for transference to the agar medium.

Many agar media such as oatmeal, wood, acorn, etc., were tried, and the best results were obtained with ordinary potato agar. This was made by soaking 30 grams of shredded agar overnight in one litre of water and replacing the unabsorbed water by strained thick potato water.

Growth is rapid, the threads radiating out regularly, so that after five or six days a circular snow-white patch one-half inch in diameter is present in less than two weeks the whole slant face of agar in a quarter inch tube will be covered. Further growth results in a thick up of the layer so that the earlier fluffy appearance is somewhat masked. This layer soon becomes woven into a thin leathery sheet which is enough for the mycelium to be extracted bodily. As time goes on the surface takes on a powdery look as it conidia are being formed. All my tubes examined none were ever discovered, the powdery appearance being due to the numerous excrated crystals of calcium oxalate in the witches' broom-like branches.

*Since this was written a paper by Long and Hutchins 1934 was received describing the culture of a large number of *Fomes* of wood-eating fungi on malt. Their investigations led in view the different growth of these forms in artificial cultures, alone the cultures of *F. applanatus* on malt and wood sporophore production was indicated in 40 to 60 days.*
After about a month's culture the mycelium begins to take on a yellowish tint. Generally this is observable first in the central region, gradually extending to both ends of the sheet. The yellow color darkens, usually reaching a dark brown shade, often with a paraphyses cast. Usually these progressive color differences are expressed as a rotation. At this time the growth often exudes conspicuous glistening drops of fluid. The mycelium preserves its vitality for many months. Even after the whole culture had shrivelled up hard and dry, new cultures may be started from bits of the sheet.

Tests carefully carried through to the formation of the Lunt bodies have shown that the rather tedious pure method of starting cultures could be successfully substituted by the tissue method first described by Birkett or by using pieces of decayed wood. The easier method was to take pieces from the interior of the sporophore; these could be depended upon to grow readily, and experience brought out the fact that the pieces did not even need to be sterilized by passing through a Bunsen flame, a recommendation by Spalding. In the other method of using pieces of the decayed wood, contrary to expectation, one was seldom bothered with bacteria if the smaller pieces were chosen. Both these methods were very convenient. The character of the tube cultures derived in either of the ways was different in respect from the culture arising from pure cultures on wood. As Fomes annosus did not grow on any of the wood tested it was found necessary to complete the culture on wood. For the purpose, blocks of wood after being water-soaked were placed in rice and the whole sterilized. They were then inoculated with pieces of mycelium from tube cultures, or directly with pieces from the interior or a tainting body. This latter method repeated at intervals and once ever Reproductive of practically all the hardwood genera of North America were used, and no difficulty was found in getting the fungus to grow on any of them. Certain woods such as balsam, oak, blackwood and poplar were found more or less in that they let themselves better to the technique and accordingly these were usually used in the culture on wood. Green timber as well as dry laboratory samples were used; both white and heartwood, with the fungus existing no preference. Counterpart wood of many species were experimented with, for including pieces of pine, spruce, fir, bark, hemlock, larch, cedar, hemlock, maple, and pine. Very few growths were obtained in some instances, but that was for development of a want. Even with mycelium growing on a block of wood attacked by the monilia rotting matter reached. These experiments combined with tests of mycelium led to the conclusion that certain wood is or
questionably practically immune from destruction by this
Lgs. 2, 3).

The carrying of cultures on wood through to the production of bodies in the case of such a fungus as *Fomes applanatus* is necessi-
tated by experiment with the consequent difficulties of ex-
tinction from outside and of keeping the wood specimens from
out. At first much time was lost in carving along cultures which
dried out in the course of two or six months. Fortunately, this
will grow in quite wet wood, so that we may begin the culture with
material carrying a high percentage of water. In the successful
one here wide-mouthed jars were used with about one inch of
soaked cotton batting in the bottom. The wood blocks of some six
right cubic inches in volume were first thoroughly water logged
alternately boiled and plunged into cold water to drive out all
possible. The block was placed in the jar in a slanting position
with a quantity of water added, a cotton plug inserted, and the whole set
in the autoclave by steaming for 20 minutes after 12 pounds pressure
had been reached. During sterilization water was usually lost, a
quantity originally necessary was only learned through experience.

The importance of the amount of water lies in the fact that the culture
be carried for the better part of a year at least without being re-
after incubation. Frequently the blocks during sterilization were
completely dried out except for the lower ends and such were.
This was nearly always the case with some woods, particularly
The easiest trees to bring through sterilization in a uniformly
condition were found to be basswood, poplar, and willow, and for
was accordingly largely used in all the later work.

The jars were then usually allowed to rest and for a couple of weeks
at any interference appeared. The blocks of wood were then mexed,
to the other piece, the medium from tube A already stated three parallel series were carried through, the culture running from piece of de pared wood, an another piece of fungus body. To lessen infection from foreign fungi
found advantage to lay a piece of paper loosely on the top of the
but even then it was time. Happened that spore of *Penicillum* op-
pended in a pit, then hyphae grew down through and
on the medium. Many of such jars, of course, had to be discarded
at time were on other jars to be set aside owing to drying
Dead, cut may be readily removed by placing the jar under a
covered jar, but under such circumstances it was found that ex-
ination frequently happened owing to the moisture at the upper
of the cover plug.
The growth-layers on the surface of wood are similar to that of most other plant tissues. The annual layer begins forming in the spring, and usually extends into the fall. The thickness of the layer varies depending on the species of wood and environmental conditions. The growth-layers are best observed when the wood is split open, and the layers appear as concentric rings. These rings provide information about the age of the tree and can be used for dating purposes. In colder climates, the growth-layers are usually more distinct and regular, while in warmer climates, the layers may be more difficult to distinguish. The growth-layers are a result of the tree's efforts to balance water uptake and transpiration, as well as to support the growth of new tissues.
of *F. applanata.* The hemispherical form with a small peduncle appearing in various directions is comparatively common, but such a pedicle one may often see another of approximately the same size pushing out from a small bracket before developing pycnidia. In the case of other species, those produced by *F. applanata* are never visible. As well as such occurrences on logs, the writer has noted in the fruiting body of the fungus some eight inches in diameter with a hollow space in the upper surface of a partly-rimmed, growing on the ground attached to a small tree, or located near several inches beneath. Fig. 7 shows one of the most common shapes collected from the field.

The experience of all who have cultivated wood-inhabiting fungi throughout their life cycle under artificial conditions has been that they find that the fruiting bodies practically never assume abnormal shape. A few Lamellatae, such as *Collybia clavipes,* *Cortinarius clavatus,* and *Neoboletus cornucopiae,* as an exception to this rule, do produce normal spore-bearing ascomata. Experience, however, has shown that the sporophore of these few species have been induced to fruit are not only abnormal in shape, but usually sterile. This has been attributed to various factors such as in the unnatural conditions of their environment, such as restricted air supply, light, etc. (Ward, Price, etc.). Probably no generalisation applies, and this is likely species for each form. The taken care to find with certain *Cortinarius,* that sporophores formed in a damp atmosphere. Batten found that *Collybia clavipes* develop normally whether sterilised or not. *Lactarius deliciosus* develop a spore in the absence of light (Bulter), while *Collybia alba* (Batten and Sprent) *Lactarius deliciosus* develop well in light or out of it. There is one important factor, however, that has been overlooked by many experimenters; it has been the practice to use very small pieces of wood in their cultures, and the writer is of the opinion that many failures to get sporulation from fruit bodies have been due to the fact that the piece of wood was not attached sufficient supply of food. Culturing *F. applanata* on new material in which much larger blocks, the described above are being employed.

V. Decay.

Studies on wood destruction through the agency of fungus have shown that the phenomena of decay in the case of most fungi, when compared, vary from the factors characteristic for each individual species.
as a rule, the gross phenomena alone, or those evident without the aid of the microscope, are sufficiently characteristic to enable the wood pathologist to recognize the causal agent. These phenomena cover a wide range of features. They include, for instance, restrictions as to the species of wood attacked and the selection of sapwood or heartwood, or the absence of such a choice; they include the nature and the extent of the decay within the areas involved—completeness of the destruction varying with different fungi from changes that scarcely affect the commercial use of the wood to complete solution of the wood substance. Then, too, there are changes in color, due to the color of the invading fungus-threads, to secretions by them, to secretions by a stimulated host, or to mechanical changes produced by them; the chemical changes caused by one species result in an extraction of cellulose leaving the wood darker, and others of lignin, leaving it lighter. The texture of the residual decayed mass, its colour, water content, or mode of fragmentation, are also specific in many cases. Even the method of the dissolution of the cellular elements of the wood, and the formation of otherwise of shoots or strands of mycelium by the fungi in the product of its handwork are characteristic for most species.

Fomes applanatus conforms to the general rule, and it is of special interest to note in a form that attacks so many different species of host that not only are the phenomena of decay produced by this fungus characteristic but that in the score or more species of host on which observations have been made they are essentially identical in all. It has also been of interest to discover that when F. applanatus is acting in living wood it produces one important phenomenon of decay that is not shown when acting in dead wood. Such a difference in behaviour is manifested by several other species, but apparently attention has been rarely called, if at all, to this feature.

The only account of the decay caused by Fomes applanatus found in the literature is a brief one by Heald (20) with reference to a disease of the crottlewood ascribed to this fungus. He describes the fungus as attacking certain areas more severely than others, rendering the wood soft and punky in the former and brittle in the latter, and states that chemically the action is one of delignification followed by a partial digestion of the cellulose walls. In describing the rot he says his material showed "the severely infected portions of the wood to be arranged in quite marked horizontal strata. The difference between the two regions (i.e., the cuttara and the sounder intervening wood) is so marked that at the first examination it was thought that the tree was infected with borers and that they were responsible for this effect." The earlier
The characteristic decay produced by the fungus is not mentioned, apparently having studied material in an advanced stage of decay. Indeed, there is a possibility that other fungi were associated with F. applinatus in the stage of decay described by him as indicated by the presence of characteristic black lines that run in a general transverse direction. The black lines which were mentioned as prominent features of the decomposition by this fungus show in histological sections as yellowish deposits in the lumen of the ducts and cells.

Heald suggests that these deposits represent endowments to the tree to check the advance of the fungus. The writer, in further search among hundreds of cases of F. applinatus in the field, has been unable to verify Heald's observation on this point. Heald's rule is repeated, but other evidence shows that there do occur more than one species of fungus at work. They are produced at the point of contact of two invading fungi in the case of tan color of wood destroying fungi, a phenomenon well known to pathologists.

Field observations indicate that Fomes applinatus usually begins its attacks in wounds, on a root near the collar or on the trunk, at its base, that it may with some reason be regarded as the cause of a root. It works inward to the heartwood and thence upward, and as it advances outward involving the lower sapwood. The decay is largely confined to the lowermost few feet of the tree, but may occasionally extend upward some 12 or 15 feet.

The wood attacked very early exhibits a mottled appearance with a distinct characteristic to enable the recognition of this fungus; but the mycelium forming the white threads begins to turn. The effects produced in heartwood and sapwood are the same. The appearance here described is in all probability the cause of the mycelium growing inward and outward, involving the lower sapwood. The larger the mycelium growing in heartwood, the more the sapwood, and the more the heartwood. Accordingly, a trunk windthrown or otherwise extensively attacked in any direction (Fig. 8) shows a characteristic texture with the piece removed in parallel to the radial surface. This stage of the decay, the wood is still quite hard and heavy, the color change of color being the only physical alteration evident.

As decay progresses with the fungus extending, the border of the primary light-colored area at the expense of the intervening tissue, the original regularity of the area in the more advanced stages of this process is lost.
of decay becomes less and less. The wood substance has been gradually disappearing from these portions leaving localized pockets which may eventually become almost one-quarter of an inch across. Into these spaces, at the same time, the hyphae have been steadily gathering and forming into tough leafy strands which may be picked out in their entirety, leaving channels not unlike larval borings, especially since the original rectilinear directions of the most severely attacked regions have been lost with the progress of the disease (Fig. 9). This feature of the decay agrees with Heald's observation. Since the hyphal cores are of the same whitish colour as the surrounding cellulosic elements, this phase of the work of the fungus is easily overlooked macroscopically. The uniform whitish colour is very rare in coming and indicates the final stage of decay. By this time the wood has become very soft and light in weight and rather spongy. No further destruction goes on, the complete disintegration and disappearance of wood substance being always localized.

The moulded type of rot is not restricted to Fomes applanatus; several other fungi produce a moulded rot, but so characteristic in each case as to be distinguishable from one another and from the decay of the term under consideration. Thus, F. tomentarius produces a moulded rot but it is a very much finer moulding; with the progress of the disease, however, it early passes into a uniform white rot, which perhaps in most cases could not be identified with certainty at that stage. The moulding caused by P. squamosus is very much finer still, and more in the form of white lines with the general direction tangential, not radial as in F. applanatus. In conifers it is also finer, but mostly radially, and since there is complete dissolution locally with no core of fungus threads left, the mould is a sort of pin hole or shot hole effect, as though the wood had been shot through with fine bird shot.

A study of the living wood of trees attacked by F. applanatus shows, as I have already indicated, a feature not found in dead wood. I refer to a brown discoloured zone which marks the extreme limit of advance of the fungus, making the line of demarcation from the sound and yet uninfected wood very distinct (Figs. 15, 16). In cross section the discoloured region appears as a brown band one quarter of an inch or more wide, similar in appearance to the band in living wood routed by F. comatus, though possibly not quite so sharply defined as in the case of the latter. This band is something altogether different from Heald's "black line" which he describes as running in a general transverse direction; an
which, as has already been pointed out, are commonly encountered.

Two wood-destroying fungi are at work together.

The dark colour in this band is due to a deposit of so-called "wound gum", a secretion or a decomposition product of host origin in the newly attacked by the parasite. A microscopic examination showed that the "wound gum" is most abundant in the lumina of parenchyma cells and in the vessels, though it may be found in any cellular element (Fig. 18, Text Fig. 2). It occurs in the form of yellow-brown drops, few or many in a cell and varying from points to masses large enough to occlude the cell cavities. It is absent from the normal uninvaded wood and so it is to be regarded strictly pathological phenomenon.

As the anterior margin of the creeps forward, keeping pace with the advancing hyphae, the posterior margin advances with equal rapidity leaving no trace of the disease in the tissues behind; the "wound gum" is either bleached or a part of the food of the fungus; at all events remains of it are not to be seen by the aid of any of the lunes or other microscopes employed in studies of the diseased wood.

Tyloses constitute another remarkable feature of the brown zone. I have found them in attacked sapwood and heartwood of many species in which search was made to include beech, sugar maple and red oak, but not in the wood of the apple or crowd the lumina of the vessels, containing them as with a continuous growth. The "wound gum" found in the vessels part at least, located in the growing Tyloses do not occur in the sound tissue behind the brown band. It is also striking how large extent the tyloses are seen deep by the occupying fungi - for a short distance behind the brown band may be but few traces of them left. A close examination made to discover whether or not the "wound gum" and tyloses might not be formed just before the tissues in question were invaded by the hyphae, but all the evidence obtained negatived any such appearance. The brown band is the first stage in the destruction of the wood, but more than that, the "wound gum" and tyloses are of importance in interpreting the nature of the fungus, and significance from this point of view will be dealt with in the sequel "Parasitism".
The microscopic features of wood attacked by *F. applanatus* are illustrated in Figs. 10 to 14. The hyphae seem to advance primarily along the medullary rays and vessels, more particularly the former, but all kinds of cells are penetrated. On visualizing the advance of the fungus threads as a whole, one does not perceive any particular evidence of chemotropic attraction exerted on the hyphae. Here and there one meets with appearances in the sections which could be so interpreted, but such are the exception, not the rule. The passage from cell to cell is in no way contingent on connecting pits, for the end of a hypha appears to penetrate the cell wall wherever it may happen to reach it. The hole is small at first, narrower than the normal diameter of the hypha, for the portion of the hypha filling the perforation is more or less reduced. An examination of the tissues taken from the advancing area of decay shows that the cells are perforated with multitudinous holes, the hyphae advancing parallel across the grain in close array. This wholesale perforation is very striking under the microscope and constitutes the first stage in the destruction of the wood. The perforation of the tissue is succeeded by a progressive solution of the cell wall itself. In the neighbourhood of any particular hypha there is a steady reduction of the cell wall so that the originally narrow perforation now becomes a large irregular hole, many times larger in area than at first. With the enlarging of the perforations, contiguous openings frequently merge; a cell wall at this stage presents a very much riddled and corroded appearance. The solution of the cell wall proceeds in a constant manner, but the inner laminæ disappear rather more rapidly than the middle lamella. The destruction continues in extreme cases till nothing is left but the outer parts—the angular "gussets" at cell corners and pieces of middle lamellæ. This is the stage observed in sections including the local pockets already mentioned.

The first chemical change in the wood during its destruction is a progressive delignification, as shown by the usual chemical tests for lignin and cellulose. Sections treated with phloroglucin and hydrochloric acid show a very faint red colour in the primary areas of attack; the colour increases in intensity in the tissue farther and farther away from these areas. On the application of chlor-zinc-iodide solution the wood takes on a bluish colour which is deepest in the primary areas of decay. But the delignification is never wholly complete, for in the most thoroughly rotted wood, in the centre of large strands of hyphae there are always some fragments which still give the reaction for lignin. The cellulose resulting from delignification is in turn finally dissolved, but only locally completely so.
In working out the diagnostic marks of the decay caused by
*F. applanatus* certain pitfalls have been discovered when checking
results over by culture tests—pitfalls that are doubtless to be Encountered
in the study of all similar fungi, and which must be carefully avoided.
Descriptions of decay are to be of value. The most important of these
has to do with the recognition of the action of secondary agencies—
thereby finding of a fruiting body on a diseased area is by no means
evidence that all of the effect apparent is due to this one fungus, nor, even
in such a conclusion be extended to most cases in which the effect is
uniform accompaniment of a certain species of fruiting body. Of the
diseased areas where the rot is of a very distinctive type such an association may
be accepted as fairly adequate evidence, though even in such cases caution is
necessary. Most of the wood-destroying fungi act rather slowly, and
many years often elapse before the sporophores appear, and during
this time secondary purely saprophytic bacteria and fungi have ample
opportunities to make their entrance. Cultures made from most wood-
advanced stage of decay almost invariably reveal the presence of
secondary agencies, thus raising a question as to the value of
descriptions of decay which so commonly are based on late stage,
leading to the conclusion that some of the culminating features of
are often to be attributed to other organisms than the primary. In
such cases, doubtless, the earlier marks are much more distinctive
of greater value in a diagnosis of the disease than the later. The
situation certainly applies to *F. applanatus*.

In correlating decay and causal agent in the case of *F. applanatus*
the most extensive tests were made on Lombardy poplar—a freshly
planted tree that had borne fruiting bodies of *F. applanatus* for years and
had been infected by the other species. Pieces taken from the inner core
selected from the upper limits to which the disease had progressed,
which showed the characteristic mottling, were cultured on potato
agar and on sterile pieces of wood through to fruit and spore production
and no question remained as to the identity of the causal agent—
cultures made from such a source contamination by bacteria or
ticks rarely appears. Cultures made from mottled areas in many
woods likewise always showed an almost constant freedom from
ticks and bacteria. On the other hand, cultures made from wood
showing uniform white stage of decay sometimes practically nowhere
appear. It is reasonably certain that we may conclude that causing
destruction in the case of *F. applanatus* after the uniform white stage
reached may in part be the work of combined agencies.
The distinction between parasitic and saprophytic fungi is based on the nature of their nutrition. But between strict parasites, which are completely dependent on living hosts, some of them such as the F. graminearum are cultivable on dead substrata, and strict saprophytes, which undergo none of their development in vital connection with a living host, there is a vast assemblage of forms that exhibit the possibilities of either a parasitic or a saprophytic mode of existence. Further, these forms, in their greater tendency or preference towards the one or the other relation, present such a variation that the extremes of strict parasitism and strict saprophytism are bridged by a closely intergraded series. These intermediate forms have been provisionally classified as homosaprophytes or facultative parasites, that is, those normally saprophytic but which may live at least partially as parasites, and hemoparasites or facultative saprophytes, that is, those normally parasitic but which may live for a time as saprophytes. As an example of the first class might be mentioned *Polyergus scissorius*, one of our most widely distributed species and most cosmopolitan in respect to its choice of hosts; it is classed as one of our commonest saprophytes, but occasionally exhibits parasitism (described by von Schrenk as a wound parasite causing a heart rot of *Catalpa species* and like). On the other hand we have forms such as *Fomes annosus* (*T. radicicola*) which, while an unmodified parasite of conifers, occurs also as a typical saprophyte on converted timbers. But this classification into hemi-forms is at best an approximation and is valueless in the case of many forms because of our want of a standard, with regard to their exact nutritive relation, or because the two potentialities are so evenly balanced in their constitution. Such an even balance is to be found in forms like *Fomes igniferus* or *Polyergus saprophytus* which continue growth and produce fruiting bodies long after the death of the living hosts.

But in practice any imperfection in the classification of this intergradational series is of little importance in comparison with the ability to distinguish the facultative parasite from the strict saprophyte, for the one wrongly classified and so removed from critical surveillance is likely in consequence to be allowed to continue its destructive work unchecked, and conceivably might even be unsuspectingly brought into new conditions under which it would prove to be a troublesome pathological problem. This applies with especial force to the fungi that occur on trees. On such large plants considerable amounts of dead tissue may be endured by them without seriously impairing their health, and these dead
areas may, and often do, serve as the harbours for many kinds. Obviously it is a matter of considerable consequence to distinguish the fungi that are strictly saprophytic and unable to pass the dead areas from those that are capable of encroaching on tissues and of insidiously though none the less certainly ensuring the life of their hosts. Unfortunately, in a very large number there are no known marks whereby the potentially parasitic forms are recognized with certainty. This difficulty has been encountered by students of tree diseases, but as yet no satisfactory applicable solution has been proposed. Distinguishing data have been proposed by von Schrenk and Spanholing 

which grow on dead wood, including both wood from the living tree, and in some cases dead heartwood or actually exposed to the air but still forming a part of the tree. The classification here is satisfactory, but an attempt to recognize the parasite from the directions given for its presence leads to much uncertainty—no better illustration of this could be found than that of F. applanatus.

Among the fungi attacking trees there has been no greater unity and difference of opinion with regard to its ability to parasitize than in the case of Fomes applanatus. Thus, Spanholing says "Fomes applanatus attacks dead wood in living trees, when the trunk has been injured, causing large wounds which extend-outwards to the sapwood and eventually kill the tree". If, however, a true heart-rotting fungus, its attacks are made in dead sapwood. It is not, however, a true heart-rotting fungus, and the wood which it attacks is dead sapwood rather than dead heartwood. Von Schrenk, after mentioning its occurrence on dead counters, says: "it is occasionally taken from dead parts of living trees". Hedgecock writes "Fomes applanatus has rarely been found limiting or living (a statement not borne out by the author's experience). The writer, to verify the view of von Schrenk and Spanholing that this fungus does not cause a disease in the sense that the roots produced by F. igniarius and F. trypographus are diseases. It attacks readily both sap and entering the sap on dead exposed roots or in dead areas of the heartwood of trees." But two years later he writes: "after making further observations concerning the effect of this fungus upon living trees, the writer b.
kinds of fungi were found attacking these trees, but I have not investigated them in detail, so I cannot pass beyond the general statement that they are harmful to living trees. The fact of their presence provides a clue to the problem of diseases of living trees, which is one of the most important problems in forestry today.

In many cases, the fungi live on dead wood and are not harmful to living trees. However, in some cases, they can cause considerable damage. The most common type of disease caused by fungi is known as "dead heartwood." This occurs when the wood is no longer alive and is attacked by fungi that feed on dead wood.

A. ivor. I

I. ivor. I

ON THE BIOLOGY OF LOMES APPLANTUS

The sap and heart of many living trees. (No statement gives the grounds on which this conclusion is based.) It is able to enter such trees only through wounds. In the majority of instances, however, the fungus acts only as a saprophyte. Heald considers it a facultative parasite, stating that it would seem probable that the fungus is not able to attack young healthy trees of cottonwood, but that it can become parasitic on older trees in which the vitality has been considerably lowered, or that have reached the maximum of their development. Von Schrenk and Sprankling dissent from this view. In many recent descriptions of diseases of forest trees, reference is made to fungi which in the opinion of the writers must be considered strictly saprophytic forms which occur only on dead wood. A striking instance of this is Fomes applanatus. This fungus is frequently found on living trees, but a careful examination always shows it to be growing on wood which is actually dead, and generally on the outer sapwood. So far as the writers have been able to observe, F. applanatus does not cause what may be called a disease of living trees. The same is true of many other fungi. The writers believe, or that most of these forms, if not all, will not grow on a tree until it has already been so weakened by other factors that to all intents and purposes it is dying or dead, with the possible exception of cases where the fungi grow on dead patches of wood caused by some injury, as in the case of trees injured by fire. Neuman (34), after speaking of finding the fungus growing out of wounds in the trunks of living oaks and cottonwoods, states, "A young apple tree had been looking sickly for the past two or three years, but I found no external fungus growing upon it until a pith of F. applanatus appeared on the trunk. The heartwood of the tree was badly decayed . . . and the trunck was attacked to the living bark as though it was a parasite."

In attempting to solve the problem as to whether or not F. applanatus may act as a parasite, I have followed three lines of inquiry: first, evidence of apparent parasitism as judged from the mode of its occurrence and the fact of its hosts (the only kind of evidence alluded to in the literature reviewed above); second, a direct investigation of the invaded tissue of the living host to determine whether or not it could be established with certainty that these tissues were living, and third, the results of inoculating healthy trees with the mycelium of the species of the fungus.

Thus, trees of nearly all the common broad-leaved species have been found bearing sporophores and in some localities the percentage of such
trees is quite high. In one park in Toronto practically all the leaves
and many of the beeches have shown turning leaves of this mnr
year, and of another, and the trees are slowly dying and being re-
placed. In some, maple, beeches, poplars, willows, birches, elms, chestnut, o. r., even the resistant Gleditsia, Robinia, and Morus,
attacked. One of the most interesting cases in this connection is
a large well-kept apple orchard many of the trees of which in
vigor of maturity had been injured by a severe wind-storm. 

*applicatus* established itself in practically every one of these trees
within four years.Gumrotes were forming on the trunk, and these
were rapidly spreading. A study of the course of the disease in
these trees showed the central upper portion of the trunk badly
damaged, and with the characteristic mottled appearance. The outer
growth of the tree was unharmed, but in place of the disease had progressed outwardly
bark, involving the cambium. This had been attacked by the
fungus and destroyed locally, more or less islands of living cambium
being left. The power to act parasitically was very evident.

Gumrotes do not invariably arise from dead exposed meristems,
resulting from injury, but often emerge from bark covering wound
early killed by the injuring agent.

Opportunities were afforded for a study of several large
beeches, maple, and red oak, and also for observing
many park trees which were being prepared by "tree surgery" for
hinging. In the case of none of these trees was any other abnormal
notions, any visible cause other than *F. applicatus* attacked the tree.
Likewise, the course of the disease was similar in all cases.
The region may be located in the lower few feet of the trunk, and was
distinctly in shape with the basal portion most rotten and the apex
least injured. But in other cases the tree was clearly diseased, not only by the disease,
but also by the brown zone at its periphery. The
fungus evidently worked progressively upward in the heart and out
eventually involving the sapwood. It is to be particularly noted that
the heathwood was affected by *F. applicatus* in all of these trees.

*F. applicatus* only in observation distinctly at various
stages of gumrotes of your Schrenk and Supplee's that it always grows on
which it is usually dead and generally on the outer sapwood, and
why it is that these zones have been attacked. The gumrotes would be little, perfectly sound and healthy physiology.
more especially. The fungus may have commenced in activity
of gumrotes, but was with little question in this stage, playing the
part...
The above facts regarding its occurrence in the tree of the trees are strongly in favor of a parasitic relation on the part of F. applanaus. At all events, it is on precisely similar evidence that we recognize the presence of the so-called "wound parasites" of tree roots, such, for example, as Fomes annosus, and Polyporus suillus. But while such evidence is generally conclusive it fails to carry the case in its entirety, and there remains for differences of opinion. A study of the brown band itself, however, to close the gap in the case of F. applanaus, and to indicate the possible conclusion that it is a wound parasite. The very existence of the brown band in connection with F. applanaus is shown by its presence on the wounded surface of the wood, and on the ground. The formation of wound gum and tyloses in this band, as already described (p. 17), would seem to permit of no other explanation.

Wound gum or balsam has been investigated cautiously by L. Church, in a large number of beech-leaved trees, where a blue spot on the wound around the dead wood in the neighborhood of the wounded place. The conclusion in all cases that it is a sign of the living protoplasm. If this be true, then there can be no question that F. applanaus acts on the cell, and after stimulating them to the production of the wound gum, destroys them. March 20. hold a different view to the cause of the wound gum in that he maintains that in any tree after the death of the cell, to an oxidation product of their content, of which there is not necessarily conflict with the conclusion to the cause of the death of the cell. For it to be borne in mind that wound gum does not necessarily occur only by means of the dead tree. Tyloses, fortunately, do not suffer in this way, for they can be produced only by living cells. Their occurrence then, proves that the invaded tissue is living, and more even that the wound gum is not reconstituted after death, but on the death of the producing cell. The tyloses arise at the result of a circulation primarily induced by the fungus, with which they are to be regarded with more or less completely contained, even more quickly than the cells from which they originate. The brown band with its wound gum and tyloses may rightly be regarded the best criterion we have at present in a decision as to the former cause or not of the attacking fungus.

Of the means of proving such facts in none could appear to be more direct than observations on the readiness of muculation with the wound gum under consideration. But for some reason the difficulty of technical
to be overcome have proved to be very serious, and our knowledge of the conditions that prevail in nature is very imperfect. As the term is used, it is not always easy to make an inoculum with its contamination, much more difficult to prevent its subsequent contamination during the month or even year through which the latter runs, and at the time to be sure of maintaining the moisture and temperature necessary for the introduction of the disease. Moreover we are very uncertain as to the extent of the influence exercised by the host in both ways, and a more definite method should be.

A survey of the literature discloses a few records of the type of disease in connection with the wound parasites of trees. Mayne reports the introduction of wood rotting by *Phaeolus chrysophyllus* and tree with resulting discoloration of the tissue and partial disintegration of the medium for a very short distance. Mr. Baylis. on experiment in *Picea* and a birch tree, makingiset in the branches in which *Penicillium nigricans* were placed, but the results were not very successful. For some time it was supposed that the inoculation was made with a coniferous tree, but it could be determined by recent tests made on the living tree, and conclude that the experiment was not so.

March 17, a report of the only instance who has repeated the experiments of inoculation experiment on the same tree in a number. He used several species of fungi, of his method within a healthy tree, and then to place the living part of which the medium was to be grown. The last were cooked out, and the whole operation had to be repeated any accidently existing spores which might exist in the soil to any considerable extent. He found that a very distinctive type of the fungus took place around the wound, and evidently showed it to be due to the presence of wound and a very characteristic of the content after the cell structure had been killed. If so, the medium accordingly takes the brown color and a rare coloration of the whole.

He also found that after two or three years very pronounced swelling and aether appeared on that tree, marking the point of infection. This he explained as due to extensice activity arising from the structure of the tissue excitation, and to the swellings and the tree and the long time. One is supposed that he is not meant the
ON THE BIOLOGY OF SOME APPANATUS.

The writer made similar experiments extending over three seasons with various species of trees of different age classes totalling several hundred borings. The species used were *Fagus grandiflora*, *Liriodendron tulipifera*, *Populus deltoides* var. *balsamifera*, *Populus trichocarpa*, *Picea engelmanni*, *Abies concolor*, *Pseudotsuga taxifolia*, *Thuja mexicana*, and *Larix occidentalis*. The procedure consisted in first smoothing the spot on the bark and rubbing it with 95 per cent alcohol, and afterwards boring with a quarter inch bit which had been sterilized by dipping in alcohol and then turning the alcohol off. The miteum was then inserted, using a cork press, and the hole plugged with a sterile cork. A variety of materials were used—pieces of raw bearing muceleum, piece of wood or which muceleum had been cultured, pieces of wood naturally ticked, and pieces of the trunk body. Some trees were handled, using cotton stop which had been run through a melted red gum, wax, and in these cases the holes were left unmarked. The soundness of the trees was examined by the boring. In each tree control were made. The experiments were made at different seasons of the year in the expectation that this one might be dependent upon the functional activity of the seasons of the tree.

The results of these inoculations may be briefly stated. Nothing occurred at the sites of the controls. As for the hardwood in many instances from whatever cause, the muceleum died without causing injury. But in others, around each hole a deep brown discoloration of the muceleum took place, this extended a short distance radially and periphery but considerable distance in the longitudinal direction. The discolored volume was that of two half cubic inches placed tree to tree. It can be gathered from the figures, which are strikingly similar to March's, and it shows that the discoloration is due to the process of wound gauze. The hole contained a thin layer of the muceleum, and microscopic examination showed hyphae present throughout the browned tissue. In addition, in the case of beech there was a very large number of tubules, while on the other hand there were none. One further characteristic of the browned volume of wood is worthy of mention. When sectioned, my co-workers showed that the discoloration extended further and farther in a long, narrow direction than the normal. The presence of the heart of the tree. The layers of wood formed after the muceleum have always remained in color, as well as more rapidly, and in inspection revealed no tufts of thread (fig. 17).

As compared with the controls, however, the above method was not a means by which one could. All controls showed a similar
The maximum browning obtained in the controls is illustrated in Fig. 20. Microscopic study showed hyphae to be present sometimes, but not nearly so commonly in the incubated borging. There again in the controls were in all probability due to some uptake of organic, or due to imperfect inoculations, since the bark would sooner or later crack open somewhat above and below the borging. In addition there were always the mummic phenomena, so similar, though on a smaller scale. The controls were never discolored nearly as far as the experiments. The holes made in the phloem, mentioned by Munich, so far has not appeared in my test tree, though the swollen bogs of trees which he considers mummic were very intriguingly present in the case of the red oaks, which were so badly infected with *Apples*, in the Park to which certain reference was made.

It will be seen that the results obtained correspond very closely with those of Munich on beech. The fact that can be claimed for these experiments with Munich's is that they indicate the power of the fungus to destroy living tissue. But whether or not under the conditions chosen by the operator the fungus will be able to fully establish itself and overcome the resistance of the vigorous spruce is, of course, to be seen. So far no living bodies have been formed. Munich explained the feature on the assumption that the introduced fungus now proceeds with a great activity after it has exhausted the gum in the borging, a great activity which has not been taken into account of the resting influence of the host.

How much time is necessary to a living tree to establish itself in the lower part of a tree, as stated elsewhere and through the agency of spores. Attenuated were able to cultivate the gum in the soil, but without success. It is certain that *Apples* does not invade the soil by means of these spores. Nor do we know to what extent infection is possible from wound. It may be that the fungus most readily establishes itself dead tissue, and then the attack the remaining living tissues, whereas the tree may possibly be but weakened through infection, or even cured of the fungus. This attack and destroyed are not restricted to heart or spored, but the weaker or weakened tissues, wherever they may be, undoubtedly lose their vitality. By ever increasing the degree of invasion the resistance of the tree is gradually undermined, usually even the most resistant tissues are unable to combat the organism, so in the case of the apple tree described fall prey to the patho-
ON THE BIOLOGY OF Toms AppLAnnus

167

The struggle between host and parasite may sometimes persist over a long period of years, and the termination of the struggle is very largely determined by the resisting powers of the host. Apparently, in certain cases, the host seems able to hold the parasite in check almost indefinitely, counterbalancing by the season's growth what it loses by the extending mould of the fungus.

The most practicable control measures in the case of park, street, and oak trees would seem to be the building up of the vigour of infected trees, and the prevention of the spreading of the disease to new hosts; by re mueving the formation of barren bodies. Surgery has been largely employed with such trees; but to be successful must be absolutely thorough.

VII. Summary

1. Fomes applannus is a perennial polypore of wide distribution and of common occurrence in North America and in Europe is responsible for the decay of very large quantities of wood annually. It attacks practically all coniferous species and several coniferous species, both dead wood and live trees. This fungus, heretofore commonly regarded as a pure saprophyte, has now for the first time been comprehensively studied, the investigation recorded in this paper has followed along three main lines of inquiry. (1) a study of the morphology and the ecology of F. applannus; (2) of the action of the fungus on its hosts; (3) a determination of its ecological relations by cultural methods, and a testing of the applicability of these methods to a study of the timber destroying fungi. (4) the investigation of the possibility of finding criteria by which we may determine the parasitic action on wood from saprophytic.

2. Fomes applannus produces basidiospores only; conidia are not produced by the mycelium, nor, as is commonly assumed, on the upper surface of the sporophore. The basidiospores are not of the ordinary type; each consists of a yellow, papillated, thick-walled chlorovolpospore within a thin hyaline wall. The so-called "truncale" base is in reality the upper end of the spore.

Spore discharge is enormous and continues for 1-2 for the longest period recorded for fungi. It is continuous day and night for about 1-2 months. In vigorous fructifying bodies a sporocarp cloud. Discharge is not affected by variations in light, humidity of the air, or temperature, within the very wide limits; frost causes an instant cessation of spore discharge; for however long the sporocarp is exposed to the weather the parasite,
The spores were not found to retain their viability for more than 4 or 5 months. They germinate in water and various other media within 48 hours after sowing, but the percentage of viable spores is very low, and their behaviour with respect to germination is erratic.

3. No difficulty was experienced in culturing *F. appplanatus* on various types of media or on wood.

Three parallel series of cultures were carried through in sporulation with mycelium obtained from old spores, (a) pieces of spore, (b) pieces of diseased wood.

1. Wood rotted by *F. appplanatus* exhibits a mottled appearance sufficiently characteristic to permit of its recognition when compared with other rots.

In the case of living wood the area of attack is delimited by a dark band.

Histologically, the decay is characterized by a proliferation and erosion of the element culminating in disappearance of the tissue localized pockets into which the mycelium grows forming strands.

Chemically, the change is one of delignification followed by an aggressive solution of the resultant cellulose wall except for a few resins.

In the later uniform white stage of decay, the threads of *F. appplanatus* were always found to be accompanied by other destructive agents or fungi.

5. The particular type of decay in timber due to *Fomes appplanatus* has now been linked with a causal agent by natural culture.

6. *Fomes appplanatus* has been proved to be a wound parasite, a southern Ontario at least, is one of the commonest and most destructive of this type. The proof rests on three grounds: (a) the convention applied to other such fungus the mycelium works upward most rapidly by the way of the heartwood causing a characteristic decay and cutting into the sapwood, eventually reaching the cambium, and is apparent the cause of the death of the tissues it has entered by it; (b) a broad band of resin in the wood of living trees along the advance line of invading mycelium - this fungus. Within this band there is a copious production of brown wound gum and an excessive multiplicity of tyloses. This band steadily moves forward with the advancing line the tyloses and wound gum being destroyed by the mycelium at the posterior margin as rapidly as they are formed along its anterior margin.

The tyloses and possibly the wound gum also occur to the invasion of the invaded tissues, their production can be ascribed only influence of the fungus, and the invasion of these tissues and the
On the Biology of Fomes Applanatus

more than media within the tree is very low.

on artificial media through to appearance compared by a wide range and corro-
rates in the emulsions.

by a process of a few resistant agents.

mature, and in most destructively conventional test most readily and outward apparent is apparently broad brown line of the apparently a copious multiplication of young hyphae.

along its anterior edge only to the and then late
LITERATURE CITED

7. BUNN, C., Untersuchungen aus dem Gesamtgebiet der Mykologie. Heft 8, 1895.
12. COSTANTIN, M. M., Culture d'un Champignon lignicole. Comptes Rendus, 110, 752-753, 1890.
16. LAW, R. S., Report of Florida Agricultural Experiment Station for 1908. (Pub. 88).
17. HARRIS, R., Wichtig Erkankungen der Waldlinie. 1874.
18. HARRIS, R., Dieleungserkankungen des Holzes. 1878.
32. MORRILL, W. A., Northern Polypores. 1913.


EXPLANATION OF PLATES.

Fig. 1 Illustrating great variation in width of sterile band in Fomes applanatus; \( \times 2.3 \).

Fig. 2 Tilia americana, 14 days after inoculation with agar bearing mycelium; \( \times 7.8 \).

Fig. 3 The same test with Tsuga canadensis, thus illustrating relative immunity of conifers; \( \times 7.8 \).

Fig. 4 F. applanatus cultured from spore to spore under artificial conditions throughout (7 months). The spore deposit is to be seen on the glass and on the cotton batting. Jar not opened between inoculation and sporation; \( \times 7.9 \).

Fig. 5 Enlargement of porel surface of the preceding; \( \times 5 \).

Fig. 6 Showing sterile "humps" usually obtained in cultures; \( \times 4.5 \).

Fig. 7 A reserve form assumed by F. applanatus in nature; \( \times 1.4 \).

Fig. 8 Lombardy poplar attacked by F. applanatus, in an early stage.

Fig. 9 A very advanced stage of the decay, in beech; \( \times 1 \).

Fig. 10 Cross section of beech wood showing first stages of decay: elements perforated and reduction of wall thickness just beginning; \( \times 212 \).

Fig. 11 An advanced stage of the same; elements gone locally except for more resistant portions; \( \times 212 \).

Fig. 12 Longitudinal section corresponding to Fig. 10, and showing extensive perforation; \( \times 212 \).

Fig. 13 Longitudinal section of advanced stage of decay: perforations have merged and walls very much reduced in thickness, with some entirely gone; \( \times 212 \).

Fig. 14 Composite drawing to illustrate successive steps in decay.

Fig. 15 Radial view of block from living hard maple attacked by F. applanatus; dark band marks advance line of fungus working outwards from the heartwood; \( \times 1.5 \).

Fig. 16 Same feature in red oak.

Fig. 17 Piece from trunk of sound young hard maple tree 12 months after inoculation with F. applanatus; the discoloured volume has been attacked; note that the wood laid down after the experiment was begun resisted attack; \( \times 1 \).

Fig. 18 Radial view in region of dark band shown in Fig. 15; on the right tissue vigorously attacked, and on the left sound tissue showing tyloses and wound gum; \( \times 212 \).
Fig. 19. Cross section of young maple trunk showing affected areas some distance above inoculation point; × 1.

Figs. 20 and 21. Illustrate the result of inoculation in sound young hard maple trees; Fig. 20 shows the maximum discolouration obtained longitudinally among all the controls in all the test trees; × 1.
some

hard

ob-

test