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On the Biology of *Fomes Applanatus*
(Pers.) Wallr.

LEWIS WHITE, M.A. B.Sc.

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On the Biology of *Fomes Applanatus* (Pers.) Wallr.

BY
I. H. WHITE, M.A., B.Sc.

*A Thesis submitted in partial fulfillment of the requirements for the Degree of Doctor of
Philosophy in the University of Toronto*

ON THE BIOLOGY OF FOMES APPLANATUS

ON THE BIOLOGY OF FOMES APPLANATUS (Pers.) Willd.

BY

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

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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 polypores 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, Faull, 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 propinquity of fruiting bodies; in contrast to the investigations of other plant diseases there has been very little work by the application of bacteriological method—establishment of 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 polypore that attack our structural and standing timber there is none more conspicuous owing to the large size of its perennial applanate bracket, or more frequent, than the species *Elvela mialoma*, 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 fruiting bodies are to be seen in great abundance on tree trunks, stumps, dead stubs and logs. It grows more frequently on deciduous than on coniferous species, and while it usually attacks dead wood it is 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 Hedd's studies (20) on its relation to a disease of cottonwood, no intensive investigation has been heretofore undertaken on the form. This may be accounted for by the fact that its ravages in Europe do not appear to be as great as in America, consequently receiving little attention there, or because of the reiterated 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 forms there have been so far no reliable criteria for distinguishing between the two, and so there have been meagre grounds for combating any widely accepted view either one way or the other.

The present investigation on *Fomes applanatus* comprises 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 saprophytism.

II. SPECIES INVESTIGATED

a) 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 *Lomes applanatus* has been questioned. Thus, Merrill (30) considers it an entirely distinct species—a position based on the creation of the species *meialoma* in 1846 by Fèveille (23) on material sent him from north-eastern America. It is of interest to note in this connection that Fèveille found specimens in the same consignment which he regarded as being identical with the European *E. applanatus*; that is, in one lot of American plants sent to him he regarded some as being identical with the European *E. applanatus* and others as belonging to a new species, restricted to America, and named by him *Polyporus meialoma*. The differences noted by Fèveille had to do with the colour of the cup and the pores and the width of the sterile border underneath. However, American mycologists (including Merrill) today consider that Fèveille 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 (2) in 1908 would appear to establish its identity with the European form, thus reducing *P. meialoma* to a synonym—a view contrary to that held by Merrill, already stated, who regards our form as different from the European and restricted to America. The writer has examined hundreds of fruiting bodies in this region, and finds that the characters of the fruiting body are fully as variable as stated by Atkinson. In particular there is much variation in the width of the sterile band, as illustrated in Fig. 1; moreover, on the same pileus the band is wider early in the growing season than later; it is generally wider in one-year-old piles than in older ones; occasionally one finds narrow and wide banded piles growing mixed on the same log, though this is not the rule. Further, an examination of the Swedish 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 form, at least as yet a constant feature has been described that would distinguish between the two, and I quite agree with Atkinson in relegating *P. meialoma* to the rank of synonymy and in calling our plants *Lomes applanatus*.

b) Hosts. Various partial lists of hosts are on record by different writers. Farlow and Seymour (14) in their Host Index recorded 4 or

negrum, *A. saccharum*, *Quercus alba*, and *Tsuga canadensis*. Hedgecock (21) gives the most complete list, including species of *Acer*, *Alnus*, *Betula*, *Crataegus*, *Fagus*, *Fraxinus*, *Hicoria*, *Liriodendron*, *Morus*, *Nyssa*, *Populus*, *Pyrus*, *Quercus*, *Salix*, *Robinia*, *Filix*, and *Umbellaria*; and of conifers, *Abies*, *Picea*, *Pseudotsuga* and *Tsuga*, or 53 species in all. Atkinson (1) Spaulding (15), Weir (50), Rhoads (30), and others, also record in one connection or another the occurrence of *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 are to be added three species of conifers, viz.: *Tsuga canadensis* (stumps and wood on the ground, in localities near Toronto); *Pinus Strobus* (planking supporting a lawn, Toronto); *Picea* (probably *P. rubra*—bridge timber in Adirondacks, N.Y., collected by Professor J. H. Faull, 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 incidental records, have been published from this distinctive point of view. Heald (20) in 1906 reported finding it on cottonwood. Newman (33) records it on apple, oak, cottonwood and willow; while Hedgecock (21) enumerated *Liquidambar styraciflua*, *Pyrus malus*, *Morus rubra*, *Populus tremuloides*, *P. trichocarpa*, *Quercus rubra*, *Acer saccharinum*.

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

<i>Acer saccharinum</i> .	<i>Pyrus aucuparia</i> .
<i>A. saccharum</i> .	<i>Quercus rubra</i> .
<i>Aesculus hippocastanum</i> .	<i>Q. velutina</i> .
<i>Betula alba</i> var. <i>papyrifera</i> .	<i>Robinia pseudacacia</i> .
<i>B. lutea</i> .	<i>Salix nigra</i> .
<i>Carpinus caroliniana</i> .	<i>Filix americana</i> .
<i>Fagus atropurpurea</i> .	<i>Ulmus americana</i> .
<i>Gleditsia triacanthos</i> .	Cultivated varieties of <i>Malus</i> .
<i>Liriodendron tulipifera</i> .	Cultivated varieties of <i>Prunus</i> .
<i>Morus alba</i> .	
<i>Populus alba</i> .	
<i>P. balsamifera</i> .	
<i>P. grandidentata</i> .	
<i>P. nigra</i> var. <i>italica</i> .	

(c) *Related Species*: The genus *Phoma*, as defined by Murrill (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, *F. fasciata* and *F. tornata*, are tropical or subtropical forms, appearing to replace respectively the northern *fomentaria* and *applanata*. Of *F. tornata* 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 *tornata*, if indeed distinct, has been differentiated as *F. Lionnetii*. Fawcett (16) has reported that *F. fasciata* is frequently a parasite of orange trees and water oaks in Florida; it also occurs on dead wood. *F. lobata*, a species found from New York to Iowa and south, but so far not recorded for Ontario, occurs on diseased trunks of certain deciduous trees, especially the white oak, as well as perhaps more commonly on dead deciduous wood. Of it Murrill (30) says, "Facts thus far collected indicate that *F. lobata* is a southern form and confined to a much more restricted area than *F. megaloma*, while within this area it is often abundant and quite destructive to the oak, its favorite host." *F. fomentaria* (recently elevated to a new genus, *Elfungiella*, by Murrill 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 echinulate 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 echinulate 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 endospore is formed. The spore "wall" in one sense then is accordingly double. As the endospore 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 so 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, "truncate at the base." This view has been taken by Patouillard (36), Bresadola (8), Merrill (31), Overholts (34), and others. Atkinson, however, on critically examining the shapes of 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 spore layer of an actively sporulating fruiting body reveal spores in all 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 "truncate base" is in reality the apical end of the spore.

(b) *Sporophore*: The sporophores of *F. applanatus* are perennial and so a new tube layer is formed during the growing season of each year of its 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. igniarius*, 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. lobatus* which lasts but a single season, but which organizes, however, a new pileus 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 polypores *Fomitiporia laminata* 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 1-16 inch is commonly found by the first or second week in May, and the fall of spores from the new hymenial surfaces has already commenced. In this connection it may be stated that Buller (10) found *P. squamosus* 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 3-8 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) *Spore 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 Buller was astonished to find discharge going on for sixteen days and estimated three weeks as the probable limit. During this period 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. An 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 cigarette smoke as long as one cares to watch them. I have observed these in the field 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 material caught on a glass slide in 24 hours is ordinarily sufficient to render it opaque. Buller, from a count estimate in the case of *Polyporus squamosus*, a form which also exhibits spore clouds, concluded that at least 1,700,000 spores were discharged from one tube in three days. A similar calculation with *F. applanatus* give the incomprehensible number of 30,000 million spores liberated in 24 hours from a fruiting body with a pored 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 60 average-sized active fruiting bodies of *F. applanatus* on a single chestnut log in the wood—it is easy to appreciate the surety with which some

spores will drift into places where conditions are favorable for their germination and growth; and of the chance that the infection will be able to establish 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 *E. applanatus* develop normally in total darkness we know from Spankling's observations on mine fungi (46). That spore discharge is immaterially 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 9.10 p.m. to 9.30 the next morning, with temperature changes from 9° C. down to 3° and up again to 15° 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 Buller (11) found that some *Hymenomyces* continued to shed their spores at the freezing point of water, though at a very diminished rate, while Overholts (33) as well as Buller 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 a very few spores were invariably found on my slides left for a week under a fruiting body of *E. applanatus*, 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 (41) on *P. squamosus* who could detect no change in spore discharge 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 by frost, a certain minimum spore production is checked, and is not resumed until the normal rate until the necessary amount of water is restored. Fruiting bodies in unshaded positions in dry weather throw spores sparsely; no doubt the explanation of this is to be looked for in their low moisture content. It further happens occasionally that sporophores growing in unfavorable conditions produce few spores or none at all. It is not probable 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, *Fomes applanatus* is stated to produce conidia on the dorsal surface of the pileus. Schulzer-Muggenberg (42) was the first to make this statement in 1880. Merrill in his specific description says that the upper surface of the fruiting body is conidia-bearing and usually brownish during the growing season from the covering of conidia. This brown coating is infrequently to be seen, but examination showed that in every case it is composed of basidiospores. These are mechanically deposited by the currents of air after they fall from the hymenial tubes. This can be easily 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 surface of such an organization as not to favour spore production, becoming heavily encrusted during its first season. Young fruiting bodies in the early stages of development, as well as very many others of various 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 Yeast-Fieghem cells was used. Various media were tried, including distilled and tap water, solutions of grape sugar, cane sugar, maltose, peptone, meat extract, acids, alcohol, alkalis, etc., in various graded percentage strengths. Decoctions 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.

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put up for invalids, but then only with the spores from some of my traps. The percentage of germination at best, however, was always low, usually a fraction of one per cent. No difference was observable in the appearance of those spores which would germinate and those which would not; nor between those taken from traps with viable spores and those from traps with none but non-viable spores. Spore collections which exhibited viability in the above mentioned malt extracts would also germinate at times in distilled or tap water, on potato agar, and on moist sterilized wood. This behaviour differs from that of spores of *P. squamosus*. Buller (10) was able to germinate these in a malt-wort extract but not in water or on fresh wound surfaces.

The most puzzling behaviour on the part of the spores was encountered. The great majority of the collections made on glass slides failed to exhibit any germination. Once one had located a spore slide collection which showed germinating powers one could go on daily for weeks with practically uniform success. Sooner or later, however, germination ceased abruptly. There was no uniformity of age at which viability ended. The oldest viable spores encountered had been kept six and one-half months after collection in a laboratory hotter and drier than most rooms. It may be noted that Price (38) found the spores of *P. squamosus* had lost their viability in 79 days, and Miss Bayliss (4) those of *Polystictus versicolor* 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 vaseline 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 explainable 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, the tube always issuing from the "truncated" apical end of the spore; the wall appears to be lighter in color and apparently thinner, and it almost equals in diameter. In the earlier stages, in general, 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 commences 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 a direction at right angles to the long axis of the spore; branching begins earlier and results on the average in a more symmetrical system. Gradually these types are not much mixed in the same culture, as a

Text Fig. 1. — *Phragmotroch varians*. Stage of germination. Object plant 72 hours.

appearing in separate cultures. Practically all the germination obtained in a given month is in evidence in 48 hours, though a few related ones are encountered; and since growth proceeds at a fairly uniform rate any particular hanging drop presents a rather definite picture at any given stage. The spore features and the germinating hyphal system are so characteristic that one readily notices any fore spore or its product.

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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 Waldbaume" in 1874 and his "Zersetzungserscheinungen 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 appearance 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 or no work on the causal forms has been done.

In 1897 Ward (40) opened up a new field in connection with the study of wood destroying fungi, by proving that such forms are capable of artificial culture. His studies were on *Stereum hirsutum*. He first of all germinated the spores on gelatine and agar media, using sugar or rye juice 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 cultures. Although abnormal in shape, it is true, but which nevertheless sporulated, the first time a basidiomycetous wood destroying fungus was cultured on its host from spore to spore. Ward's purpose, however, was merely to test the possibility of such artificial cultures. He had not in view a demonstration that the features of decay usually associated with a fungus were really traceable to it, but rather to show that the culture technique employed in the study of other fungus diseases was likewise applicable in the study of the diseases of wood.

Contrary to hopes that might be aroused by Ward's success with *Stereum hirsutum*, experience has shown that similar attempts with higher fungi commonly lead to disappointment, so that, as yet, reports of successful cultures, with the sporulating fruiting body as an end attained, constitute 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 environmental factors conducive to fructification. 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 moulds or bacteria. In the 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 a report on account of similar work in relation to the action of *Collybia velutipes* on wood of *Aesculus*. He germinated the spores in hanging drops of a 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 sporophores were produced within a month. Four years previously Constantin and Matruchot (12) had exhibited normal fructifications of this same species obtained on artificial cultures in two months.

Biffen (6) has similarly investigated *Bulgaria polymorpha*. The spores in this case were germinated in beerwort 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.

Falck (13) in 1902, reported culturing three agarics 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 Autobasidiomycetes, 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 hymenia in the laboratory." Spaulding (43) in 1905 reported culturing *Schizophyllum commune* successfully, but in later cultures of another agaric, *Lenzites sepiaria*, on sterilized pieces of wood he got only abnormal sporophores which he does not mention as sporulating (44). The highly destructive *Lentinus lepideus* 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 *Lenzites sepiaria* from spore to spore. Buller (10) has given us a very interesting biological paper on *Polyporus 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 dried 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 on occasion demanded. The glassware used in the germination cell was sterilized, the malt extract was sometimes sterilized and sometimes not; it seemed to give a rather higher percentage germination when not sterilized, and for all practical purposes served equally well, for the proportion 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 its 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, but 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 in four 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 thickening up of the layer so that the earlier fluffy appearance is somewhat lost. This layer soon becomes woven into a thin leathery sheet which is strong enough for the mycelium to be extracted bodily. As time goes on the surface takes on a powdery look as if conidia were being formed. In all my tubes examined none were ever discovered, the powdery appearance being due to the numerous excreted crystals of calcium oxalate. The witches' broom-like branches.

*Since this was written a paper by Long and Hatch (21) has come to hand concerning the culture of a large number of forms of wood rotting fungi on agar media. Their investigations had in view the differentiation of these forms by cultural characters alone. In the cultures of *F. applanatus* on malt and wood, sporophore production was indicated in 40 to 45 days.

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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, finally reaching a dark brown shade, often with a purplish cast. Usually these progressive color differences are expressed as a zonation. 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 has shrivelled up hard and dry, new cultures may be started from bits of the sheet.

Tests carefully carried through to the formation of the fruit body have shown that the rather tedious pore method of starting cultures could be successfully substituted by the tissue method first described by Duggan, 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, as recommended by Spaulding. In the other method of using pieces of the decayed wood, contrary to expectation, one was seldom bothered with bacteria if the sounder pieces were chosen. Both these methods were very convenient. The character of the tube cultures derived in either of these two ways differed in no respect from those originating from pores.

Cultures on Wood. As *Lomus applanatus* did not fruit on my agar, tried out it was found necessary to complete the cultures on wood. For the purpose, blocks of wood after being water-soaked were placed in rum and the whole sterilized. They were then inoculated with pieces of mycelium from tube cultures, or directly with pieces from the interior of a fruiting body. This latter method is perfectly satisfactory and a time-saver. Representatives of practically all the hardwood genera of northern North America were used, and no difficulty was found in getting the fungus to grow on any of them. Certain woods, such as bass-wood and poplar, were found more suitable in that they lent themselves better to the technique, and accordingly these were mainly used in the culture on wood. Green timber as well as dry laboratory samples were used, both sapwood and heartwood, with the fungus exhibiting no preference. Contrasting wood of many species was also experimented with, the list including pieces of pine, spruce, tamarack, hemlock, fir, and several members of the cedar tribe. A very scanty growth at best was obtained in some instances, but that was due to poor development of a went. Even with mycelium originating from a hemlock limb attacked by this fungus nothing material resulted. These experiments, coupled with field observations, lead to the conclusion that coniferous wood is un-

questionably practically immune from destruction by this (Figs. 2, 3).

The carrying of cultures on wood through to the production of bodies in the case of such a form as *Fomes applanatus* is necessitated experiment with the consequent difficulties of exclusion from outside and of keeping the wood specimens from drying out. At first much time was lost in carrying along cultures which dried out in the course of five or six months. Fortunately, this will grow in quite wet wood, so that one may begin the culture with material carrying a high percentage of water. In the successful one litre wide-mouthed jars were used with about one inch of soaked cotton batting in the bottom. The wood blocks of some six or eight cubic inches in volume were first thoroughly water logged alternately boiled and plunged into cold water to drive out all possible air. The block was placed in the jar in a slanting position, a quantity of water added, a cotton plug inserted, and the whole sealed 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-inoculated after inoculation. Frequently the blocks during sterilization were completely dried out except for the lower ends and such were useless. This was nearly always the case with some woods, particularly oak. The easiest woods to bring through sterilization in a uniformly moist condition were found to be bass wood, poplar, and willow, and bass was accordingly largely used in all the later work.

The jars were then usually allowed to stand for a couple of weeks if any infection appeared. The blocks of wood were then inoculated by transferring to them pieces of agar bearing mycelium from tube or plate. As already stated three parallel lines were carried through, in a culture originating from spores from pieces of dried wood, and in a piece of fruiting body. To lessen infection from foreign fungi the jars were found very convenient to fix a piece of paper loosely on the top of the jar, but even then it sometimes happened that spores of *Penicillium* or *Aspergillus* germinated in a plug, then hyphae grew down through and on the inner side. Most of such jars, of course, had to be discarded as time went on, but it had to be at least a week owing to drying. Drying can now be greatly retarded by placing the jar inside a covered jar, but under such circumstances it was found that extraneous infection frequently happened owing to the moisture of the upper of the cotton plug.

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The growth behaviour on the surface of wood is similar to that on agar. The hyphae grew out from the inoculation material forming white circular patches, steadily enlarging. The fastest rate recorded was one in which a piece of mycelium about 3.8 square inches in size in the course of ten days covered an area of five square inches. Eventually the same color changes ensue as has been noted for the cultures on agar. In the majority of the wood cultures, however, only a small portion of the surface of the block is overgrown by the mycelium. Usually the transferred mycelial bits were placed on the transverse face of the block for it was found that the hyphae penetrate into the interior much more quickly than when a longitudinal face of the block is inoculated and with better results. In the latter case more of the exterior becomes overgrown though this is of no special advantage.

In due time, from two months onward in the case of successful culture, small white hemispherical humps appear here and there on the surfaces of the block. The number on different blocks varies from two or three to eight or ten. Their appearance is spread over a considerable period of time, during which some might be produced simultaneously. Some cease growth very shortly after their formation, while others continue for some weeks and then come to a standstill. In these, with cessation or increase in size a thin leathery outer layer is organized. Sectioning reveals the same color zonation of tissue as one sees in that portion of the pileus above the first tube layer in any fruiting body of *L. applanatus*. As a rule one or two humps grow steadily larger at an appreciable rate till they reach their maximum for the growth condition.

about one inch in diameter in the case of the blocks of the volume used. It was evident that the size depended upon the number of humps in relation to the food supply. In some jars these humps grew superimposed on one another producing quite bizarre shapes. In others the humps appeared more in the nature of cushions or ridge-like expansion (Fig. 6). In the great majority of jars this was the limit of increase attained, but in others in the course of some even to nine months possible to make their appearance (Fig. 7) from my first successful culture. The deposit of brown spores on the side of the jar was in evidence very shortly after the porol area began to form, and judged by the increasing density of the coating spore discharge lasted two months at which time the experiment was terminated and the spores examined. They were found to be typical *Lomes applanatus* spores.

Before mentioning yet, though, the typical bracket form appeared. The form assumed by the fruiting bodies under these artificial conditions can, however, be largely duplicated in the forest on logs bearing bracket

of *F. applanata*. The hemispherical form with a small pore appearing in various directions is comparatively common, such a specimen one may often see another of approximately the same size pulling out into a small bracket before developing pores, and in a case of more tool being within the influence of the latter than the cake-like form developed in some cultures is also to be noticed. As well as such occurrence on logs, the writer has collected a body of this shape some eight inches in diameter with upper surface pored, growing on the ground attached to a mushroom several inches beneath. Fig. 7 shows one of the most typical 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 normal shape. A few lamellate forms such as *Collybia velutipes* (Cortina et Matruchot), and *Sclerophyllum commune* (Sp.) as exceptions to this rule, do produce normal sporophores. The experience likewise has been that the sporophores 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 in the unnatural conditions of their environment, such as restriction of supply, light, etc. (Ward, Price, etc.). Probably no generalization applies, the causes being likely specific for each form. The writer has found with certain *C. pruni* that sporophores formed and matured by a damp atmosphere. Bitten found that *Collybia* develop normally whether aerated or not. *Lentinus lepideus* develop a pulvis in the absence of light (Buller), while *Collybia* (Bitten) and *Strombosia* (Ward) do equally well in light or dark. There is one important factor, however, that has been overlooked by most experimenters; it has been the practice to use very small pieces of wood in their culture, and the writer is of the opinion that many failures to get normal fruiting bodies have been due to the fact that the pieces of wood do not afford a sufficient supply of food. Cultures of *F. applanata* are now in progress in which much larger blocks than described above are being employed.

V. DECAY.

Studies on wood destruction through the agency of fungi have shown that the phenomena of decay in the case of most fungi, when taken from the first, are characteristic for each individual species.

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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 recognise 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 chemical changes produced by them; the chemical changes caused by some species result in an extraction of cellulose leaving the wood darker, and in others of lignin, leaving it lighter. The texture of the residual decayed mass, its odour, 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 sheets or strands of mycelium by the fungus in the product of its handiwork 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 (26) with reference to a disease of the cottonwood 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 strata and the sounder intervening wood) is so marked that at the first examination it was thought that the tree was infested with borers and that they were responsible for the effect". The earlier

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 *P. applanatus* in the stage of decay described by him, as indicated by his statement that "the naked eye examination of the cut surface at the point of contact of the fungus with the wood shows the presence of characteristic black lines that run in a general transverse direction The black lines, which were mentioned as a prominent feature of the decomposition by this fungus show in microscopic sections as yellowish deposits in the lumen of the ducts and in the cells." Heald suggests that these deposits represent an endeavour on the part of the tree to check the advance of the fungus. The writer's assiduous search among hundreds of cases of *P. applanatus* in the field, has been unable to verify Heald's observation on this point. Black lines are encountered, but cultural or other evidence shows that wood decay does occur more than one species of fungus is at work. They are present at the point of contact of two invading fungi in the case of many of the wood destroying fungi, a phenomenon well known to pathologists.

Field observations indicate that *Tomex applanatus* 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 rot. It works inward to the heartwood and thence upward, and as it progresses the decay extends outward involving the lower sapwood. In the case of the trunk 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, sufficiently characteristic to enable the recognition of this fungus long before fruiting bodies begin to form. The effects produced in heartwood and sapwood are the same. This appearance is best described by a transverse section (Fig. 8). The lighter colored areas in the mottling indicate the location of the majority of the hyphal threads, though the colour is due not to the threads, but to the reduced density of the wood and its consequent softening consequent on the extraction of lignin. These areas forming a system more or less rectangular, with the general direction tangential and radial. Accordingly, a trunk windthrown or cut into exhibits a characteristic fracture with the pieces removable in a parallelepiped, and trees overthrown generally break off square. In this stage of the decay the wood is still quite hard and heavy, the change of colour being the only physical alteration evident.

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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 leathery 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 cellulose element, this phase of the work of the fungus is easily overlooked microscopically. The uniform whitish colour is very late 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 mottled type of rot is not restricted to *Fomes applanatus*; several other fungi produce a mottled rot, but so characteristic in each case as to be distinguishable from one another and from the decay of the form under consideration. Thus, *F. tomentarius* produces a mottled rot but it is a very much finer mottling; 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 mottling caused by *P. squamosus* is very much finer still, and more in the form of white lines, with the general direction tangential, and in dried wood it appears as fine depressed lines; while that of *P. conialis* in conifers is also finer, but mostly radially, and since there is complete dissolution locally with no core of fungus threads left, the final result is a sort of pinhole 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 brownish discoloured zone which marks the extreme limit of advance of the fungus, making the line of demarcation from the sound and yet uninvaded 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 rotted by *P. tamaris*, 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, and

which, as has already been pointed out, are commonly encountered when 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 newly attacked by the parasite. A microscopic examination shows that the "wound gum" is most abundant in the lumina of parenchymatous cells and in the vessels, though it may be found in any cellular elements (Fig. 18, Text Fig. 2). It occurs in the form of yellowish 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 as a strictly pathological phenomenon. As the anterior margin of the rot creeps forward, keeping pace with the advancing hyphae, the posterior margin advances with equal rapidity leaving no trace of the discoloration in the tissues behind; the "wound gum" is either bleached or secreted as part of the food of the fungus; at all events remains of it are not readily detected by the aid of any of the stains or other reagents commonly 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 a number of species in which search was made for them, including beech, sugar maple and red maple, but not in the wood of the apple. They crowd the lumina of the vessels, controlling them as with a continuous growth of tissue. The "wound gum" found in the vessels is part at least, located in the in-growing tissue. Tyloses do not occur in the sound tissue beyond the brown band. It is also striking to a large extent the tyloses are soon destroyed by the occupying fungus—for a short distance behind the brown band there may be but few traces of them left. A close examination was made to discover whether or not the "wound gum" and the tyloses might not be formed just before the tissues in question were reached by the hyphae, but all the evidence obtained negated an assumption. The brown band is the first stage in the destruction of living wood, but more than that, the "wound gum" and tyloses are features of importance in interpreting the nature of the fungus concerned. From this point of view will be dealt with in the section "Parasitism."

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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 laminae disappear rather more rapidly than the middle lamella. The destruction continues in extreme cases till nothing is left but fragments of the most resistant parts—the angular "gussets" at cell corners and pieces of middle lamellae. 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. The mere 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 if such a conclusion be extended to most cases in which the effect is accompanied by a uniform accompaniment of a certain species of fruiting body. Of course, where the rot is of a very distinctive type such an association may be accepted as fairly adequate evidence, though even in such cases confirmation is necessary. Most of the wood-destroying fungi act rather slowly, many years often elapsing before the sporophores appear, and during this time secondary purely saprophytic bacteria and fungi have ample opportunity to make their entrance. Cultures made from most woods in an advanced stage of decay almost invariably reveal the presence of such secondary agencies, thus raising a question as to the value of descriptions of decay which so commonly are based on late stages of decay, leading to the conclusion that some of the culminating features of the decay are often to be attributed to other organisms than the primary cause. In such cases, doubtless the earlier marks are much more distinctive and of greater value in a diagnosis of the disease than the later. This 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 cut tree that had borne fruiting bodies of *F. applanatus* for years and in which there was no other species of fungus. Pieces taken from the interior of the wood, selected from the upper limits to which the disease had progressed, and which showed the characteristic mottling, were cultured on potato and on sterile pieces of wood through to fruit and spore production. It was found that no question remained as to the identity of the causal agent, for in all cultures made from such a source contamination by bacteria or other fungi rarely appears. Cultures made from mottled areas in many other woods likewise always showed an almost constant freedom from such secondary fungi and bacteria. On the other hand in cultures made from woods in a uniform white stage of decay bacteria and other forms practically always appear. It is reasonably certain that we may conclude that complete destruction in the case of *F. applanatus* after the uniform white stage is reached may in part be the work of combined agencies.

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VI. PARASITISM.

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 *Uredineae* not even 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 hemisaprophytes or facultative parasites, that is, those normally saprophytic but which may live at least partially as parasites, and hemiparasites or facultative saprophytes, that is those normally parasitic but which can live for a time as saprophytes. As an example of the first class might be mentioned *Polystictus versicolor*, 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 (40) as a wound parasite causing a heart rot of *Catalpa speciosa* and lilac). On the other hand we have forms such as *Fomes annosus* (*F. radiciperda*) which, while an undoubted 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 uncertainty 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 ignarius* or *Polyporus sulphureus* 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 intermediate 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 pabulum for many kinds. Obviously it is a matter of considerable consequence to distinguish the fungi those that are strictly saprophytic and unable to pass the dead areas from those that are capable of encroaching on the living and of insidiously though none the less certainly encroaching on the life of their hosts. Unfortunately, in a very large number of cases there are no known marks whereby the potentially parasitic form can be 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 many investigators in this field, but they fall short when an attempt is made to apply them. This is aptly illustrated in a review of diseases of deciduous trees by von Schrenk and Spaulding (41). These authors make two groups of wood destroying fungi, viz., wound parasites and "those fungi gaining entrance through wounds or branch stubs into the centre of a tree and causing a heart rot which extends outwards to the sapwood and eventually kills the tree" and "saprophytes" "which grow on dead wood, including both wood exposed from the living tree, and in some cases dead heartwood or wood actually exposed to the air but still forming a part of the living tree". The classification here is satisfactory, but an attempt to recognize the parasite from the directions given for its recognition leads to much uncertainty—no better illustration of this could be given than that of *F. applanatus*.

Among the forms attacking trees there has been no greater uncertainty and difference of opinion with regard to its ability to be a parasite than in the case of *Fomes applanatus*. Thus, Spaulding says "*Fomes applanatus* attacks dead wood in living trees, especially when the trunk has been injured, causing large wounds which are favorable to its entrance. It is not, however, a true heart-rotting fungus as its attacks are made in dead sapwood rather than dead heartwood" (50) after mentioning its occurrence on dead conifers, sapwood occasionally taken from dead parts of living trees". Hedger writes "*Fomes applanatus* has rarely been found fruiting on living trees" (a statement not borne out by the author's experience). "To verify the view of von Schrenk and Spaulding that this fungus does not cause a disease in the sense that the rots produced by *F. igni* and *F. traxinophilus* are diseases. It attacks readily both sapwood and heartwood entering the sap on dead exposed roots or in dead areas at the base of the trees." But two years later he (21: 145) "after making further observations concerning the effect of this fungus upon living trees, the writer has

kinds of fungi distinguish among to pass beyond thing on living encompassing number of cases the forms can be countered by all able solution has posed by some attempt is made of diseases of These authors and parasites on stubs into the wards to in and s wood removed od or sapwood of the living in attempt to its recognition could be given to greater uncertainty to act as a Spaulding (45) trees, especially and which are rot-rotting fungus and heartwood". ters, says "it is Hedgcock (21) on living trees". This tends his fungus does *F. igniarius* and sap and heart, s at the base of further studies writer has come

to the conclusion that very frequently it attacks with the sap and heart of many living trees. (No statement is given 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 "it would seem probable that the fungus is not able to attack young healthy trees (of cottonwoods), 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 Spaulding 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 form 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

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 331, 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 growths upon it until a pileus of *Fomes applanatus* appeared on the trunk. The heartwood of the tree was badly decayed . . . and the fruiting body was attached 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 fate 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 if so, whether or not their subsequent fate was contingent on the action of the occupying fungus; third, the results of inoculating healthy trees with the mycelium or the spores of the fungus.

Living trees of nearly all the common broad-leaved species have been found bearing sporophores and in some localities the percentage of such

tree is quite high. In one park in Toronto practically all the beeches and many of the beeches have shown fruiting bodies of this fungus (year after year), and of no other, and the trees are slowly dying and being replaced. In the region, maple, beeches, poplars, willows, birches, elm, chestnut, etc., even the resistant *Gleditsia*, *Robinia* and *Morus*, are attacked. One of the most interesting cases in this connection is a large well-kept apple orchard, many of the trees of which in their vigour of maturity had been injured by a severe wind storm. *F. applanatus* established itself in practically every one of these trees within four years; perithecia were forming on the trunk, and the trees were rapidly succumbing. A study of the course of the disease in these trees showed the central upper portion of the trunk badly affected, and with the characteristic mottled appearance. The outer growths were in order, but in place; the disease had progressed outward, involving the cambium. Thus had been attacked by the fungus, and destroyed locally, none but small islands of living cambium being left. The power to act parasitically was very evident. Perithecia do not invariably arise from dead exposed areas, but result from injury, but often emerge from bark covering wood entirely killed by the fungus itself.

Opportunity was afforded for an analysis of several large trees of beech, hard maple, and red oak, and also for observation of many park trees which were being prepared by "tree surgeons" for felling. In the case of none of these trees was any other disease observed, nor was there any visible cure other than *F. applanatus* on the trees should die. The course of the disease was similar in all. The region involved was the lower few feet of the trunk, and was conical in shape with the basal portion most rotted and the apex least. The decayed mass was clearly distinguished, not only by the characteristic mottling, but also by the brown zone at its periphery. The decay evidently worked progressively upward in the heart, and eventually including the sapwood. It is to be particularly noted that the heartwood was affected by *F. applanatus* in all of these trees. *F. applanatus* only—an observation distinctly at variance with the statement of von Schrenk and Spaulding that it always grows on wood which is actually dead and generally on the outer sapwood." It is clear, whether they held their conclusion that it is never anything but saprophytic. Outside the upper apical portion attacked, and a little wood would be found perfectly sound and healthy physically microscopically. The fungus may have commenced its active saprophytic life, but was with little question in this stage playing the parasite.

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The above facts regarding its occurrence and the life of the trees point strongly to a parasitic relation on the part of *F. applanatus*. At all events, it is on precisely similar evidence that our recognition of the parasitism of the so-called "wound parasites" of trees rests, such for example, as *Fomes igniarius*, and *Polyporus sagittarius*. But while such evidence is reasonably conclusive it falls short of a complete demonstration, leaving some play to individual judgment in the matter, and ground for differences of opinion. A study of the brown band (Fig. 18, 19) that mark the advance limit of decay in living trees seems, however, to close the gap in the case of *F. applanatus*, and to fully establish the conclusion that it is a wound parasite. The very existence of the brown band in connection with *F. applanatus*—for it was shown by cultural tests that this was the only organism present—is strong prima facie evidence that the fungus is acting parasitically. But the formation of wound gum and tyloses in this band, as already described (Fig. 18), would seem to permit of no other explanation.

Wound gum or balsam has been investigated carefully by Church (1917) in a large number of broad-leaved trees, where it is produced commonly in wood in the neighborhood of a wounded surface. He considered in all cases that it is a secretion of the living protoplasm. If this be true, then there can be no question that *F. applanatus* acts on living cells, and after stimulating them to the production of the substance, in turn destroys them. Munch (20) holds a different view as to the origin of the wound gum in that he maintains that it originates after the death of the cells as an oxidation product of their contents. A view that does not necessarily conflict with the conclusion as to the cause of the death of the cells, for it is to be borne in mind that wound gum does not form most readily in fallen dead trees. Tyloses fortunately do not suffer from this opinion; they can be produced only by living cells. Their occurrence, then, proves that the invaded tissue is living, and moreover, that if the wound gum be not a secretion it follows very closely on the death of the producing cell. The tyloses arise as the result of a stimulation primarily induced by the fungus, what purpose they serve the host it may not be apparent, for they are soon destroyed and more or less completely consumed, even more quickly than the cells from which they originate. The brown band with its wound gum and tyloses may readily be recognized as the best criterion we have at present in a decision as to the presence or not of the attacking fungus.

Of all the means of proving parasitism none could appear to be more direct than observation on the results of inoculation with the organism in under consideration. But for some reason the difficulties of technique

to be overcome have proved to be very serious, and our knowledge conditions that even infection is very imperfect. As to the form difficult enough to make an inoculation without contamination, much more difficult to prevent subsequent contamination during month or even year through which the test must run, and at the time to be sure of maintaining the moisture and in fact to introduce. Moreover we are very uncertain as to the extent of the actual influence exerted by the host in technical inoculations should be.

A survey of the literature discloses few records of this type of infection in connection with the wound parasites of trees. May (1884) records the introduction of wood rotted by *Polyporus betulinus* into a sound tree with resultant discoloration of the tissue and partial mycelium for a very short distance. M. Rayless (1) experimented upon a birch tree making it in the branches in which *Polyporus* or *Arctia* were placed, but the results were inconclusive. Stoddard was unsuccessful in his inoculation test with *Arctia* on a maple. Spackling (11) says in connection with his test of *Arctia* on long leaf pine "absolutely no results could be detected in several trees made in the living tree" and concludes that the fungus is a saprophyte.

March (27) is perhaps the only investigator who has reported carrying out of inoculation experiments on living trees in a systematic manner. He used several species of fungi and his method was to bore into healthy trees and then to place in the boring place on which the mycelium was grown. The holes were corked and sealed with lead line, the whole operation being completed with the purpose of preventing any infection by foreign species. March's experiments rewarded with only tolerable success. He found that in a distinct rowing of the tissue took place around the inoculation and examination showed it to be due to the presence of wound has already been mentioned. March considered the wound zone then produced the contents after the cells have been killed by wood accordingly takes the browning as a sure indication of infection. He also found that after two or three years a very pronounced white swelling appeared on his test trees marking the point of infection. This he explained as due to extraordinary activity resulting from the stimulus of the fungus exertion. He concluded that it was a response to callus and other growth from fungus often seen in nature and to the swollen parts of trees at fungus rot. One result appeared that he does not mention the

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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 *Acer saccharum*, *Betula atra*, *Juniperus*, *Larix canadensis*, *Pinus Strobus*, *Betula lutea*, *Populus nigra*, etc. The procedure consisted in first smoothing the spot on the bark, then rubbing it with 95 per cent alcohol, and afterwards boring with a one-quarter inch bit which had been sterilized by dipping in alcohol and then turning the alcohol off. The inoculum was then inserted, using sterile pieces, and the hole plugged with a sterile cork. A variety of material was used—pieces of agar bearing mycelium, pieces of wood on which mycelium had been cultured, pieces of wood naturally rotted, and pieces of the fruiting body. Some trees were bandaged, using cotton strips which had been run through a melted grafting wax, and in these cases none of the holes were left uncorked. The soundness of the trees used was judged by the borings. In each tree controls were made. The experiments were made at different seasons of the year in the expectation that success might be dependent upon the functional activity of the tissues of the tree.

The results of these inoculations may be briefly stated. Nothing resulted in the case of the controls. As for the hardwood in many instances, from whatever cause, the inoculum died without causing infection. But in others, around each hole a deep brown discoloration of the tissue took place, this extended a short distance radially and peripherally, but a considerable distance in the longitudinal direction. The shade of the discoloured volume was that of two half cere placed one to the other, as can be gathered from the illustrations, which are strikingly similar to Michx's, and its colour was determined to belong to the presence of wound gum (figs. 17, 19, 21). The hole contained a fungus with the mycelium, and microscopic examination showed hyphae present throughout the browned tissue. In addition, in the case of beech there was a very large number of tyloses, while outside the affected area there were none. One further characteristic of the browned volume of tissue is worthy of mention. Median radial section invariably showed that the discoloration extended farther and farther in a longitudinal direction the nearer it approached the heart of the tree. The layers of wood formed after the inoculation were always normal in colour, as well as microscopically, and inspection revealed no fungus threads (fig. 17).

Contrasted with the controls, however, the above results were not conclusive as one could wish. All controls showed a similar

discoloration, though of much less extent. The *maximum* brown obtained in the controls is illustrated in Fig. 20. Microscopic studies showed hyphae to be present sometimes, but not nearly so commonly in the inoculated borings. The results in the controls were in all probability due in some cases at least, to infection from other organisms due to imperfect inoculations, since the bark would sooner or later crack somewhat above and below the boring. In addition there were always the traumatic phenomena, so similar, though on a smaller scale, to the control, never discolored nearly as far as the experiments. The ridge-like swelling phenomenon, mentioned by Munch, so far has not appeared in my test tree, though the swollen butt of trees which he considered to be very strikingly present in the case of the red oaks, which were so badly infected with *T. applanata*, in the Park to which our reference was made.

It will be seen that the results obtained correspond very closely with those of Munch on beech. The most that can be claimed for the present test tree with Munch's is that they indicate the power of the fungus to destroy living tissue. But whether or not under the conditions chosen by the experimenter the fungus will be able to fully establish itself and overcome the resistance of the vigorous sapwood tissue remains to be seen. So far no fruiting bodies have been formed. Munch explained this feature on the assumption that the introduced fungus had lost its activity after it has exhausted the air in the boring—the mycelium died. But this appears to be an assumption unsupported by any reliable fact, and open to one very forcible objection in that it does not account of the resisting influence of the host.

How infection takes place in nature is not altogether certain. Apparently infection is by way of wound—usually in the lower part of the tree, scattered elsewhere—and through the agency of spores. Attempts were made to cultivate the fungus in the soil, but without success, and it is certain that *T. applanata* does not traverse the soil by means of rhizomorphs. Nor do we know to what extent infection is possible through wounds. It may be the fungus most readily establishes itself in dead tissue, and from the attack the surrounding living tissues, which may possibly be first weakened through excretion or excretion of the fungus. The tissue attacked and destroyed are not restricted to heart or sapwood, but the weaker or weakened tissue wherever they are undoubtedly the most easily invaded. By ever increasing the extent of invasion the resistance of the tree is gradually undermined, and finally even the most resistant tissue such as the cambium is observed in the case of the apple trees described, fall a prey to the parasite.

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That the struggle between host and parasite may sometimes persist over a long period of years is certain, and the termination of the struggle is very largely determined by the resisting powers of the host. Apparently, in some 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 inroads of the fungus.

The most practicable control measures in the case of park, street, and fruit 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 retarding the formation of fruiting bodies. Surgery has been largely employed with such trees, but to be successful must be absolutely thorough.

VII. SUMMARY

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1. *Topia applanatus*, 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 deciduous species and several coniferous species, both dead wood and living trees. This fungus, heretofore commonly regarded as a pure saprophyte, has now for the first time been comprehensively studied, the investigations recorded in this paper have followed along three main lines of inquiry, (1) a study of the morphology and the ecology of *T. applanatus* and of the action on its host, (2) a determination of its ecological relationships by culture methods, and a testing of the applicability of such methods to a study of the timber destroying fungi, (3) an investigation of the possibility of finding criteria by which we may distinguish parasitic action on wood from saprophytic.

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2. *Topia applanatus* produces basidiospores only; conidia are not produced by the mycelium, nor, as is commonly affirmed, on the upper surface of the sporophore. The basidiospores are not of the ordinary type, each consists of a yellow, papillate, thick walled chlamydospore within a thin hyaline wall. The so called "truncate" base is in reality the apical end of the spore.

Spore discharge is enormous and continues for by far the longest period recorded for fungi. It is continuous day and night for about six months, visible more vigorous fruiting bodies as spore clouds. Discharge is not affected by variations in light, humidity of the air, or temperature within very wide limits; frost causes an instant cessation and thereafter there is no further spore fall until a new set of pores is organized.

The spores were not found to retain their viability for more than 6 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. applanatus* on artificial media or on wood.

Three parallel series of cultures on wood were carried through sporulation with mycelium obtained from (a) spores, (b) pieces of sporophore, (c) pieces of diseased wood.

4. Wood rotted by *F. applanatus* 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 perforation and erosion of the element, culminating in disappearance of the tissue, localized pockets into which the mycelium gathers forming strands.

Chemically, the change is one of delignification followed by a progressive solution of the resultant cellulose wall except for a few resistant fragments.

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

5. The particular type of decay in timber due to *Fomes applanatus* has now been linked with its causal agent by actual culture.

6. *Fomes applanatus* has been proved to be a wound parasite; in 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 fungi—the mycelium works upward most rapidly by the way of the heartwood causing a characteristic decay and on into the sapwood, eventually reaching the cambium, and is apparently the cause of the death of the tissues traversed by it; (b) a broad band is present in the wood of living trees along the advance line of invading mycelium—the fungus. Within this band there is a copious production of brown wound gum and an excessive multiplication of tyloses. This band steadily moves forward with the advancing heartwood, the tyloses and wound gum being destroyed by the mycelium at its posterior margin as rapidly as they are formed along its anterior. The tyloses, and possibly the wound gum also, certify to the living condition of the invaded tissues, their production can be ascribed only to the influence of the fungus, and the invasion of the elements and the

demonstrates directly its ability to act as a parasite; (c) inoculations with the spores and mycelium of *F. applanatus* into living trees resulted in an extensive browning of the inoculated wood with a multiplication of releases both far in excess of similar phenomena due to traumatic stimulation.

7. The occurrence of wound gum and the multiplication of tylose in a tree marking the advance of a wood-destroying fungus in a living tree would appear to furnish an unerring criterion for the recognition of the fungus as a parasite.

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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 sporulation; $\times 7-9$.
- Fig. 5. Enlargement of pored surface of the preceding; $\times 5$.
- Fig. 6. Showing sterile "humps" usually obtained in cultures; $\times 4-5$.
- Fig. 7. A freak 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; $\times 1\frac{1}{2}$.
- 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. Illustration of 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 .

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