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PITH-RAY FLECKS IN WOOD.

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PITH-RAY FLECKS IN WOOD.

PREVIOUS INVESTIGATIONS.

Pith-ray flecks, or medullary spots, often render lumber unfit for certain uses. They are common in many of our native woods (Pl. I, fig. 1), appearing in transverse sections of logs or lumber as crescent-shaped, discolored areas, and in tangential, or bastard cut, boards as brown streaks running usually in a vertical direction (Pl. I, fig. 2). The pith rays, passing outward toward the cortex, end blindly in the discolored areas, and it is comparatively easy with a microscope to detect the connection of the two.

The observance of pith flecks appears to be coincident with the early systematic study of wood. Theodore Hartig, noting them as early as 1840 in *Corylus, Betula,* and *Alnus,* designated them "Zellgange," or cellular passages. He described them as similar to the passages of barkbeetles, extending down into the roots for 5 feet or more and up into the stem. The cells, he says, are rich in starch, and contain brown masses of an unknown substance insoluble in alcohol or water.

Ratzburg found similar markings in wood which he received from Russia in 1852. He suspected their pathologic origin and named them "Braunketten;" that is, "brown chains of cells." Nordlinger also called attention to them in his "Querschnitt von hundert Holzarten," but applied to them the name of "Markfleckchen." In spite of the generally accepted belief in the pathologic origin of these markings, attempts were made by some writers to use them to identify species. Kienitz published a key of the most important German woods, in which he endeavored to separate some species of *Prunus* and *Salix* by the presence of pith flecks.

Kienitz, in 1883, submitted the first convincing proofs of the pathologic origin of pith flecks. He found that they were due to the work of the larvæ of dipterous insects [1] living in the growing cambium and eating passages in this layer while in search of food. According to his observations the insect passes the winter in the pupal state in the ground. The adult forms appear in the spring and deposit their

[1] These insects consist probably of one or more species which as yet have not been classified and named.

eggs singly, apparently in the young branches of the tree. Kienitz, unfortunately, failed to observe the manner of entrance into the cambial layer, but found the young larvæ in infested trunks as early as May, eating passages in the cambium and in the soft tissue of the inner bark. At first these passages are narrow, only a few cells broad, and lead downward. As the larvæ proceed downward they grow but slightly in thickness, though considerably in length. Finally each one becomes 2 or 3 cm. long. The passage, Kienitz says, gradually widens as the insect grows in size. It spreads out laterally as the larva turns as far to left or right as its worm-shaped body will permit. In a radial direction the wound is always slight, since the larva attacks only the growing cells of the cambium. After it has proceeded a certain distance downward, the larva abruptly turns, and, without forming a loop, starts upward. The size of the passage is increased only slightly at this turning point.

The position of the turning point in the tree varies. Often it is at the dividing point between root and stem, or else in a lateral root. Sometimes the larva turns but once or twice, while in other cases it may turn a number of times. Finally it assumes a somewhat shorter and more compact form, bores through the bark, emerges from the narrow opening, and falls to the ground. Kienitz did not observe the adult form.

Investigations of the insects involved are being carried on by the Bureau of Entomology through its branch of forest insects.

ORIGIN OF PITH FLECKS.

The present investigation confirms the conclusion of Kienitz, published in 1883, that pith flecks are caused by the larva of a dipterous insect living in the cambium during the growing season. Specimens of river birch were examined as early in the season as April 25. Growth had then begun, as shown by the ease with which the bark peeled from the wood. At this time the larvæ were burrowing vertically downward in the cambium and had already reached a point about 6 feet above the ground. They were 1½ cm. long, 1 mm. in width, and pure white, except for the dark mouthparts.

To determine the manner in which the larvæ obtained entrance into the cambium, a number of mines were traced back to their source. This could be done with reasonable care, because at this early date growth had not progressed far enough to cover up or obliterate the mines. They had their origin invariably in the upper part of the tree's crown and on branches of about 5 years' growth. In such cases the mine could be traced to a suppressed lateral twig. At the point of attachment of this to the main branch, and always on the side toward the ground, a dark coloration could usually be detected extending from the outer bark into the cambium. This appeared like a puncture of some sharp instrument. The coloration resulted from the decay of the injured cells. Whether the larva first hatches out of the egg outside the bark and then bores into the cambium, or whether the adult female deposits the egg in the cambium itself, can not be determined from the present investigation.

Observations were next made about two weeks later—that is, about May 10. The larvæ had increased slightly in length, but scarcely at all in diameter. Some had already reached the base of the tree and started back, following for a short distance a path parallel to the old mine, and then branching off obliquely (Pl. II, fig. 2). Very few had gone far down into the roots at this time, but were burrowing in the growing layer near the base of the tree. This was expected, since the larvæ were evidently guided in their movements by the food supply.

During May there were examined specimens of black cherry, wild plum, serviceberry, red maple, and wild apple. From all of these species larvæ were secured similar to those already described. The mines that were still free from wound tissue were readily followed as the bark was removed. Often the larvæ were secured by thus tracing a mine to its termination. The number of larvæ in each case varied with the tree species and individual. In Maryland and Virginia river birch appears to be the favorite host, with wild plum, serviceberry, black cherry, red maple, wild apple, and silver maple following in the order named. Certain specimens in a few localities were almost free from larvæ, while others seemed to be favorite hosts year after year, as shown by the number of pith flecks in previous rings of growth.

During the period between May 25 and June 25 the larvæ continued to mine back and forth, seldom going more than 10 feet above the ground. As the larva grew larger the mines gradually increased in diameter up to several millimeters and often crossed one another. The appearance of the wood was often misleading as to the number of larvæ actually at work, since one larva, working up and down, may make several flecks within the same annual ring.

Pupation began about June 25. After this date the time of pupation seemed to depend somewhat on the age of the tree. In young trees with relatively thin bark it occurred first, while larvæ were secured from older trees with thick bark as late as July 20. The larvæ proceeded down into the roots for varying distances. When the roots are exposed, as along the banks of streams, the mines often continue for a number of feet until they enter the ground. In trees growing on flat land the roots are seldom penetrated for more than 3 feet. In such instances the larvæ generally return to a position near the base of the trunk and pass out through the cortex.

Pupation takes place in the ground. The larvæ bore a small hole through the bark and come out in the earth. The end of a mine is generally marked by a small black spot where the cambium is exposed to the air. A number of puparia were secured in proximity to the bark and always close to the termination of a mine. Pupation occurred, as already stated, almost immediately after the larva emerged.

OCCLUSION OF THE LARVAL PASSAGES.

Soon after the passage of the larva the healing process begins. The larva destroys only those cells in its immediate path through the inner bark. Cambial activity proceeds as usual on both sides of the passage. As the cambium layer moves outward radially, the passage left by the larva increases in diameter. For this reason, when growth is very rapid, the pith-fleck spots are larger than when it is slow. Mines produced in early spring are larger radially than those made later in the season, when diameter increase is slower.

The healing process proceeds mainly from the bast pith-ray cells in the bark which are in direct communication with the reserve food supply. During this healing process made by the division of the bark cells toward the wood, growth is proceeding in the cambium on each side of the wound. The cambium becomes united again toward the periphery of the annual ring, and wood elements are formed in the usual way. Thus the cambium, reuniting around the passage, leaves the latter behind in the annual ring. And the passage, although thus wholly independent of the new cambium, becomes filled with new cellular tissue. This process can be followed macroscopically by removing the bark from the infested trees. For a short distance back of the larva the mine is free of all cell growth, and appears like a small groove under the bark. Soon, however, wound tissue is formed, and the space is filled with young cells similar in character to those in pith rays. This tissue clings to the inner bark when the latter is removed from the tree, and appears like a ridge upon the smooth surface. After a distance of a few feet the wound tissue gradually passes over into the wood or older portion of the annual ring. The farther the mine is traced backward the deeper is it buried, and in fast-growing trees it often disappears completely in the wood.

Some idea of the microscopic appearance of pith flecks in transverse section may be had from Plates II, III, and IV. The thick-walled cells are occasionally separated by layers of a compact, yellowish-brown substance, the remains of dead cells and excrement of larvæ. The size of the cells filling the wound does not depend upon the size of the wound itself, but upon the nature of the tissue surrounding the wound; that is, upon the size of the ray cells and the diameter of the vessels. Where the ray cells are compact and short, such as in wild plum (Pl. III, fig. 1), the successive divisions in the healing process give rise to cells of small dimensions. But when they are

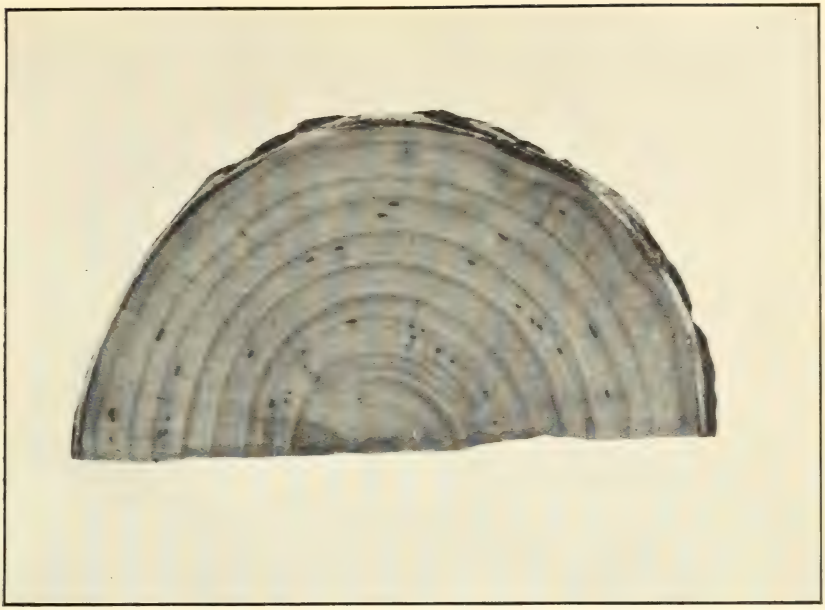


FIG. 1.—TRANSVERSE SECTION OF A BRANCH OF RIVER BIRCH, SHOWING PITH FLECKS. NATURAL SIZE.

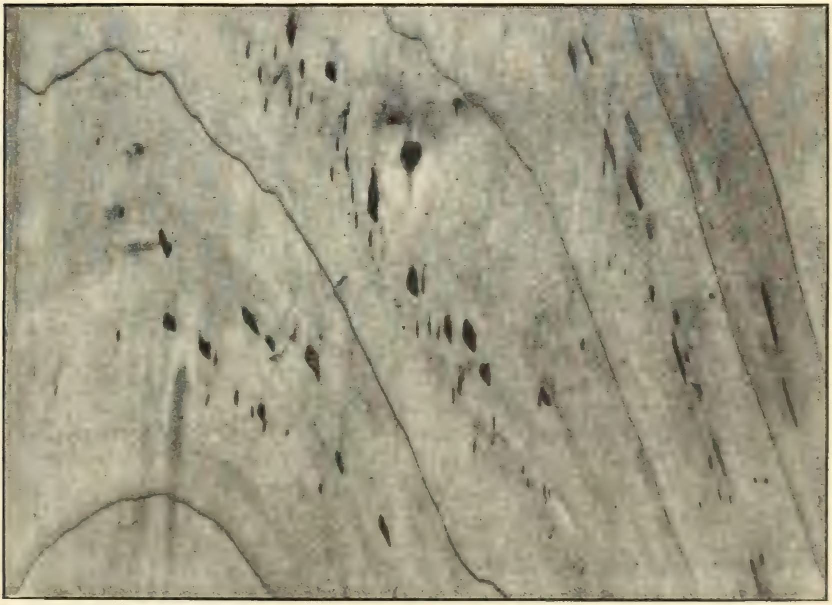


FIG. 2.—TANGENTIAL SECTION OF THE TRUNK OF SILVER MAPLE, SHOWING PITH FLECKS. NATURAL SIZE.

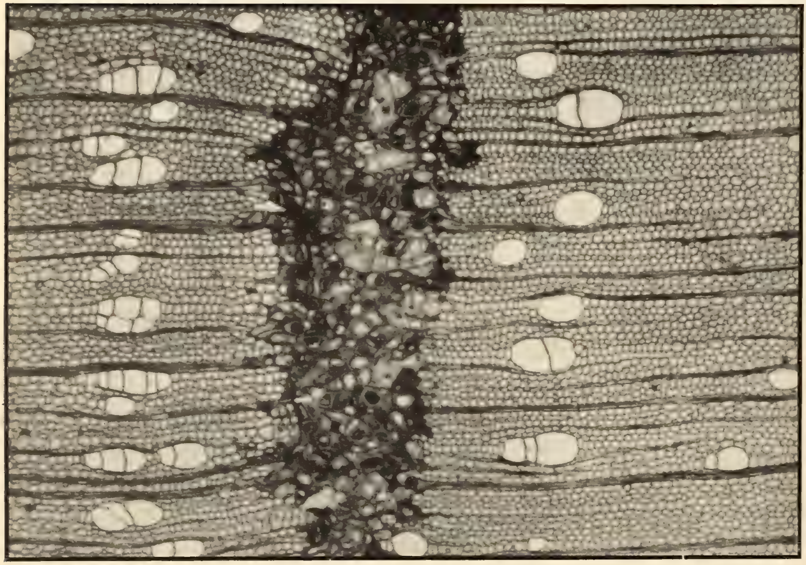


FIG. 1.—TRANSVERSE SECTION OF RIVER BIRCH, SHOWING PITH FLECKS. MAGNIFIED 60 DIAMETERS.

FIG. 2.—BARK OF RIVER BIRCH REMOVED, SHOWING DISTRIBUTION OF THE MINES OF LARVÆ.

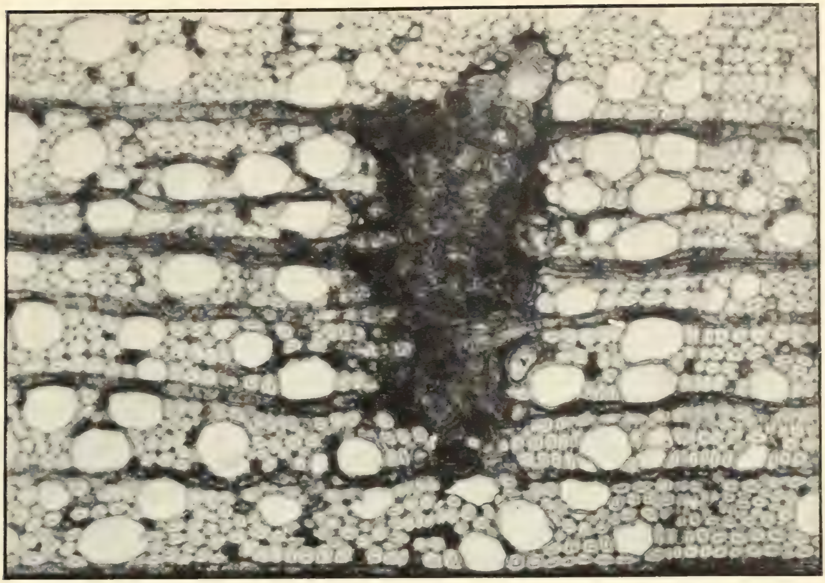


FIG. 2.—TRANSVERSE SECTION OF SERVICEBERRY, SHOWING ONE PITH FLECK. MAGNIFIED 120 DIAMETERS.

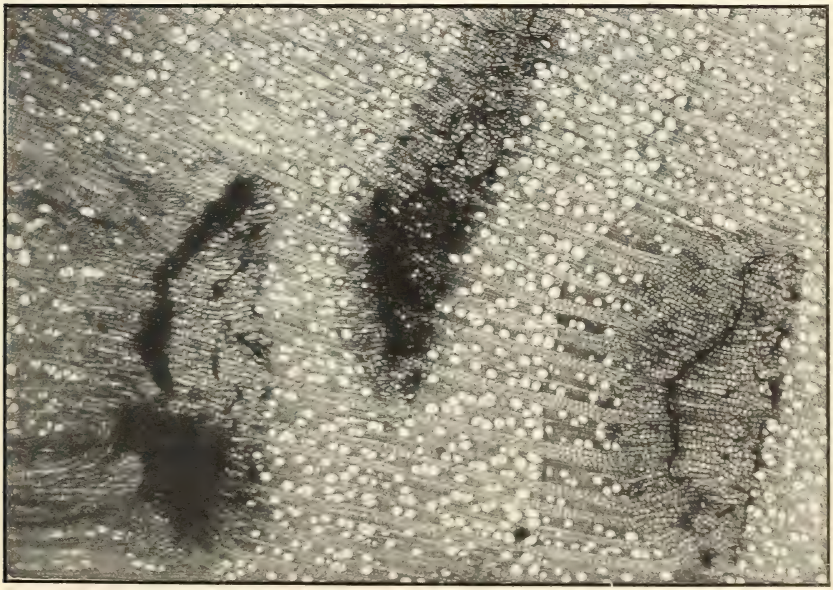
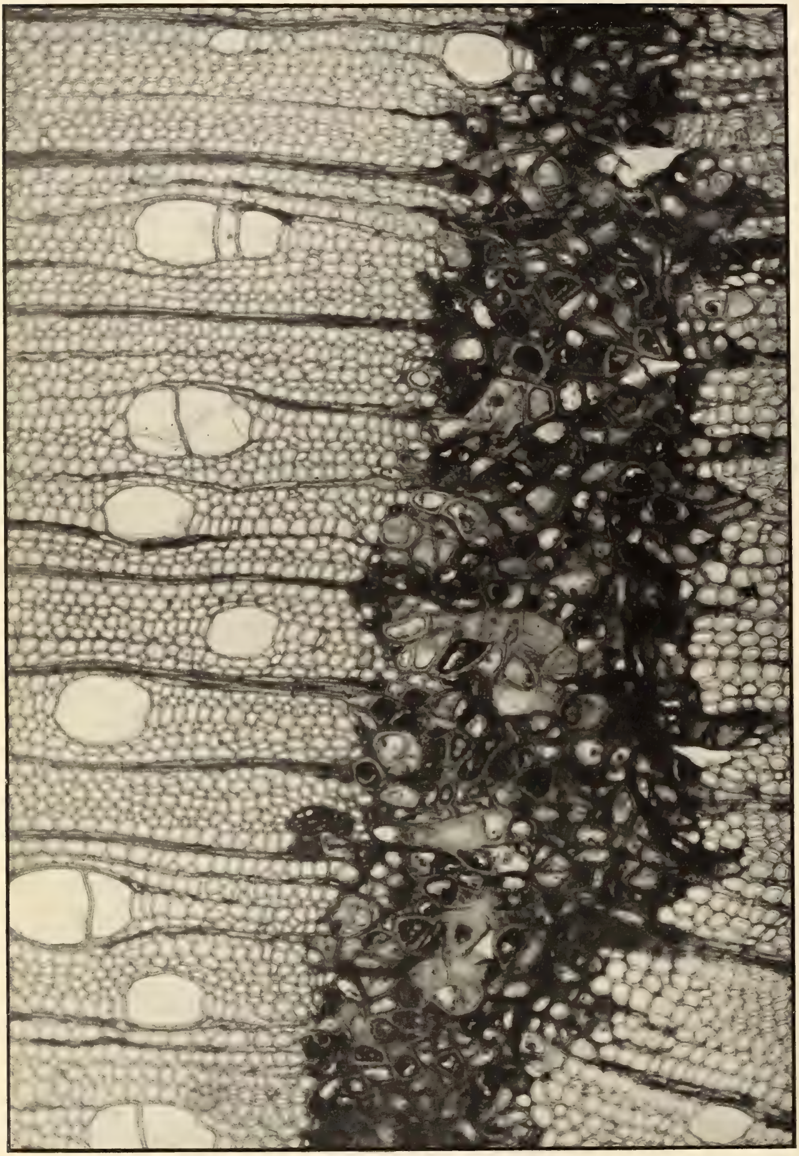


FIG. 1.—TRANSVERSE SECTION OF WILD PLUM, SHOWING THREE PITH FLECKS. MAGNIFIED 30 DIAMETERS.



TRANSVERSE SECTION OF RIVER BIRCH THROUGH PITH FLECK, SHOWING CONNECTION BETWEEN WOUND TISSUE AND PITH RAYS. MAGNIFIED 150 DIAMETERS.

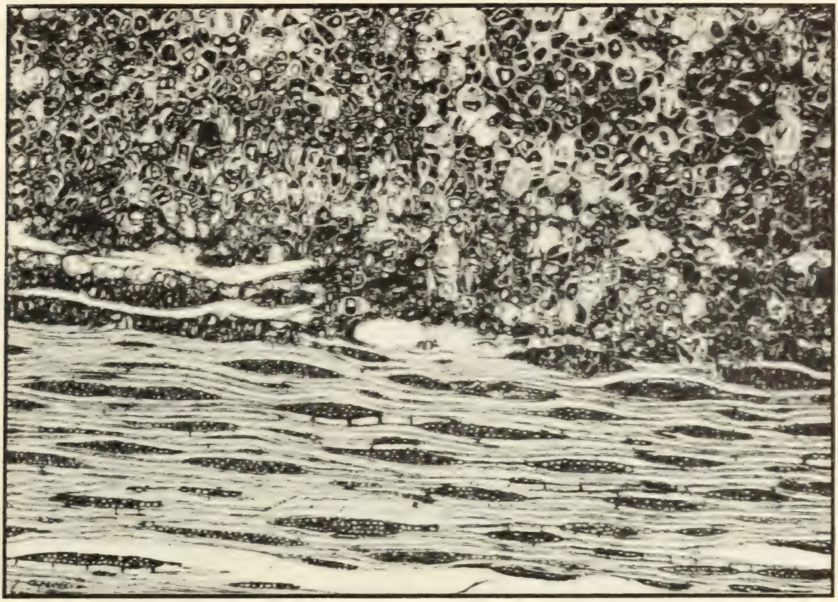


FIG. 2.—TANGENTIAL SECTION OF RIVER BIRCH THROUGH WOUND TISSUE OF PITH FLECK AT THE TOP. MAGNIFIED 120 DIAMETERS.

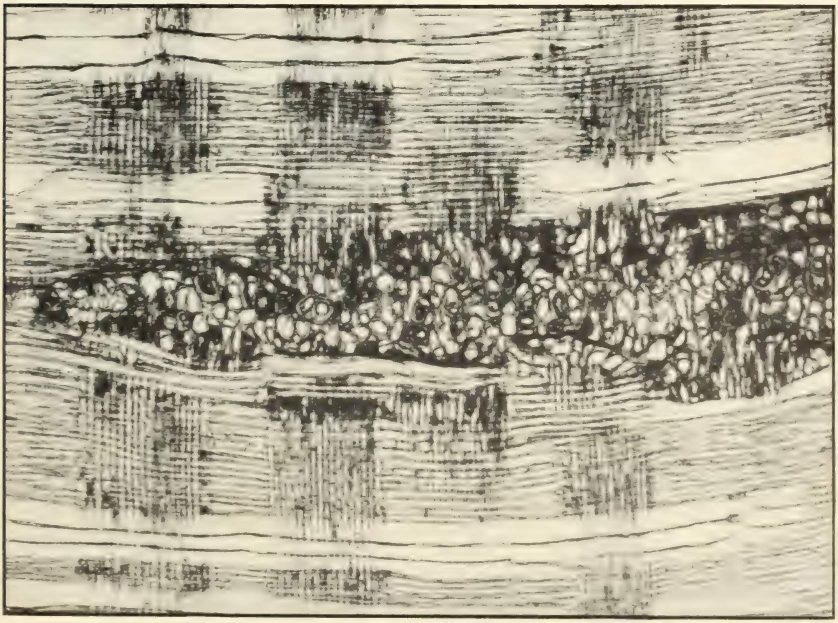
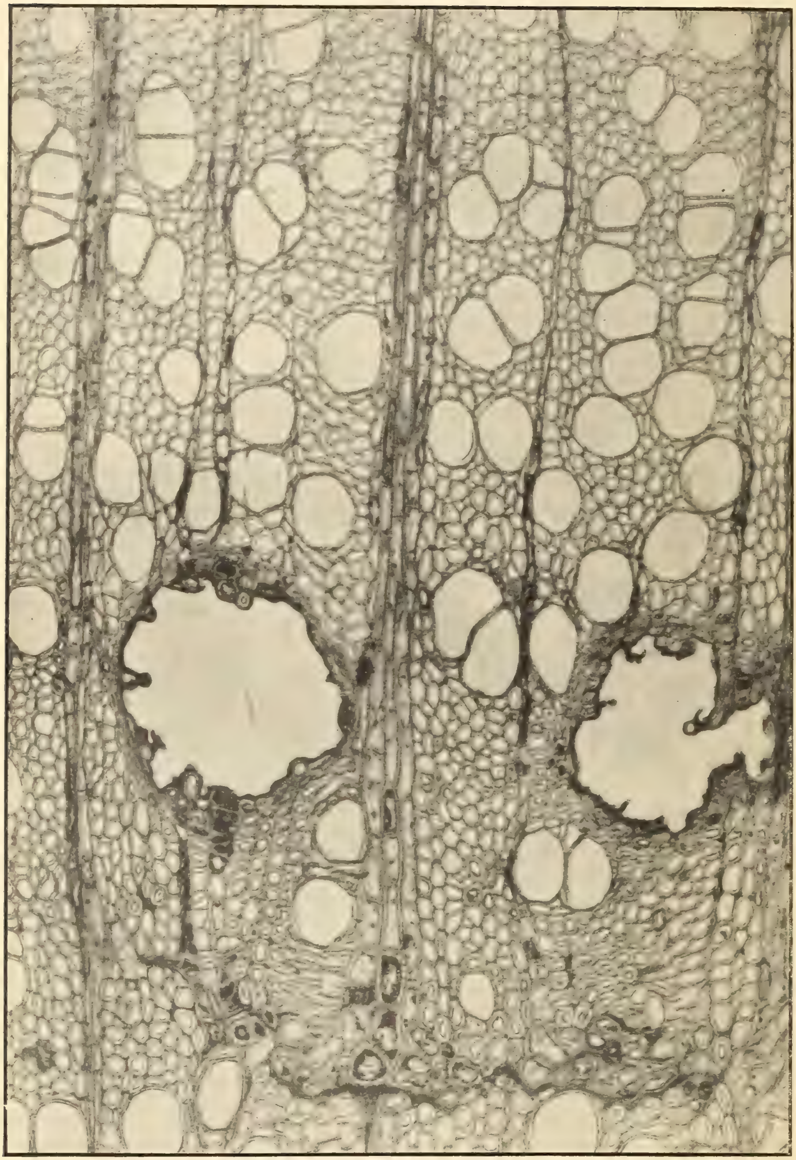


FIG. 1.—RADIAL SECTION OF RED MAPLE THROUGH A PITH FLECK, SHOWING CONNECTION WITH PITH RAY. MAGNIFIED 120 DIAMETERS.



TRANSVERSE SECTION OF BLACK CHERRY, SHOWING TWO CAVITIES CAUSED BY GUMMATION OF WOUND TISSUE. MAGNIFIED 150 DIAMETERS.

long, as in river birch, the wound tissue consists of cells with correspondingly larger cavities. Division in this case takes place more tardily. Even under the stress of wound stimulus, the inherent character of cell formation persists. There seems, then, to be a definite relation between the ray cells and the cells of the wound tissue. The relation, however, of the vessels to wound tissue is more obscure. In woods with small vessels there is usually a corresponding reduction in the cells of the wound tissue; while in woods with large vessels the reverse is true. Though no logical reason can be given for such a relation, present observations confirm it.

When viewed in tangential (bastard) section, the passages appear as broad bands of wound tissue. All appearance of pith-ray formation is lost. The cells are commonly isodiametric and polygonal in form (Pl. V, fig. 2), resembling in some respects the cells of the pith or medulla. A radial view (Pl. V, fig. 1) presents no new characters. The wound tissue is not as extensive in this section, however, since the larva works only in the cambium.

GROUPS AND SPECIES OF TREES AFFECTED.

Pith flecks are present in a greater number of tree species than is generally supposed. Nordlinger reported them as occurring in 41 genera, included in 27 families. A critical examination of sections prepared by him increased the list of hosts still further. It is possible that the markings found are all the work of the larvæ of a dipterous insect, but only extensive observations can determine this. That they are all caused by cambium miners is, however, apparent. No other injury would heal in the manner described.

As far as determined by the present investigation, pith flecks occur in only 5 families of trees in the United States, namely, the Salicaceæ, Betulaceæ, Rosaceæ, Aceraceæ, and Tiliaceæ. The following is a tentative list of woods indigenous to the United States in which pith flecks were observed:

SALICACEÆ.

Common name.	Botanical name.
Bebb willow	*Salix bebbiana* Sargent.
Long leaf willow	*Salix fluviatilis* Nutt.
Hooker willow	*Salix hookeriana* Baratt.
Smooth leaf willow	*Salix lævigata* Bebb.
Black willow	*Salix nigra* Marsh.
Nuttal willow	*Salix nuttallii* Sargent.
Silky willow	*Salix sitchensis* Sans.
Narrowleaf cottonwood	*Populus angustifolia* James.
Balm of Gilead	*Populus balsamifera* Linn.
Cottonwood	*Populus deltoides* Marsh.
Largetooth aspen	*Populus grandidentata* Michx.
Aspen	*Populus tremuloides* Michx.
Black cottonwood	*Populus trichocarpa* Torr. & Gr.

BETULACEÆ.

Common name.	Botanical name.
River birch	*Betula nigra* Linn.
Paper birch	*Betula papyrifera* Marsh.
White birch	*Betula populifolia* Marsh.
Hornbeam	*Ostrya virginiana* (Mill.) Koch.
Lanceleaf alder	*Alnus acuminata* H. B. K.

ROSACEÆ.

Serviceberry	*Amelanchier canadensis* (Linn.) Medic.
Western serviceberry	*Amelanchier alnifolia* Nutt.
Mountain ash	*Pyrus americana* (Marsh.) de C.
Narrowleaf crab	*Pyrus angustifolia* Ait.
Wild apple	*Pyrus malus* Linn.
Oregon crab	*Pyrus rivularis* Dougl.
Elderleaf mountain ash	*Pyrus sambucifolia* Cham. & Schl.
Allegheny sloe	*Prunus alleghaniensis* Porter.
Wild plum	*Prunus americana* Marsh.
Sweet cherry	*Prunus avium* Linn.
Sour cherry	*Prunus cerasus* Linn.
Western choke cherry	*Prunus demissa* (Nutt.) Walp.
Bitter cherry	*Prunus emarginata* (Dougl.) Walp.
Garden wild plum	*Prunus hortulana* Bailey.
Hollyleaf cherry	*Prunus ilicifolia* (Nutt.) Walp.
Wild red cherry	*Prunus pennsylvanica* Linn.
Black cherry	*Prunus serotina* Ehrh.
Choke cherry	*Prunus virginiana* Linn.
Summer haw	*Cratægus æstivalis* (Walt.) Torr. & Gr.
Dotted haw	*Cratægus punctata* Jacq.

ACERACEÆ.

Striped maple	*Acer pennsylvanicum* Linn.
Red maple	*Acer rubrum* Linn.
Silver maple	*Acer saccharinum* Linn.

TILIACEÆ.

Basswood	*Tilia americana* Linn.

GEOGRAPHIC DISTRIBUTION OF THE CAMBIUM MINER.

The geographic distribution of the cambium miner can not be definitely fixed at present, because of the uncertainty of the source of many of the wood samples examined and of the difference in susceptibility of the same host in different situations. Nordlinger's list of woods includes species that grow throughout a vast area, and shows that pith flecks occur in wood of all tropical and temperate regions. Many European species examined contained them. Further investigations of foreign woods will doubtless increase the number of host trees. From the list of indigenous trees given it is seen that the insect producing these flecks is quite generally distributed over the United States. The extent to which different genera and different species of the same genus are affected varies. Wood specimens of red maple from Pennsylvania and from Florida were abundantly infested, while those of the western maples were comparatively free. No western species of *Cratægus* seem to be immune, but this conclusion can be established only by further investigation. The genus *Pyrus* leads in number of species affected. It does not follow, however, that trees of this genus form the favorite hosts. As already mentioned, river birch is most often infested in Maryland and Virginia. There appears to be a peculiar local susceptibility of certain species. White birch, for example, is quite commonly infested throughout the New England States, but near the southern limit of its range the wood is usually entirely free of mines. Its successor in range farther south, river birch, becomes the favorite host. It is probable that this peculiar distribution of the insect's work holds also for the willows and poplars.

FACTORS AFFECTING LOCAL DISTRIBUTION OF LARVÆ AND PASSAGES.

Topography has little to do with the local distribution of the larvæ. Trees growing on uplands were found to be infested fully as often as those at lower elevations. It is not at all probable that bark characteristics have anything to do with the likelihood of infestation, since the mines can be traced to the young bark, which in thickness and smoothness is much the same on all trees. Organic infiltrations in the cortex may cause immunity in certain hosts. Tannin, perhaps, accounts for the total absence of the mines in American oaks. Resin is doubtless a preservative. Kraus reported pith flecks in the firs, spruces, and cedars (*Juniperus*), but later writers contradict this. Penhallow notes the formation in some coniferous woods of traumatic resin canals, which might be easily mistaken for pith flecks in a cursory examination.

The distribution of pith flecks in individual trees is readily inferred from the life history of the larvæ. Samples of wood taken from near the transition point of root and stem in infested trees show the mines in the greatest abundance. This is due to the frequent trips by the larvæ back and forth prior to pupation. The number of mines decreases rapidly after the first 10 feet above the ground. Above that distance, in transverse section, there is usually only one pith-ray fleck per larva.

The adult evidently deposits its eggs in the younger branches of the tree's crown. The larva, upon hatching out, burrows straight downward until near the ground, then makes several turns, as previously described. In red maple and river birch mines were traced about 40 feet down the stem with only slight deflections, and without a turn before reaching the base of the tree. The tangential diameter is at first very small and rarely over 5 mm. even in the roots. The majority of mines are well within the margin of annual rings of growth; they rarely border on the spring or autumn wood of other rings. The larva begins its wanderings some time after growth begins and stops before the end of the growing season.

Nordlinger states that in certain species the mines are always in close proximity to the pith. This doubtless was correlated with bark characteristics because certain hosts were attacked only during their early existence. The present investigation, however, indicates that pith flecks in the eastern American hosts at least occur throughout the whole transverse section of the basal log. A large specimen of river birch was examined on July 22. The age could not be accurately determined, but a conservative estimate would place it at about 110 years. Many mines were observed at the base of the tree in the last season's growth. Other trees ranging from 10 to 80 years were found to be infested with the larvæ. In at least one species, river birch, both the young and the old trees are frequently attacked.

TAXONOMIC VALUE OF PITH FLECKS.

Early writers on wood ascribed a taxonomic value to pith flecks and efforts were made to use them in separating genera and species. If the distribution in certain genera were constant, the importance of these markings would be readily apparent. Record has pointed out, however, that they are of no value in this connection. The present investigations confirm his observations and considerably enlarge the list of infested woods. Pith flecks are clearly of pathologic origin, and their distribution in genera, species, and individuals is extremely irregular and uncertain. Their presence or absence, therefore, can not be used to identify woods.[1]

DETERIORATIVE EFFECT ON QUALITY OF WOOD.

Among the important quality factors of wood are strength, elasticity, texture, and freedom from knots and discolorations. Any agent that adversely affects one of these qualities may decrease the commercial value of the wood. Pith flecks may mar the natural beauty of woods by causing discolorations. In some woods pith flecks cause definite areas of disintegration in which normal tissues become involved. Intercellular spaces or cavities may thus arise.

The discoloration due to the work of dipterous larvæ arises from two causes. In all native species (except the willows and poplars) marked with pith flecks (pp. 9 and 10) the cavities of the newly formed wound cells become filled with a dark-brown substance responding to tannin

[1] Logically, of course, no pathologic condition or other accident could have any taxonomic value.

reactions.[1] This color serves to differentiate sharply the wound tissue from the normal cells surrounding it and renders the closed mines conspicuous in transverse sections (Pl. III). This is true particularly of light-colored woods, such as birches and maples. In cherry, however, owing to the similar color of the wood, the mines are quite inconspicuous, provided other pathological changes described herein, do not occur.

In maple (Pl. I, fig. 2) and birch the mines stand out in tangential or radial sections as brown spots or lines of varying magnitude, which run in the direction of the fibers. This renders the wood inferior in quality and useless for the finer grades of cabinetwork. The defect is emphasized for woods finished in the natural color, since filling and varnishing renders the spots still more distinct. Pith flecks are, however, frequently seen in all the cheaper grades of furniture. In veneers the injury is a still greater factor. Badly infested cherry is often useless for this purpose.

Another cause of discoloration is the result of interference with the normal physiological activities of the tree [2] where the medullary rays are broken by mining larvæ. The wood adjoining the mine for varying distances toward the center darkens prematurely and changes into heartwood. These discolored areas rarely cover more than two annual rings of growth, but in some of the poplar woods they were observed to extend through as many as eight annual rings. In other wood the discoloration, as a rule, is comparatively slight, serving mainly to render the occluded mines more conspicuous and rarely extending beyond the growth of the season.

Disintegration of woody tissue due to pith flecks was observed only in the wood of cherry. In various species of this genus there is a breaking down or disintegration of the tissue, accompanied by the usual formation of "cherry gum." This process is technically known as "gummation."[3] The correlation of pith flecks with the disintegration or liquefaction of normal woody tissues was probably first noted by Wiegand in 1863. He found that in sweet cherry pith

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[1] In willow and poplar wood the occluded mines are often quite inconspicuous, owing to a lack of coloring matter in the wound tissue.

[2] The medullary rays of the wood continue out through the growing layer into the inner bark. Here they are in direct communication with the sieve tubes of the bast, and serve to conduct food material elaborated in the leaves to the growing layer of the wood. They consist of comparatively thin-walled cells that form, with the wood parenchyma, the living portion of the xylem. The other wood elements lose their protoplasmic contents soon after their formation, after which they perform the function mainly of water and air conduction. The wood parenchyma, however, lives for a number of years intimately associated with the physiological activities of the tree.

[3] Many conflicting opinions are held regarding the origin of cherry gum. Mikosch considers it a pathological product which follows the wounding of the cambium, and asserts that its formation takes place within the inner portions of the cambial layer. Rant ascribes its formation to three factors: (*a*) new formation of tissue, (*b*) liquefaction, (*c*) activity of the dead cells as a wound stimulus through necrosis. The latter may result through physiological influences or through the traumatic working of foreign organisms, such as bacteria, fungi, or animals. Ruhland further infers that oxygen is necessary for the process, and that in wounds where air is excluded no gummation results.

flecks are the principal starting points in gummation. His observations have been confirmed by more recent investigations.

In the present studies of the wood of cherry some mines were found filled with wound tissue of the usual type, while in others gummation was well under way (Pl. VI). There was apparently no distinction in species or individuals as regards the formation of gum. All species of cherry subject to pith flecks are also susceptible to the breaking-down process. This can be expected from the results obtained by Mikosch and Rant.[1]

The discolored spots produced by gummation in cherry wood often render it unfit for the finer grades of furniture. This defect is often directly traceable to pith flecks. Where the mines remain occluded with normal wound tissue, little injury results, owing to the similar coloration of the surrounding wood with that of the wound tissue. It is with the inception of gummation that the injury really begins. The disintegration thus started often spreads until the sound tissue is affected.

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[1] As previously noted, the larvæ live in the cambial zone and destroy the growing or dividing cells by sucking their contents. The burrow thus formed by the larva is partially filled with the remnants of dead cell walls and excrement of larvæ. It is still open to doubt whether gummation begins immediately before the wound tissue forms or whether the latter first fills the mines and then breaks down. Mines were found which presented all stages of development. Some were completely filled with normal wound tissue; while in others disintegration had affected a part of the cells. In some instances no wound tissue was in evidence; here the mines in cross section appeared like openings in the otherwise normal tissue. It is difficult to say whether the gum in such instances arose from the liquefaction of the dead cell walls or, as is more probable, from the wound tissue formed subsequent to the passage of the larvæ. Either theory may be reconciled with the deductions of Mikosch and Rant.

Regarding Ruhland's theory concerning the necessity of oxygen in the process, little can be said. It perhaps accounts for the absence of gum formation in some of the mines. Where gummation does occur it can hardly be ascribed to atmospheric oxygen. It is highly improbable that the latter would penetrate the mine for any great distance, owing to the small opening at its inception and to the rapid formation of wound tissue after the passage of the larva.

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