THE DEVELOPMENT OF SOME SPECIES OF AGARICS

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The species of Agaricaceae whose lamellae are endogenous in their origin have in recent years been given considerable attention. The structural variation of a number of forms has been observed and studied. As a result a number of interesting morphological features have been explained and their development demonstrated. But very little attention has been given to those species whose lamellae are exogenous in their origin. It is important that the morphological characters of both forms be studied from their origin, beginning with the young, undifferentiated basidiocarp and tracing their development to the mature fruit body.

Hoffmann was the first to give serious attention to the development of Agaricaceae. In 1856 (13) he described *Panus torulosus*, showing that the lamellae are exogenous in their origin. He observed the hyphae of the young basidiocarp to diverge at the apical end, and noted the subsequent development of the pileus.

In 1860 (14) and 1861 (15) he followed this work with a description of a number of forms, the greater portion having an exogenous origin of the lamellae. He observed the early stage of the palisade layer, preceding the origin of the lamellae, to be level.

DeBary in 1859 (6) and 1866 (7) described *Nyctalis asterophora*, *N. parasitica*, *Collybia dryophila*, and others. In the main he agreed with Hoffmann’s observations, with the exception of the condition of the palisade layer just previous to the development of the lamellae. DeBary stated that this layer was folded from the first. He later (8, 9) agreed with Hoffmann.

Fayod (11) in 1889 described a number of forms. He concludes that the pileus primordium is endogenous in origin in all Agaricaceae.

Since Fayod’s work there are no published studies on the development of exogenous forms. In view of these facts, it appeared to me that it would be interesting to study the development of certain species whose lamellae are exogenous in origin.

Material.—Basidiocarps of three species in all stages of develop-
ment were collected, August and September, 1915, near Seventh Lake, Adirondacks, N. Y. One species, *Clitocybe adirondackensis*, was collected late in September of the same year in Coy Glen, near Ithaca, N. Y.

*Omphalia chrysophylla* was found growing on a coniferous log which was not very far along in decay. The season being unusually wet, quite sufficient moisture was present, which produced a very luxuriant growth. The cells and structure of this species stand out with unusual clearness, due, very likely, to the firmness of the cell walls.

*Clitocybe adirondackensis* was found growing gregariously among leaves on a steep hillside under coniferous trees. The whitish mycelium growing through and among the decaying leaves, spread over a space equal to about three square feet.

*Clitocybe cerussata* was growing in leaf-mold under coniferous trees. The mycelium was very abundant and spread in all directions.

*Clitopilus nubeculosus* was growing in leaf-mold in a mixed forest. Its habit is gregarious. The white mycelium in forms of hyphal strands permeated the substratum, covering an area equal to about four feet square.

The basidiocarps were fixed immediately in Carnoy's fluid, cleared in cedar oil, embedded and sectioned in paraffine.

**Omphalia chrysophylla** Fries

*Basidiocarp Primordium.*—The youngest stages obtained of this species were small, elongate bodies, averaging 50μ in diameter and 780μ in length (Fig. 1). They are larger at the base and gradually taper to a blunt point at the apex. At this stage of development they consist of a homogeneous web of slender threads, measuring 3.5μ in diameter. Their general direction is parallel with the axis of the young fruit body. The number of hyphae is increased by branching which takes place more abundantly toward the base in the young basidiocarp. The more peripheral hyphae end on the surface at varying distances from the tip, while central ones converge at the apex (Fig. 18), thus giving to the young fruit body its slender form.

*Stipe Primordium.*—The stipe primordium develops by continued growth of the hyphae that compose the undifferentiated basidiocarp and is not differentiated as such, until the origin of the pileus primordium; even then there is no definite line separating it from the pileus (Fig. 3).
In Figure 2, a slightly older stage, the hyphae at the base are more loosely interwoven. This results largely from the increase in the length of the threads and contributes to the enlarging of the base of the young basidiocarp. As the plant develops the hyphal cells increase in size until in the stage represented by Figure 3, they average 4 to 5μ in diameter and 10 to 20μ in length. The hyphae near the surface are more closely interwoven.

*Pileus Primordium.*—In Figure 19 (a higher magnification of a portion of the apex of Fig. 2) the apex has increased in breadth by a slight spreading of the hyphae and by interstitial growth of its elements. There is no differentiation in staining, but the whole structure has the appearance of very active growth. In a little later stage, Figure 20, the growth direction of these apical threads is out and upward, with a slight tendency, of the lateral ones, to epinasty. At the same time profuse branching takes place which supplies new elements that interlace and ramify among the older ones. Thus, in a longitudinal section, a weft of closely interwoven hyphae is presented, except at the periphery where the terete ends of hyphae, advancing in growth, project (Figs. 20 and 21). This divergent growth of the hyphae at the apex of the young fruit body marks the origin of the pileus and differentiates it from the stipe primordium. The origin of the pileus primordium corresponds very closely to that described by DeBary in *Nectalis asterophora, N. parasitica* (6), and *Collybia dryophila* (8, 9).

*Further Differentiation of the Pileus.*—By continued growth of the primordial elements the pileus is delimited from the stipe in the following manner: The central hyphae continue to grow toward the surface, some curving outward more than others. This growth is accompanied with vigorous branching and interlacing of hyphae, which add new elements. In this way the inner structure of the pileus is formed (Figs. 3–6). At the same time the hyphae, by branching and growing in a radial direction, accompanied by strong epinasty, curve downward and form the margin of the young pileus (Fig. 22). By this radial and downward development of the margin of the pileus an annular groove, Figure 6, is formed on the surface of which is the hymenophore primordium. Figures 3–6 show the gradual development from the primordial condition of the pileus to that stage in which it is well differentiated from the stipe.

The pileus continues to increase in thickness and diameter in a
manner similar to that described above and gradually changes to a broadly convex form with an incurved margin (Figs. 7–10).

**Hymenophore Primordium.**—Simultaneously with the formation of the annular groove by epinastic growth of the marginal hyphae, the hymenophore primordium is differentiated by the rich content in protoplasm of the hyphae forming the external annular zone in the furrow. They are crowded, and stained deeply as shown in longitudinal section (Fig. 6).

The annular region is composed of more or less blunt and cylindrical ends of numerous hyphal branches which have their origin both in the stipe and pileus elements. Their growth direction is obliquely out and downward. The oldest are on the stipe and by centrifugal development new elements are added to this area near the margin of the pileus which continues to curve down over this surface. Figure 22 is a median longitudinal section of the fruit body at this stage of development and shows this structure in detail.

At first this annular primordial layer curves out and upward at an angle of about 45°. As the pileus expands and becomes more convex, new primordial elements are introduced by branching and interstitial growth in centrifugal succession as above described. This causes it to curve in the form of an arch (Figs. 7–8).

Since the development is centrifugal it must be borne in mind that, at the time this layer is in the primordial stage at the margin of the pileus, near the stipe it will be further differentiated.

**Palisade Layer; Origin and Development of the Lamellae.**—The hyphae of the hymenophore primordium branch in a digitate manner. By this branching new elements are interpolated in the spaces between the older hyphae. This process continues gradually until a compact layer of short hyphae is formed. Simultaneously with this the cells enlarge, especially the terminal ones, and the surface smooths up into an even, compact layer (Fig. 23). This is the palisade layer and precedes the origin and development of the lamellae, as has been described for a number of endogenous forms. The differentiation of the palisade layer appears first near the stipe and progresses centrifugally toward the margin of the pileus, as did the development of the hymenophore primordium. As the cellular elements of the palisade layer increase in size, a great pressure is produced within this structure. This pressure is released to some extent by the palisade layer being thrown into equally spaced, radial folds beginning near the stipe (Fig. 12).
Simultaneously with this, subadjacent hyphae along radial areas corresponding with the gill areas, by elongation, push their way downward and govern the origin of the gill salients. Figures 24 and 25 show this feature in excellent detail. These down-growing salients of the level palisade layer are the first evidence of the appearance of the lamellae. Continued growth of these salients produces the lamellae, as observed in species of Agaricus (1, 2, 4), Coprinus (5), Cortinarius (10), etc.

The subhymenial hyphae are branched in a corymbose manner, Figure 27, and supply new elements within the hymenophore layer. Figure 28 is a higher magnification of a portion of Figure 27 and shows in detail the corymbose branching.

Growth in width of the lamellae occurs by the further elongation of the trama of the lamellae which branch as above described. These new elements are interpolated between the older hyphae at the edge of the gill.

The development of the lamellae is centrifugal as are the structures preceding their origin. Therefore the oldest portions of the lamellae are nearest the stipe and proceed in a radial direction to the margin. Since the margin of the pileus is involute, a tangential section through that portion of the fruit body parallel with the axis of the stipe will present an appearance as represented by Figure 16. Below, it shows a portion of the inrolled pileus edge. This relation of the gills to the involute margin of the pileus has been adequately described by Atkinson for Agaricus rodmani (4).

Structure of Stipe and Pileus.—As the basidiocarp grows the stipe becomes even in diameter. This results largely from the elongation of the peripheral hyphae and more abundant branching in the upper portion of the stipe, together with the enlargement of the cellular elements. The process is a gradual one, as Figures 3–9 show.

The pileus at the same time increases in all its dimensions and becomes more expanded (Fig. 10). The general direction of its elements is horizontal and radial (Fig. 29). Those on the surface are more closely interwoven, and this serves to produce a smooth surface. Figure 30 is a high magnification of a portion of the pileus which shows this structure very clearly. The hyphal cells have very firm walls and are exceedingly large, measuring 7 to 8μ in diameter.
CLITOCYBE ADIRONDACKENSIS PECK

Basidiocarp Primordium.—The undifferentiated basidiocarps of this species are long, slender bodies, tapering toward the apex. They are usually curved or bent in various directions. Those studied measure 60μ in diameter and 1 mm. to 2 mm. in length. The hyphae are very slender, wavy threads, averaging 1.5μ in diameter. They run in a longitudinal direction (Figs. 31 and 41). The central hyphae extend to the apex where they converge into a blunt point. The peripheral ones end in such a manner as to form a slanting surface from the base to the apex. There is no differentiation at this time, the whole fruit body staining homogeneously.

Pileus Primordium.—At the time the stipe fundament is delimited from that of the pileus, the apical hyphae grow upward and spread out in all directions. In this feature it is similar to that of Clitopilus novoboracensis, which is described below. The hyphal elements are long, slender and terete. This is the pileus primordium (Fig. 84). By continued radial and diverging growth of its elements the pileus fundament increases in size (Figs. 72, 77). This gives rise to a hemispherical body which is delimited from the stipe by the annular groove (Figs. 72-74). Further epinastic growth causes the margin to curve inward toward the stipe (Fig. 76). At this time the plant has assumed a beautiful and symmetrical form. In Figure 77, the pileus has enlarged and the margin has become so strongly involute that the edge turns upward against the gills. The hyphae do not grow out from the margin of the pileus nearly so strongly as in Clitopilus novoboracensis.

Hymenophore Primordium.—The hymenophore fundament is differentiated in the annular groove between the pileus and stipe and stains deeply. This area develops in a radial manner, following the centrifugal growth of the pileus, characteristic of the Agaricaceae. This area consists of short hyphae perpendicular to the surface of the annular groove. It becomes more dense by interpolation of new elements which are formed by digitate branching of the primordial hyphae.

Palisade Layer; Origin and Development of Primary Lamellae. — As the hymenophore becomes more compact by intercalary growth, the cells themselves increase in size. The end of the hyphae reach the same level and form an even palisade layer, as shown in Figure 78. A higher magnification is shown in Figure 85. The hyphal elements that compose this layer are longer than those of the other species described in this paper, and are comparatively slender. As the elements increase in number and size, the resulting pressure is partly relieved by the level palisade layer bulging out into radial fold-like ridges. These ridges are the gill fundaments. In this species, as in Clitopilus novoboracensis, they occur first on the stipe very near the angle between the latter and the lower surface of the pileus (Fig. 79). Later the gill salients of the primary lamellae appear.

Further differentiation of the pileus is the result of continued growth of this primordial tissue. Around the upper lateral surface of the stipe primordium and on the under side of the young pileus, the ends of the diverging hyphae stain deeply and mark the origin of the hymenophore fundament (Fig. 33). The central apical hyphae continue their growth upward and by profuse branching add materially to the thickness of the pileus, while the intermediate elements bend gently outward.

By continued branching and interstitial growth of its elements the pileus increases in diameter. At the same time the central hyphae, as compared with those of the periphery, elongate less rapidly. Thus the intermediate and peripheral threads, growing upward and outward at an oblique angle of about 45°, cause the pileus to become plane on its upper surface (Fig. 35). The marginal hyphae at the same time continue to curve abruptly downward. In this way a shallow and very narrow annular groove is formed.

In later stages in the under portion of the pileus next the stem, hyponasty replaces epinasty. The form of the pileus consequently changes from plane to umbilicate, and then to infundibuliform, while
epinasty continues to have its influence on the thin younger margin which is incurved or involute.

Structure of the Stipe.—At the appearance of the pileus fundament, the stipe primordium is clearly differentiated as a definite region. At this stage the apparently homogeneous structure of the stipe primordium is changed by the loosening up of its texture. There are strands of tissue running longitudinally through the stipe. These strands stain very deeply, causing them to stand out conspicuously. They intertwine with others in anastomosing fashion, thus forming intervening hyphal spaces.

The stipe elongates by the lengthening of the cells. These elements, in the stage of development represented by Figure 40, measure 3–30μ in length. The increase in width is the result of branching and interstitial growth of the hyphae, and also by the increase in diameter of the cells themselves, which average 3.5 to 4μ. In more mature plants increased thickness is chiefly the result of the latter, as Hoffmann (14) on page 394 suggested.

Hymenophore Primordium.—The organization of the hymenophore primordium occurs simultaneously with that of the origin of the pileus margin. Like it, too, the development is centrifugal. The first differentiation of this tissue is in the angle between the pileus margin and stipe and on the upper surface of the stem. Because of the active increase in its elements and their richness in protoplasm the young hymenophore primordium takes a dense stain.

As the pileus increases in width, its marginal hyphae add to this annular zone so that its surface is increased radially and upward (Fig. 43). Its elements multiply by intercalary growth and present a frizzled appearance, as observed in Coprinus comatus (5), Agaricus rodmani (4), and some other plants.

Palisade Layer, Origin and Development of the Lamellae.—By continued branching of the hyphae, the zone of primordial elements organize a definite layer of parallel threads which becomes more or less even on the surface since the ends of the hyphae reach the same level. This results in forming a compact layer of parallel threads perpendicular to the surface. Figure 44, is a transection through the upper part of the stipe and shows a portion of this structure immediately beneath the curved pileus margin. The hyphal elements of this layer are slender, cylindrical, septate threads, 4.5–6μ in diameter and 35μ in length. The terminal cell is longer than the others of the
same thread and slightly larger, which tends to give a clavate appearance to the threads. The cells are rich in protoplasm and present an appearance of active growth.

_Hymenophore Primordium._—The lamellae make their first appearance as folds of the level palisade layer. These folds are the rudiments of the lamellae themselves. They appear on the surface at or near the apex of the stipe, Figure 36, and by progressive growth extend out and upward on what is the morphological underside of the pileus. By downward growth of hyphae subadjacent to these folds, the trama of the lamellae is formed (Figs. 45-46). These tramal threads are differentiated from the other elements of the hymenophore by the fact that they do not stain so deeply. These threads branch and furnish new elements by which the lamellae grow in thickness and at the same time by apical and intercalary growth the lamellae increase in width (Fig. 47).

The tissue of the pileus and stipe subadjacent to the hymenophore is peculiar because of extraordinary large interhyphal spaces, due to the extension exerted by the pressure from interstitial growth and enlargement of the elements of the hymenophore.

The lamellae develop in length in a radial centrifugal direction, following that of the palisade layer. They are decurrent from the beginning, since the hymenophore has formed around the upper lateral surface of the stipe (Figs. 36-40). At the base of the older ones, other lamellae sometimes branch off, developing in a manner described for the primary gills (Fig. 37). These form the forked lamellae sometimes present in this species. Secondary lamellae also arise between the diverging primary gills, filling the spaces between them.

_Clitocybe cerussata Frings_

_Basidiocarp and Stipe Primordia._—The youngest basidiocarps of this species which were collected measure .5 mm. in diameter and 2 mm. in length (Fig. 70). They are composed of slender interlacing hyphae, measuring 3μ in diameter, which form a close interwoven tissue. Their general direction is longitudinal, converging at the apex (Fig. 83). This homogeneous structure is the primordium of basidiocarp and stipe.

By continued growth of this primordial tissue the stipe fundament is finally differentiated by the formation of the pileus primordium which is marked off by the divergence of the apical hyphae. As the stipe
becomes older the hyphae are more loosely interwoven (Fig. 7). Its further growth is provided for by means of branching and elongation of its elements.

Pileus Primordium.—At the time the stipe fundament is delimited from that of the pileus, the apical hyphae grow upward and spread out in all directions. In this feature it is similar to that of Clitopilus noveboracensis, which is described below. The hyphal elements are long, slender and terete. This is the pileus primordium (Fig. 84).

By continued radial and diverging growth of its elements the pileus fundament increases in size (Figs. 72, 77). This gives rise to a hemispherical body which is delimited from the stipe by the annular groove (Figs. 72–74). Further epinastic growth causes the margin to curve inward toward the stipe (Fig. 76). At this time the plant has assumed a beautiful and symmetrical form. In Figure 77, the pileus has enlarged and the margin has become so strongly involute that the edge turns upward against the gills. The hyphae do not grow out from the margin of the pileus nearly so strongly as in Clitopilus noveboracensis.

Hymenophore Primordium.—The hymenophore fundament is differentiated in the annular groove between the pileus and stipe and stains deeply. This area develops in a radial manner, following the centrifugal growth of the pileus, characteristic of the Agaricaceae. This area consists of short hyphae perpendicular to the surface of the annular groove. It becomes more dense by interpolation of new elements which are formed by digitate branching of the primordial hyphae.

Palisade Layer; Origin and Development of Primary Lamellae.—As the hymenophore becomes more compact by intercalary growth, the cells themselves increase in size. The end of the hyphae reach the same level and form an even palisade layer, as shown in Figure 78. A higher magnification is shown in Figure 85. The hyphal elements that compose this layer are longer than those of the other species described in this paper, and are comparatively slender.

As the elements increase in number and size, the resulting pressure is partly relieved by the level palisade layer bulging out into radial fold-like ridges. These ridges are the gill fundaments. In this species, as in Clitopilus noveboracensis, they occur first on the stipe very near the angle between the latter and the lower surface of the pileus (Fig. 79). Later the gill salients of the primary lamellae appear
on the under surface of the pileus as shown in Figure 8o. In this figure, on each side of the salients, a portion of the palisade layer is shown. Since these structures develop centrifugally the first differentiation occurs on or near the stipe. Consequently in a tangential section the portion to the right or left would be cut obliquely and show tissue nearer the margin than that in the center of the section. Thus, the palisade layer represents a younger portion of the hymenophore, in which salients have not as yet made their appearance.

The development of the lamellae in width is as has been described for the previous species. The subadjacent hyphae by elongation, aid in the extension of the salients in width or keep pace with their growth. New elements are also added by intercalary growth to the palisade layer. Figures 85–89 show in detail the development of a gill from the palisade stage of the hymenophore through the first evidence of a gill salient to a well-formed lamella.

*Origin of Secondary Lamellae.*—As was described for the previous species, the salients of the secondary gills appear between the primary lamellae on the under surface of the pileus. Those that appear first occur near the stem (Fig. 81). Their development is exactly as described for the primary gills. They serve to occupy the spaces produced by the divergence of the primary gills as they proceed from the stipe.

*Structure of Pileus and Stipe.*—The more mature pileus is expanded and the hyphae arrange themselves in a radial horizontal direction. The trama is composed of hyphal threads that ramify and interlace among themselves. The stipe increases in width by branching and interstitial growth of the hyphae. In the more mature pileus and stem, growth is chiefly by the increase in size of the cellular elements.

**Clitopilus noveboracensis Peck**

*Basidiocarp and Stipe Primordia.*—The fruit bodies representing the primordial stage of the basidiocarp become comparatively large, .6 mm. in width and 2 mm. in length, before differentiation of the pileus occurs. They are elongate bodies which taper gradually to a point at the apex (Fig. 48). The young basidiocarp presents a closely interwoven structure composed of slender hyphae averaging about 3μ in diameter at the base; toward the apex they are not so stout. The general direction of the hyphae is parallel with the direction of the growth of the fruit body (Fig. 64). The whole extent of the apical
end and a portion of the peripheral hyphae stain deeply, which indicates an area of active growth.

This fundamental tissue is soon differentiated by growth direction of the apical threads as stipe primordium. At this time the inner structure of the stipe fundament is a woof of slender homogeneous hyphae, while some of the hyphal threads near the surface of the stipe, growing more rapidly than the other elements, extend outward and form a loose floccose layer. Figure 49, a median longitudinal section, shows this layer as a narrow zone which stains more deeply. This structure is composed of the dead ends of these hyphae which extend beyond the immediate surface of the stipe and is very ephemeral.

Pileus Primordium.—The origin and development of the pileus fundament agrees with the preceding species. The elements extend outward in all directions with a slight tendency to epinasty. In this species the fundament consists of a peripheral zone of long radiating hyphae and a dark staining central portion. The hyphae of both the loose and the more dense regions have the same origin; i. e., the elements of both regions are the result of radial diverging growth from the stipe fundament.

Further development of the pileus is by the continued radial growth of the hyphae. At the margin by epinastic growth the hyphae curve downward, forming the annular groove (Figs. 50, 51). In the stages represented by Figures 52–54, the hyphae branch profusely and are organized in a very compact structure, except a very thin, loose surface zone. The pileus margin develops by centrifugal growth. On the surface of the annular groove in the angle between the pileus and stipe the hymenophore fundament is organized.

In a later stage of development, represented by Figure 55, the pileus margin is so strongly involute that the edge is curved upward against the lamellae. The marginal hyphae span the intervening space between the pileus margin and the gills. At this stage of growth these hyphae function as a marginal veil, though this veil is very different in origin from the marginal veil of those species with endogenous origin of the hymenophore. They do not, at any stage of development which I have examined, interlace with the hyphae of the stipe, as Hartig suggested for Armillaria mellea (12). Such an interlacing might occur in case the margin curved down against the stipe below the hymenophore area. In all the specimens examined, however, the pileus margin curves up toward the hymenophore. Hypo-
nastic growth of the older portion of the pileus begins soon, causing it to expand, thus lifting the margin up and outward far away from contact with the hymenophore. The growth of the pileus in thickness is primarily the result of the enlargement of its elements accompanied by branching and intertwining of the threads.

_Hymenophore Primordium._—Soon after the origin of the pileus primordium, the ends of the peripheral hyphae which are perpendicular to the surface of the annular groove, are rich in protoplasm and stain deeply. This is the region of the hymenophore primordium. This region, as in _Omphalia chrysophylla_ and _Clitocybe adirondackensis_, develops centrifugally and adds new elements by intercalary growth.

_Palisade Layer._—By continued introduction of new elements, this layer becomes compact and the free ends reach the same level (Fig. 66). The increase in size of the cellular elements and the extending downward of the subadjacent hyphae produce regularly spaced, radial folds in the palisade layer (Figs. 57, 58). These folds are the salients of the primary lamellae and appear first on the stipe very near the angle between the latter and the under surface of the pileus. Thus, the gills are decurrent from their very first appearance.

At this period of development the hymenophore layer on the under surface of the pileus is in the level palisade stage, near the stipe (Fig. 56). It gradually grades off into the primordial condition at the margin. Therefore, since the gills follow the same centrifugal succession as did the structures preceding their origin, the salients continue their development toward the margin of the pileus. Thus, Figure 58 (a little later stage than Fig. 57) shows their first appearance on the under surface of the pileus.

Further growth in width of the lamellae is brought about by growth of the tramal hyphae in these folds. This growth aids in pushing the palisade layer outward at the edge of the salient. By corymbose branching new elements are introduced into the palisade layer by intercalary growth. The hyphae that grow down into the lamellae from the trama of the pileus form the trama of the gills. Figures 67–69 show a serial development of a gill from the origin of the salient to a lamella fairly well along in growth.

_Origin and Development of Secondary Lamellae._—As the primary gills advance from the stipe to the margin of the pileus, they diverge from each other. In the spaces so produced on the under surface of the pileus near the stipe, the secondary lamellae arise. Figure 59, a
transverse section through the stipe and pileus, shows the primary lamellae as "bars" extending between the pileus and the stipe. Between the "bars" on the morphological under surface of the pileus, down-growing salients of the secondary gills are shown. They develop and progress radially, as do the primary lamellae. Figure 61 is a slightly oblique transection through the margin of the pileus and upper portion of the stipe and shows the increase in number of lamellae on the pileus margin as compared to the number of primary gills on the stipe.

Further Growth of Pileus and Stipe.—The pileus elements in the more mature stage have in general a radial, horizontal direction. The trama of the pileus increases by branching and elongation of its elements. The size of the stipe increases likewise by branching and interstitial growth. The lengthening or elongation of the stem, as in the previous species studied, is the result of the extension in length of the cellular elements.

Summary

1. The young basidiocarp and stipe primordium consist of a homogeneous weft of slender, terete, interlacing hyphae. The general growth direction of the elements is parallel with the axis of the young fruit body. The hyphae converge at the apex. The cellular elements are comparatively short, cylindrical cells, rich in protoplasmic content.

2. The pileus primordium is differentiated by the divergence of the apical hyphae which grow upward and laterally. This divergence serves to mark the origin of the pileus and differentiates it from the stipe fundament.

Further differentiation of the pileus is the result of continued growth of the primordial tissue. By profuse branching and interstitial growth of the elements, an intricately interwoven tissue is produced. At the same time the lateral hyphae by epinastic growth bend downward, forming the annular groove.

3. The primordium of the hymenophore is organized simultaneously with the origin of the pileus margin. The first differentiation of this tissue is on the surface of the annular groove in the angle between the pileus and stipe. This annular layer progresses centrifugally.

4. By continual branching of the hyphae, the hymenophore primordium changes to a definite layer of parallel threads, perpendicular to
the surface. By the enlargement of the cells of these parallel hyphae, and the evening up of the hyphal elements, a level palisade layer is produced.

5. The primary lamellae originate as evenly spaced, radial folds of the level palisade layer. The first folds that appear are the rudiments of the primary gills. Their further development is produced by the elongation of the subadjacent hyphae of the pileus which push their way into the salients and form the trama of the gills. These trama hyphae branch and furnish new elements by which the lamellae grow in thickness and at the same time by apical and intercalary growth increase in width.

6. The secondary lamellae arise as down growing salients of the palisade layer on the under surface of the pileus near the stipe between the primary gills. They develop as do the primary lamellae.

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immediately below the margin of the pileus. This shows the palisade layer which is formed by the gradual increase of primordial elements by intercalary growth. At the same time the cellular elements, which result in a compact layer. X 300.

Fig. 45. A cross-section similar to the above only of a slightly older stage. It shows the first appearance of gill salients, which are the outfolding of the palisade layer. Subadjacent hyphae grow into this fold, and by elongation force the salient outward, at the same time branching in a corymbose manner, new elements are added. X 300.

Fig. 46. A cross-section of the pileus which shows further growth of the gill salients. The hyphae that force their way down into the salients from the pileus elements do not stain so deeply and are easily distinguished. They form the trama of the lamellae. X 300.

Fig. 47. A cross-section of a little older stage than the preceding figure. This shows the apical development of the gill by which the lamellae increase in thickness.

Plate IX.

Figs. 48-63. Clitopilus novehoracensis.

Fig. 48. A median longitudinal section, showing the homogeneous weft of slender, interwoven hyphae. The peripheral hyphae end at varying distances from the tip, so that the surface slants gradually from the base to the apex. X 20.

Fig. 49. A median longitudinal section, showing the flaring of the hyphae at the apex which serves as a line of demarcation between the pileus and stipe primordia. On the surface of the stipe primordium is a very narrow zone of tangled hyphae which stain more deeply. This is composed of the ends of hyphae which project farther than those that compose the weft. X 20.

Figs. 50-54. Median longitudinal sections, showing older stages of development. The marginal hyphae by epinastic growth turn downward, forming the annular groove on whose surface is the hymenophore primordium.

Fig. 55. A median longitudinal section of a more mature plant, showing its general habit. The margin turns in and upward towards the gills. The marginal hyphae extend outward as a loose weft and span the space between the pileus margin and gills. At this stage it has the function of a marginal veil. X 13.

Fig. 56. A tangential section through the pileus near the stipe, showing the palisade layer. X 20.

Fig. 57. An oblique transection through the margin of the pileus and upper part of the stipe. The cavity within represents the annular groove. On the surface of the stipe the palisade layer has been thrown into folds. These folds are the gill salients. Thus the origin of the primary gills is on the stipe. X 20.

Fig. 58. A tangential section of a young pileus, showing the origin of the primary gills as they extend from the stipe on the lower surface of the pileus toward the pileus margin. X 20.

Fig. 59. A slightly oblique transverse section through the pileus margin and upper part of the stipe, showing the origin of the secondary lamellae between the primary gills. The primary gills appear as "bars," connecting the pileus and stipe. X 20.

Fig. 60. A tangential section through the pileus, showing the decurrency of the gills; also the incurving of the pileus margin. X 20.
PLATE VII

Figs. 18–30. Omphalia chrysophylla.

Fig. 18. A higher magnification of a portion of the apex of Fig. 1. It shows the converging of the apical hyphae and homogeneous nature of the whole structure. × 100.

Fig. 19. A higher magnification of a portion of the apex of Fig. 2. The threads are spreading apart slightly and have increased in size. This differentiation marks the region of the pileus and stipe primordia. × 300.

Figs. 20, 21. A higher magnification of a portion of the apices of Figs. 3–4, showing the further growth of the primordial hyphae of the pileus. They grow radially outward and by epinasty curve downward. × 300.

Fig. 22. A higher magnification of the pileus margin of Fig. 8, showing the annular groove on the surface of which is the hymenophore primordium. This primordium is composed of the ends of hyphae whose origin is in the pileus and stipe elements. They are rich in protoplasm and stain deeply. The hyphae of the pileus margin by strong epinasty curve down by which the annular groove is formed. × 230.

Fig. 23. A tangential section of the pileus near the stipe which shows in detail the structure of the palisade layer. This layer is formed by branching and interstitial growth of the primordial hyphae. As the cells themselves increase in size the layer becomes compact and even. × 300.

Fig. 24. A tangential section of the pileus showing the beginning of a gill salient. The pressure within the layer is relieved by this downward folding of the level palisade layer. At the same time subadjacent hyphae by elongating push down into this fold forming the trama of the gills. × 300.

Fig. 25. A tangential section showing a salient a little further developed. In this section the detail of the structure stands out so definitely that there can be no possible mistaking as to how the gill salient proceeds in developing. The tramal hyphae can be easily traced from the pileus elements above down into the palisade layer itself. In this way new elements are introduced in the periphery of the salient and also the trama of the gill is produced. × 300.

Figs. 26, 27. Are tangential sections showing further development of the gill salients. The tramal hyphae are evident and the corymbose branching, by which new elements are added to the palisade layer of the gill, is clearly shown. × 300.

Fig. 28. A higher magnification of a portion of the palisade layer of Fig. 27. The corymbose branching of the tramal hyphae and the intercalary growth of the elements are well shown. × 720.

Fig. 29. A median longitudinal section which shows the structure of the pileus and its relation to the palisade layer between the gills. The hyphae branching in a corymbose manner supply elements to the palisade layer. × 230.

Fig. 30. A high magnification of the edge of the pileus surface of Fig. 10. The very large and stout hyphae are well shown. The hyphae on the right side of the figure are interwoven and serve to produce a smooth surface. × 720.
THE DEVELOPMENT OF SOME SPECIES OF AGARICS

PLATE VIII

FIGS. 31-47. Clitocybe adirondackensis.

Fig. 31. A median longitudinal section of a young basidiocarp. It represents the primordial stage at which time it is composed of a loose weft of wavy, slender, and homogeneous hyphae. × 32.

Fig. 32. A median longitudinal section which shows the pileus primordium at the apical end, differentiated from the stipe primordium. The apical threads are spreading and serve as an arbitrary line of demarcation between the areas of the two primordia. × 32.

Fig. 33. A median longitudinal section showing further development of the pileus and stipe. By continued growth of the central primordial hyphae umbonate pileus is produced. Between the margin of the pileus and stipe an area of densely staining hyphae is shown. This is the hymenophore primordium which develops centrifugally as the pileus continues to grow. × 32.

Figs. 34, 35. A median longitudinal section of later stages. The pileus has increased in thickness but the expansion is comparatively little. Since the marginal hyphae elongate more rapidly than the central ones the pileus becomes plane. The hymenophore primordium develops at the same time, advancing toward the margin of the pileus and stains more deeply. × 32.

Fig. 36. An oblique transection through the upper portion of the stipe. The lower part of the figure shows a portion of the surface of the stipe beneath the hymenophore. To the left and above this region is a portion of the palisade layer. The remaining peripheral portion shows the folding of the palisade layer and the development of the gill salients. × 32.

Fig. 37. Cross-section of the extreme lower portion of the pileus, showing the general habit of the gills and manner of development. × 32.

Fig. 38. A tangential section through the pileus and near the stipe, showing the decurrency of the lamellae and also the incurring of the pileus margin. × 32.

Fig. 39. A tangential section midway between the margin of the pileus and stipe. It shows the thickness of the pileus and the nature and general direction of the gills. Some are connected at their base which is chiefly the result of branching. × 32.

Fig. 40. A median longitudinal section, showing the general habit of the plant. The pileus is plane and the gills extremely decurrent.

Fig. 41. A high magnification of a young basidiocarp, showing in longitudinal section the structure of the primordial condition. A homogeneous weft of wavy, slender threads which converge at the apex. × 230.

Fig. 42. A median longitudinal section, showing the apical hyphae growing outward. This is the pileus primordium. × 300.

Fig. 43. A median longitudinal section, showing the hymenophore primordium. This is composed of the ends of hyphae which have their origin in the stipe and pileus elements. The margin of the pileus curves down over the surface. Thus, the marginal hyphae add new elements to the hymenophore regions, both of which develop centrifugally. × 300.

Fig. 44. A cross-section through the basidiocarp near the apex of the stem
immediately below the margin of the pileus. This shows the palisade layer which is formed by the gradual increase of primordial elements by intercalary growth. At the same time the cellular elements, which result in a compact layer. \( \times 300 \).

**Fig. 45.** A cross-section similar to the above only of a slightly older stage. It shows the first appearance of gill salients, which are the outfolding of the palisade layer. Subadjacent hyphae grow into this fold, and by elongation force the salient outward, at the same time branching in a corymbose manner, new elements are added. \( \times 300 \).

**Fig. 46.** A cross-section of the pileus which shows further growth of the gill salients. The hyphae that force their way down into the salients from the pileus elements do not stain so deeply and are easily distinguished. They form the trama of the lamellae. \( \times 300 \).

**Fig. 47.** A cross-section of a little older stage than the preceding figure. This shows the apical development of the gill by which the lamellae increase in thickness.

**Plate IX.**

**Figs. 48–63.** *Clitopilus novboracensis.*

**Fig. 48.** A median longitudinal section, showing the homogeneous web of slender, interwoven hyphae. The peripheral hyphae end at varying distances from the tip, so that the surface slants gradually from the base to the apex. \( \times 20 \).

**Fig. 49.** A median longitudinal section, showing the flaring of the hyphae at the apex which serves as a line of demarcation between the pileus and stipe primordia. On the surface of the stipe primordium is a very narrow zone of tangled hyphae which stain more deeply. This is composed of the ends of hyphae which project farther than those that compose the web. \( \times 20 \).

**Figs. 50–54.** Median longitudinal sections, showing older stages of development. The marginal hyphae by epinastic growth turn downward, forming the annular groove on whose surface is the hymenophore primordium.

**Fig. 55.** A median longitudinal section of a more mature plant, showing its general habit. The margin turns in and upward towards the gills. The marginal hyphae extend outward as a loose web and span the space between the pileus margin and gills. At this stage it has the function of a marginal veil. \( \times 13 \).

**Fig. 56.** A tangential section through the pileus near the stipe, showing the palisade layer. \( \times 20 \).

**Fig. 57.** An oblique transection through the margin of the pileus and upper part of the stipe. The cavity within represents the annular groove. On the surface of the stipe the palisade layer has been thrown into folds. These folds are the gill salients. Thus the origin of the primary gills is on the stipe. \( \times 20 \).

**Fig. 58.** A tangential section of a young pileus, showing the origin of the primary gills as they extend from the stipe on the lower surface of the pileus toward the pileus margin. \( \times 20 \).

**Fig. 59.** A slightly oblique transverse section through the pileus margin and upper part of the stipe, showing the origin of the secondary lamellae between the primary gills. The primary gills appear as "bars," connecting the pileus and stipe. \( \times 20 \).

**Fig. 60.** A tangential section through the pileus, showing the decurrency of the gills; also the incurring of the pileus margin. \( \times 20 \).
Fig. 61. A slightly oblique cross-section through the pileus margin and stipe, showing: (1) primary gills on the stipe; (2) the upper left hand portion of the figure shows two "bars" of the primary gills; (3) a secondary gill between the "bars"; (4) primary and secondary gills on the pileus margin. On the right lower hand portion of this figure is shown a part of the involuted pileus margin. × 20.

Fig. 62. A tangential section through the involuted margin of the pileus, showing the relation of the involuted margin to the gills. × 20.

Fig. 63. A tangential section through the margin of the pileus just within the limit of the involuted margin. It shows very clearly how the marginal hyphae have been pushed against the gills. × 20.

Plate X

Figs. 64–69. Clitopilus novoboracensis.

Fig. 64. A higher magnification of the apex of Fig. 48, showing the converging of the hyphae. × 200.

Fig. 65. A higher magnification of a portion of the pileus primordium, showing the spreading of the hyphae at the apex. × 200.

Fig. 66. A higher magnification of the palisade layer. Its elements are increased by intercalary growth. This, together with the increase in size of the hyphae, produces the compact palisade. × 300.

Fig. 67. A cross-section through the stipe, showing the first fold in the palisade layer. It is an outward growing salient, the rudiment of a lamella. × 300.

Figs. 68, 69. Transverse sections through the pileus margin and stipe, showing further development of the gill salient. The apical growth of the gill is well shown by which it increases in width. The tramal hyphae can be definitely made out. × 300.

Figs. 70–74. Clitocybe cerussata.

Fig. 70. A median longitudinal section of a young basidiocarp, showing the basidiocarp primordium. It is a homogeneous web of slender, interlacing hyphae, whose general direction is longitudinal and converge at the apex. × 20.

Fig. 71. A median longitudinal section, showing the diverging hyphae at the apex. This serves to separate the pileus and stipe primordia. × 20.

Figs. 72–74. Median longitudinal sections of older stages, showing the centrifugal development of the pileus. The stipe at the same time increases in thickness. The hymenophore is differentiated in the surface of the annular groove. × 20.

Figs. 75, 76. Median longitudinal sections, showing further growth of the pileus. The margin curves down and toward the stipe. × 20.

Fig. 76. A median longitudinal section of a more mature plant, showing its general habit. The strongly incurved margin is well shown. × 20.

Plate XI

Figs. 78–89. Clitocybe cerussata.

Fig. 78. A tangential section of the pileus, showing the palisade layer near the margin. × 20.

Fig. 79. A slightly oblique transsection through the pileus margin and stipe, showing the origin of the lamellae as folds in the palisade layer on the upper portion of the stipe. × 20.
Fig. 80. A tangential section through the pileus, showing the origin of the primary gills on its under surface. On either side of the down-growing salients a portion of the palisade layer is shown. $\times 20$.

Fig. 81. Transection of the pileus and stipe, showing the origin of the secondary lamellae between the primary gills which show as "bars." $\times 20$.

Fig. 82. Tangential section of the pileus, showing further development of the gill salients. The tissue below the salients is a portion of the involuted pileus margin. $\times 20$.

Fig. 83. A higher magnification of the apex shown in Fig. 20. This shows the converging of the apical threads and the general homogeneous structure. $\times 100$.

Fig. 84. A longitudinal section of the pileus primordium, showing the general growth direction of the hyphae. $\times 300$.

Fig. 85. Transection of the stipe, showing the palisade layer. $\times 300$.

Fig. 86. A transverse section of the stipe, showing the first evidence of a fold in the palisade layer. $\times 300$.

Fig. 87. Further development of a salient represented by Fig. 86. It shows the apical growth by which the elements of the palisade layer are increased by elongation of the hyphae from the trama of the pileus. $\times 300$.

Fig. 88. Represents a little older stage than the preceding one. The tramal hyphae are shown growing down into the gill and branching; thus new elements are supplied to the palisade layer. $\times 300$.

Fig. 89. A slightly older stage, showing further development of the gill. $\times 300$. 
Blizzard: Omphalia chrysophylla
Blizzard: Omphalia chrysophylla
BLIZZARD: CLITOCYBE ADIRONDACKENSIS
BLIZZARD: CLITOFILUS NOVEBORACENSIS
BLIZZARD: CLITOPILUS NOVEBORACENSIS AND CLITOCYBE CERUSSATA
THE ORIGIN AND DEVELOPMENT OF THE GALLS PRODUCED BY TWO CEDAR RUST FUNGI

J. L. Weimer

The question of the origin of the outgrowths caused by Gymnosporangium Juniperi-virginianae Schwein. and Gymnosporangium glohosum Farlow on Juniperus virginiana L. has never been settled satisfactorily. The galls produced by G. Juniperi-virginianae have been studied by several workers but there still exists considerable difference of opinion as to the method of their origin. The excrescences caused by G. glohosum have been studied but little. While making observations on these galls incident to the preparation of another paper the writer became interested in their method of origin. Observations were made throughout two summers and the earliest stages of the development of these galls were studied in the field and later microscopical studies were made. The results of these observations and studies together with a resume of the literature on the subject are given below.

G. Juniperi-virginianae Farlow (1880) states that prior to the time of writing it had been generally accepted that the cedar apples originated in the young cedar stems but that so far as he could ascertain they were deformed leaves. Sanford (1888) studied the pathological histology of the galls produced by this fungus and decided that the galls are modified cedar leaves, while Wormald (1894) after also studying these galls histologically concluded that they originated from the stem. Heald (1909) thinks that the cedar apples originate from the stem in the axis of a leaf. Kern (1911) places G. Juniperi-virginianae among the foliage inhabiting species and Coons (1912) states that while he has never observed or produced infection artificially it is evidently a leaf infection. Reed and Crabill (1915) claim that the cedar apple is nothing but a hypertrophy of a cedar leaf infected by the fungus G. Juniperi-virginianae. Giddings and Berg (1915) picture minute galls situated near the end of cedar leaves, hence apparently originating from the leaf. Steward...
J. L. WEIMER (1915), after having studied the histology of these growths, concludes that they originate as modified axillary buds; the leaf tissue becoming involved later.

The writer's observations go to show that the cedar apples caused by this species usually break through the upper or inner side of the leaves, the first evidence of infection being the discoloration of the whole or a part of a leaf, followed later by a swelling usually from the upper surface but more rarely from the sides. The young galls grow rapidly and assume the characteristic shape and color very early in their development. It was found that when the infected leaves were removed the galls remained attached (PL XII, Fig. 1). This led to the belief that they must be in very close association with the leaf and perhaps originate from it. Specimens such as are pictured by Giddings and Berg (1915) and Coons (1912), where the galls are located near or even beyond the center of the leaf, were found in considerable abundance (PL XII, Figs. 2 and 3). This strengthened the theory that these galls originate from the leaf. If these galls originated in the stem or as modified axillary buds with separate fibro-vascular systems it would be reasonable to suspect that in the very young stages at least the gall would be more firmly attached to the stem than to the leaf.

A single gall has been found by the writer which has the appearance of having originated from the stem and it may be true that this mode of origin also exists, although it is certainly not the common method about Ithaca, New York. The writer has had the privilege of examining young galls from West Virginia and Wisconsin and the method of origin herein described was also found in those galls.

Before proceeding with a discussion of the internal anatomy of these galls a brief description of the structure of the healthy cedar leaf and stem will be given. The cedar leaf is attached to the stem throughout a large part of its length, only the apical portion being free. In cross section the leaf is triangular in outline at the apex but gradually becomes four-sided toward the base. The epidermis consists of a single layer of somewhat flattened, elongate cells with the outer wall covered by a thick layer of cutin. The epidermal layer on the upper or inner side of the leaf is broken by numerous stomata. Beneath the epidermal layer is a hypodermis on all the sides except the upper. For the most part this consists of a single layer of sclerenchymatous cells. This may however be reinforced at certain places, principally at the corners and in the region of the resin duct, by additional cells.


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