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Introduction.

Cortinarius pholideus is characterized by the peculiarly strong development of dark, pointed, erect scales on the pileus and stem. This feature is unusual in Cortinarius, but is very striking in certain species of Pholiota, so that *Cortinarius pholideus* in its general aspects suggests Pholiota, the spore color in the two genera being the same. Since I have recently studied three scaly species of Pholiota (12), it therefore occurred to me that it would be extremely interesting to study the development of this species, which I found in all stages of development in the same region in which the Pholiotas[1] were collected. Especially would it be interesting to determine the formation of a cortina in a species where such a prominent, coarse, universal veil is present.

Primordium of the Basidiocarp

The very young fruit-body is elongate, composed of slender, closely interwoven hyphae, with numerous interhyphal spaces. These hyphae are, in general, parallel with the long axis of the basidiocarp; they have abundant protoplasm and are active in growth, as indicated by their deeply staining property and long slender cells. The peripheral threads, however, take the stain poorly or not at all. They turn outward on all sides, and in an extremely early stage the outermost cells are enlarged, dead, and brown in color.

This outer zone of differentiated hyphae forms a loose-meshed envelope for the entire plant, and is a universal veil. or blematogen, in the sense in which this structure has been interpreted by Atkinson (4).

Figure 1 represents a median longitudinal section through a very young fruit-body, which is about one millimeter long and half a millimeter in width. The hyphae are slender and very uniform in size, averaging about 3 μ in diameter. The loose peripheral threads belonging to the blematogen, however, are enlarged, many of them being 10 μ in diameter, dead, and brown. A conspicuous feature of

[1] Woods in vicinity of Seventh Lake, Adirondacks, N. Y.

the young fruit-bodies of this species are the numerous interhyphal spaces scattered throughout the basidiocarp.

Differentiation of the Stem Fundament

Very early in the development of the fruit-body the hyphae in the basal part increase in number and show evidence of more rapid growth, so that this portion of the basidiocarp becomes more dense in structure. This new growth is the primordium of the stipe, which, by progressive growth and differentiation, finally reaches the apex of the fruit-body. From the beginning, the structure of the basidiocarp is compact, and the gradual progressive differentiation of the stem fundament does not at first produce any marked change in appearance. In figure 2 the fundament is well differentiated nearly to the stem apex; the latter is still in the primordial condition. In figure 3 at the left is shown the compact cortex of the stem fundament, from which the looser hyphae of the inner portion of the blematogen radiate outward and upward. The cortex of the stem fundament is somewhat more dense and deeply staining than the inner portion, as shown in figure 5.

A similar, but more marked origin of the stem, has been shown to occur in two species of Lepiota (6), in *Rozites gongylophora* (11), in the three species of Pholiota already mentioned, and in five species of Cortinarius (8).

Differentiation of the Primordia of Pileus and Hymenophore

After the organization of the stem fundament the hyphae in its apical end take on more rapid growth and branch freely, as indicated by their deeper stain and by the fact that they traverse the interhyphal spaces at this time. This new interstitial growth causes a bulbous expansion of the stem apex, which marks the young primordium of the pileus (fig. 6). At the same time the peripheral hyphae of this apical region, instead of growing, in general, straight upward, as they have done heretofore during the development of the stem fundament, now grow outward in all directions (fig. 7). On the lateral surfaces they become subject to epinastic influence and turn strongly downward, forming the pileus margin, as shown in figure 8 by the small deeply stained area on either side of the pileus, beneath the blematogen layer.

Almost simultaneously with the formation of the pileus margin the hyphae of its under surface begin to grow outward and downward very rapidly. These hyphae are slender, very rich in protoplasm, crowded together, and with terete ends. Their outward growth while under the influence of epinasty causes them to curve strongly, so that the ends point downward, or even inward toward the stem. This ring of new growth surrounding the stem apex is the hymenophore primordium. A median longitudinal section at this stage shows it as a deeply stained region on either side, as in figure 10. Since the primordium of the hymenophore is formed from hyphae of the pileus margin, and at practically the same time with the latter, it is extremely difficult to point to the exact stage at which it originated. As has been stated, the hyphae of the pileus margin stain deeply and by new growth increase the density of its structure, and the beginning of this period of increased activity probably marks the origin of the hymenophore primordium.

The appearance of this new fundament definitely marks off the pileus area from the stem primordium. As development continues, the pileus broadens centrifugally and becomes more compact by interstitial growth. At the same time the hymenophore primordium, by the intercalary growth of new hyphae from the pileus, and by the increase of its own elements, likewise develops centrifugally, and keeps pace in its growth with the pileus margin.

Formation of the Palisade Layer

For a time the growth of the hyphae composing the hymenophore is very rapid and uneven, the pointed ends of some of the threads growing down beyond the others, so that the surface is rough and jagged (figs. 12 and 13). Gradually, however, the hyphae acquire a more uniform rate of growth, and the ends reach the same level, becoming clavate and crowded. This condition of the hymenophore in which the hyphal ends form an even, compact surface is the palisade stage. Such a condition is shown in figure 23. In this species, as in others previously investigated, its development is centrifugal, from the stem toward the pileus margin. Here however it develops very uniformly, so that at one time in the same fruit-body the palisade occupies the whole area of the hymenophore except the extreme margin. In all the species that have had this phase of their development described, the formation of the palisade is more gradual, so that in the same fruit-body there is present at the same time the palisade condition of the hymenophore and a considerable amount of primordial tissue.

The Annular Prelamellar Cavity

When the pileus and stem areas become differentiated from the primordial tissue of the basidiocarp, in the angle formed by the junction of these two structures a small amount of primordial or ground tissue is left. The primordia of pileus, stipe, and hymenophore grow more rapidly than does this ground tissue and as a result tensions are produced which cause it to become loose in texture and to tear apart. This results in the formation of a cavity in the form of a ring around the apex of the stem, beneath the surface of the hymenophore. In this species the formation begins very soon after the origin of the hymenophore, as shown in figures 10 and 11, where the tissue immediately below the hymenophore primordium is becoming loose through the lateral and upward pull exerted on it by the margin of the expanding pileus. In figures 14 and 15 the development has proceeded further, so that an actual cavity is formed, although still weak and spanned by hyphal threads. By the time the level palisade stage is reached the gill cavity is well differentiated and entirely free from intervening tissue, as shown in figures 16, 17 and 23. Like the primordium of the hymenophore and like the palisade, its development is from the stem toward the pileus margin, so that its earliest appearance is close to the stem. The two tangential sections represented by figures 12 and 13 show this fact; in figure 13 the cavity, while not complete, is more strongly developed than in figure 12, a section of the same fruit-body nearer to the pileus margin.

The Origin and Development of the Lamellae

At the time of the beginning of gill formation the pileus and stem are completely formed and the gill cavity is well defined. The hymenophore is in the stage in which there is an even palisade layer extending from the junction of the stem and pileus nearly to the pileus margin; near the latter the palisade grades off into the primordial condition of the hymenophore. The palisade is composed of small hyphae with blunt and crowded ends (fig. 23). The continued growth of these hyphae and the intercalation of new elements from the hymenophore above gives rise to sufficient lateral pressure to throw the palisade surface into downwardly projecting folds (fig. 24) which are the first gill salients. At the same time a more rapid growth of the hymenophore downward in radial, regularly spaced areas directs the formation of the folds, as described for *Agaricus rodmani* (5) and species of Coprinus (7), so that the gills are radially symmetrical with reference to the stipe.

The origin of the lamellae is next the stem, and by continued growth and differentiation the lamellae develop toward the pileus margin. This centrifugal manner of formation enables one to study their development by means of serial longitudinal sections from the pileus margin toward the stem, since they are youngest near the former and become progressively older as they approach the latter. Figure 23 represents a section near the pileus margin. The even palisade occupies the greater part of the hymenophore surface, with a little of the primordial tissue on either side. The gill cavity is well formed. The tissue below the latter belongs to the stem cortex and universal veil, together with some ground tissue belonging to the partial veil. Figure 24 represents a section a little nearer to the stem. The palisade is no longer level, but has an undulating surface, with two slight, very broad folds. In figure 25, still nearer to the stem, these two folds are more pronounced, and at the right the beginning of a third may be noted. The breadth of these folds, and their distance apart, can leave no doubt that they are the first salients of the lamellae themselves.

The trama of the mature gill (fig. 34) has its origin in the hyphae beneath the palisade layer which grow down into the young gill salient. Further growth takes place by the elongation and enlargement of these hyphae. Throughout the center of the lamella they are compactly interwoven, with their general direction of growth toward the edge (fig. 34). Laterally, however, they turn outward and form the hymenial layer of the lamella.

The primary gills, because of their radial arrangement with the stipe as a common center, diverge as they approach the pileus margin. Continued growth of the hymenophore results in the production of shorter secondary lamellae between their outer ends in the same way as that in which they were formed. Figures 28–32, however, show the formation of two gills in a somewhat different manner. In figure 28, a section near the stem, it will be noted that a gill salient occurs that is unusually broad. In the successive sections it can be seen that this broad salient, by branching, forms two salients, each of which thereafter develops into a lamella in the usual way. This probably illustrates the method of origin of the dichotomous or forked lamellae characteristic for Cantharellus and certain species of Russula.

Figures 35–37 illustrate a condition due to the strongly inrolled margin of the pileus. Figure 35 is of a section tangential to the pileus margin. In the center a lamella appears with a cavity on either side. Figures 36 and 37, respectively, nearer the stem, show the same condition; the lamellae appear as bars continuous from the upper to the lower part of the pileus, with separate cavities between them. The gills, however, have not become continuous with the tissue below by growing down and uniting with it. This tissue belongs to the hymenophore of what is morphologically the under surface of the pileus. The inrolling of the margin of the latter, however, has reversed the position of the hymenophore. The presence of the salients of secondary lamellae on this lower surface serves to make this more clear. The attachment of the gills below, as well as above, represents their point of origin. The sections are not cut perpendicular to these points, but are tangential to the "backs" of the lamellae; their direction of growth is not in the plane of the section, but at right angles to it. The spaces between the lamellae are extensions of the general annular cavity nearer the stem.

The Blematogen

Before any internal differentiation takes place the young basidiocarp is completely enveloped by a universal veil or blematogen. The hyphae composing this outer layer are differentiated from the other elements of the fruit-body by the fact that their cells are short and enlarged, the outer ones being dead, with thick brown walls and scanty content. The direction of these hyphae is outward and upward. They diverge at the ends, forming a loose structure easily rubbed off during growth or in the manipulation of the fruit-bodies preparatory to study.

The blematogen has a very striking appearance at about the time of the formation of the hymenophore primordium (fig. 10). The large hyphae stand straight out from the pileus surface, their clear yellow-brown walls, which do not stain at all, contrasting sharply with the deeply stained and closely interwoven elements of the pileus. At this same time the weft of hyphae between the pileus and blematogen, left when the former became differentiated from the primordial tissue, loosens, probably because of partial cessation of growth, and forms a thin layer with many interhyphal spaces extending over the surface of the pileus (figs. 17 and 19). As the plant approaches maturity the erect hyphae of the universal veil (figs. 18, 19) become aggregated into little tufts or clumps that form the erect, dark scales covering stem and pileus, so characteristic of this species.

A peculiar and interesting feature of the blematogen is its double character over the margin of the pileus, as shown in the left side of figure 14 and in figure 15. The outer layer is characteristic of the universal veil elsewhere on the plant, being composed of large, thick-walled cells that radiate outward in loose arrangement. The inner portion, however, is very different in appearance. The hyphae are slender, with abundant protoplasm and thin walls. Instead of growing outward in loose structure they lie closely side by side and passing up over the edge of the pileus margin become ingrown with the pileus surface an appreciable distance above its free edge. Kniep (10) has demonstrated that in hyphal threads bearing clamp connections, the growing end always lies in the direction in which the obtuse angle, formed by the junction of the cross wall of the hypha and the cross wall of the clamp, opens. These inner blematogen hyphae bear numerous clamp connections, whose walls all form angles opening upward; therefore these hyphae could not have grown down from the pileus, but must have had an upward direction of growth. Furthermore, in the section shown in figure 16, the free ends of some of these hyphae may be seen interlacing with the threads of the pileus surface just above the margin of the latter. It is probable that the growth of this inner layer is slow, and its union with the pileus is due to the active outward and downward growth of the hyphae belonging to the latter, which interweave with the threads of the former. A duplex blematogen has been described by Miss Douglas in *Cortinarius anfractus* and *C. armillatus* (8), differing, however, from the condition here in that the outer layer in these two species is thin and compact, while the inner part is loose and floccose.

The Marginal Veil

The marginal veil is very poorly developed in this species, as compared with *Agaricus rodmani* (5), *Armillaria mellea* (3), *Agaricus comtulus* (2), species of Hypholoma (1), and other species. After the differentiation of pileus and stem, some ground tissue is left in the angle between them. This is nearly all broken away in the process of formation of the gill cavity, but a small amount may remain attached to the pileus margin, beneath the blematogen. This is increased by the downward growth of a few hyphae from the extreme margin of the pileus, and in figures 14 and 15 it is probable that the inner layer of the veil described above does not belong entirely to the blematogen, but has on its inner surface some hyphae belonging to the marginal veil proper, as limited from the universal veil or blematogen.

The Cortina

The name "cortina" is a term applied especially in the genus Cortinarius to the veil composed of delicate silky fibrils stretching from the pileus margin to the stem. It is usually evanescent, although in a few species, like *C. armillatus*, it may persist for a long time in the form of rings about the stem. In *C. pholideus* it breaks away early, leaving a very slight ochraceous annulus around the top of the stipe that disappears with age. Occasionally a half-grown plant is found with the arachnoid veil still intact. It is light in color, almost white, and stretched tightly over the gills. The fibers composing it are very slender, and this character, together with its lighter color, distinguishes the cortina from the brown-walled, larger hyphae of the outer blematogen layer, which is external to the cortina in varying amount, depending on how much has been rubbed off during the development of the plant. The cortina is composed of the hyphae of the inner layer of the blematogen, together with whatever marginal veil may be present. In figures 20 and 21 it may be seen extending from the pileus margin to the stem. Outside is tissue belonging to the outer layer of the blematogen. Figure 22 shows a condition so common as to be almost characteristic in this species, in which the pileus margin is so strongly inrolled that it has become free from the cortina, which is attached to the pileus surface above its margin, thus showing that the cortina represents here the inner zone of the duplex blematogen.

Fries (9) must have regarded the cortina as a structure distinct from the universal veil or blematogen, for, although its presence was used by him for a generic character, only two of his six subgenera, namely Myxacium and Telamonia, are said to possess a universal veil. *C. pholideus*, however, put by Fries in the sub-genus Inoloma, has a universal veil, and the same has been found by Miss Douglas in species representing two other Friesian subgenera. No generalizations can be made until the development of many more species is known, but the evidence at hand indicates that the presence of a universal veil (blematogen) is constant for the genus. If so, it is probable that it plays some part in the origin of the cortina, as in the species studied by Miss Douglas, and as it does in this species.

In conclusion, I wish to acknowledge my indebtedness to Professor George F. Atkinson, under whose direction the greater part of this work was done at Cornell University, for his helpful interest and kindly criticism.

Summary

1. The primordium of the basidiocarp of *Cortinarius pholideus* is composed of slender hyphae interwoven into a compact structure with numerous interhyphal spaces, and enveloped in a layer of differentiated hyphae.

2. These enveloping, radiating hyphae form the blematogen or universal veil. They are loose in their arrangement, with large, thick-walled cells. Soon after pileus formation the blematogen shows a double character over the pileus margin and gill cavity. The inner layer has an upward growth direction and the hyphae of the pileus surface interlock with its upper portion.

3. The appearance of the stem fundament is the first differentiation to take place within the basidiocarp. It is formed in the base of the fruit-body, and advances to the apex by progressive growth and differentiation.

4. The pileus is formed by the expansion of the stem apex, due to interstitial and divergent growth. The lateral hyphae of the pileus fundament by epinastic growth form the pileus margin.

5. Perpendicular downward growth of hyphae from the under surface of the pileus, beginning in the angle between stem and pileus, forms the primordium of the hymenophore as an annular zone of new growth surrounding the stem apex. At first, because of unequal growth of its hyphae, the primordium is uneven and jagged, but later the ends of the hyphae grow down to the same level, forming the even palisade zone.

6. The annular prelamellar cavity is formed by the breaking away of ground tissue left in the angle between stem and pileus after their differentiation, due to the growth and expansion of these parts. A small amount of this ground tissue may remain attached to the edge of the pileus and form a slight element of the cortina.

7. The lamellae originate as downward-growing folds of the level palisade zone, through the influence of lateral pressure in the palisade, and, more particularly, by downward growth of hyphae from the hymenophore in radial, regularly spaced areas. Their differentiation is centrifugal, from the stem toward the pileus margin. The first folds or ridges in the hymenophore are the salients of the lamellae themselves. The gill trama is formed by the downward growth of hyphae from the hymenophore into the gill salient, and increases by interstitial growth.

8. The cortina is the silky veil stretching over the gills, attached on the one hand to the surface of the pileus margin and on the other to the stem. It is composed of the hyphae of the inner layer of the blematogen, together with fragments of the ground tissue below the hymenophore. It is covered externally by remnants of the outer layer of the blematogen, as indicated by the dark patches that may be attached to its outer surface.

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DESCRIPTION OF PLATES XXVIII–XXIX

The following micróphotographs were made by the author, some with the Spencer Lens Co.'s horizontal camera with Zeiss lenses, the others with a Bausch and Lomb microscope equipped with Zeiss lenses and a Bausch and Lomb vertical camera attachment.

PLATE XXVIII

FIG. 1. Primordium of the basidiocarp. The hyphae are closely interwoven to form a compact structure. Many interhyphal spaces occur, scattered through the fruit-body. On the outside are a few blematogen hyphae. ×50.

FIG. 2. A fruit-body somewhat older than the preceding. The stem fundament is differentiated to near the apex, where the hyphae are still in the loose primordial condition. On the sides may be seen the basal parts of blematogen hyphae, their outer ends having been lost. ×30.

FIG. 3. An enlargement of the right side of the preceding figure. The loose blematogen threads are shown growing out from the compact stem cortex. ×215.

FIG. 4. A young fruit-body after formation of the stem primordium. The blematogen may be seen enveloping the stem fundament. ×30.

FIG. 5. A slightly older stage, showing the blematogen radiating from the stem cortex. The latter is compact; the apex is slightly more deeply staining, showing that growth is more active at that point. ×30.

FIG. 6. A state slightly older than the one shown in fig. 5. By interstitial growth the stem apex has become bulbous, forming the pileus primordium. Outside is the blematogen. ×50.

FIG. 7. A fruit-body in median longitudinal section that is a very little older than the one shown in Fig. 6. The pileus fundament is a little larger and the hyphae in the peripheral zone are growing straight outward over its entire surface. ×50.

FIG. 8. Median longitudinal section. By epinastic growth the outer, lateral hyphae have grown downward to form the pileus margin, which appears as a small, deeper stained area on either side. ×30.

FIG. 9. An enlargement of the right side of Fig. 8. Near the center can be seen the pileus margin, whose hyphae extend in a downward and slightly outward direction. Immediately below it the ground tissue is beginning to break away to form the gill cavity. On the outside, at the right, is the loose universal veil. ×115.

FIG. 10. An older stage; the hymenophore primordium appears on either side, on the margin of the pileus. Over the pileus the brown, enlarged hyphae of the blematogen stand straight outward. ×30.

FIG. 11. An enlargement of the right side of Fig. 10, showing details of above mentioned structures and early indication of formation of the gill cavity. ×115.

FIG. 12. Tangential section, showing the uneven condition of the hymenophore. Below the ragged surface of the latter the ground tissue is beginning to break away to form the gill cavity. ×50.

FIG. 13. Tangential section of the same fruit-body, but nearer to the stem. The hymenophore is becoming more even and the gill cavity is much better formed. ×50.

FIG. 14. Median longitudinal section. On the left may be seen the duplex nature of the blematogen over the pileus margin. ×30.

Fig. 15. Left side of preceding figure, more highly magnified. On the outside are the large hyphae of the outer blematogen layer, with an outward and upward direction. Within is the inner blematogen layer, composed of slender parallel hyphae, interlacing with the surface of the pileus above its margin. Below the hymenophore is the gill cavity. ×115.

Fig. 16. Right side of median longitudinal section of a fruit-body a little older than the preceding one. The palisade zone is differentiated and the gill cavity is completed. Extending up over the edge of the pileus margin may be seen hyphae of the inner part of the blematogen. ×115.

Fig. 17. The right side of median section, showing the palisade layer and the universal veil, with the loose area between the latter and the pileus surface. ×25.

Fig. 18. Median section of fruit-body after the gills are formed. The pileus and stem have become very compact through branching and growth of their hyphae. The pileus margin is strongly inrolled, as in all the fruit-bodies sectioned at this stage. The cells of the blematogen hyphae are collapsed and shrunken and show signs of aggregation into the tufts that later become the erect squamules on the surface of pileus and stem. The narrow area of loose tissue between blematogen and pileus surface may be seen here. ×15.

Fig. 19. A fruit-body a little younger than the preceding, showing well the radiating hyphae of the blematogen. ×15.

Plate XXIX

Fig. 20. The section represented by this photograph is from a fruit-body at a stage after the gills are well formed. The margin of the pileus is strongly incurved and the edge is free from the veil. ×30.

Fig. 21. This section shows well the structure of the cortina. It is composed of the slender hyphae of the inner part of the blematogen and the marginal veil. On the outside are remnants of the outer layer of the blematogen. Since the pileus margin is not strongly inrolled in this particular fruit-body, the edge has not become free from the veil. ×30.

Fig. 22. A portion of the right side of a section showing the pileus with its edge entirely free from the cortina, due to its inrolled character. ×30.

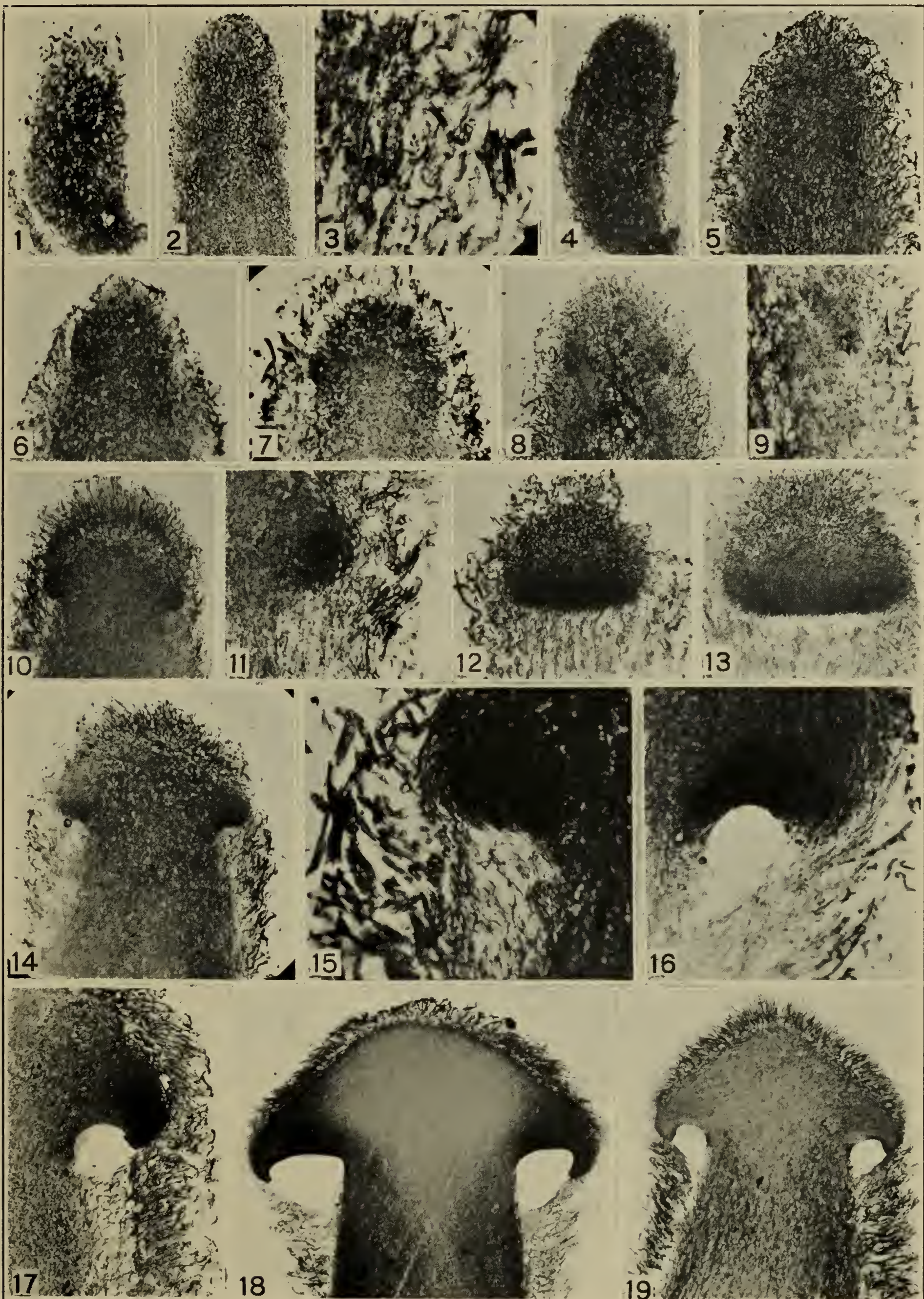
Figs. 23–27. A series of sections showing the origin and development of the lamellae. In Fig. 23 a section near the pileus margin is shown. In the center is the well developed gill cavity. Above it is the even palisade area of the hymenophore, bordered on either side by primordial tissue. Below is loose ground tissue on the stem. In Fig. 24 the first gill salients are seen as two slightly downwardly projecting broad folds in the palisade. Fig. 25 shows these two salients better developed, toward the stem, and at the right a third is appearing. Fig. 26 represents a section of the same fruit-body tangent to the stem. On the left is the level palisade and on the right development has proceeded further, so that a gill salient has been formed. Fig. 27 is of a section nearer to the center of the fruit-body, showing the same features as in the preceding section. ×112.

Figs. 28–32. Stages in the origin and development of a dichotomous gill through the branching of a gill salient. The section shown in Fig. 28 is near the stem, and the following figures are nearer the pileus margin in order. ×50.

FIG. 33. A section tangent to the stem at its junction with the pileus, showing two adnate gills. ×30.

FIG. 34. Structure of the mature gills. The hyphae of the trama turn outward on the sides and contribute to the formation of the hymenium, which shows as the deeply stained layer covering the gill. ×30.

FIGS. 35–37. Tangential sections in the inrolled margin of a nearly mature fruit-body. In Fig. 35 the section is tangent to the "backs" of the gills. In Fig. 36 the lamellae appear to grow across the gill cavity as bars, with a separate cavity between each two gills. In reality it is the backs of the gills seen in section, and their attachment below, as well as above, represents their point of origin. Due to the inrolled pileus margin the tissue at either end of the "bars" belongs to the same morphological under surface of the pileus. Fig. 37 shows the origin of secondary gills between the primary lamellae, both above and below. ×15.



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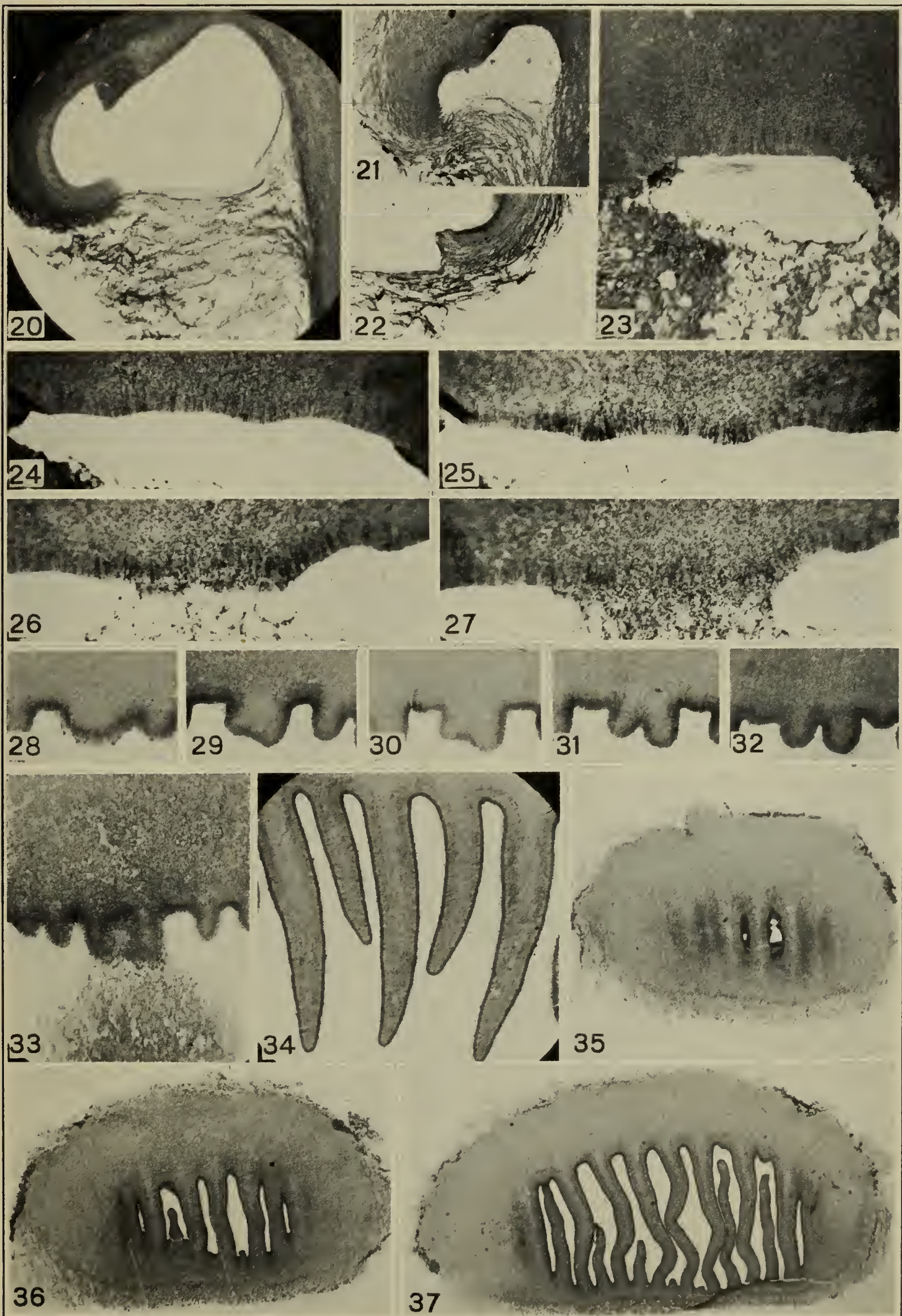

Sawyer: Development of Cortinarius pholideus.