MORPHOLOGY AND DEVELOPMENT OF AGARICUS RODMANI

(Plates VII.–XIII.)

By GEO. F. ATKINSON.

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Introduction.

Agaricus rodmani[1] was described by Peck in 1885, from specimens growing in "grassy ground and paved gutters" at Astoria, Long Island. As to its habitat and occurrence a more specific statement is made in 1897, in that it "grows in grassy ground and even in crevices of unused pavements and paved gutters in cities,"[2] from May to July, and is said to be rare. It has been observed in the city of Ithaca, N. Y., for a number of years, where it is usually found growing in the parking between the sidewalks and street curbing, or even in the crevices of stone paved streets and gutters, and also in grassy ground along the street railway or along walks on the border of groves. The material for this study was collected in August, 1914, along the Ithaca street railway and by the side of paths along the border of groves on the campus. In these places the mycelium in spots was often very abundant so that lumps of soil resembling a fine quality of spawn were exposed in digging for the young stages. The young fruit bodies collected were scattered on these cords of mycelium, the material and conditions offering very clear evidence of the normal development of the basidiocarps. The material was fixed in chrom-acetic fluid and sectioned in paraffin.

The features of interest in the morphology and development of *Agaricus rodmani* which I have considered in the present study are as follows: (1) the duplex character of the annulus, or ring, on the stem, and its significance; (2) the origin of the hymenophore funda-

[1] N. Y. State Mus. Nat. Hist. Rept., 36, 45, 1885.

[2] N. Y. State Mus. Nat. Hist. Rept., 48, 139, 1897.

ment; (3) the differentiation of parts in the primordial ground tissue; and (4) the origin and development of the lamellæ. The peculiar form and position of the annulus on the stem has suggested a resemblance to a volva, a structure not admitted in the genus *Agaricus* as now limited; while the subject of the origin and development of the lamellæ has acquired new interest in all of the Agaricaceæ since the accuracy of observations and the correctness of the statements covering a period of more than a half a century, in regard to this topic, have recently been called in question. Without further preliminary remarks we may proceed to an account of the present investigation, and to a consideration of the various matters involved.

I. The Duplex Annulus and its Significance.

The Annulus.—The annulus is situated near the middle of the short stem, or even near its base. It is usually very thick next the stem and is divided into an upper and lower limb by a deep marginal groove as is clearly seen in the photographs reproduced in Plate I. In those cases where the annulus is near the base of the stem, Peck was impressed by its suggestion of "the idea of a volva" (*l. c.*, 45). Before the expansion of the pileus, while the veil is still attached to the stem and pileus margin, a longitudinal section of the plant shows very clearly that the lower limb of the annulus lies on the outer (upper) side of the pileus margin (see Plate VII., upper right hand and lower left hand figures). The marginal veil is very thick and the epinastic growth of the pileus margin crowds the latter into the veil tissue and against the stem. The position of the lower limb of the annulus therefore corresponds to that of the volva limb of the *Amanitas*.

The plates represented in the upper group of Plate VII., were collected on the Cornell University campus, those in the upper group during August, 1911, along a path in the edge of a small wood not far from the street; those in the lower group, July, 1913, along the street railway and parking by East Avenue. In the expanded specimens, the pileus ranged from 6 cm. to 8 cm. in diameter. The plants were smaller than those represented in Plate VIII., but since they were abundant and in all stages of development they present in an excellent way the different details of the veil and annulus during expansion of the plant. Those represented in Plate VIII., were collected by Mr. Wood, June 28, 1915, in the parking between the sidewalk and street, on Stewart Avenue, in front of the Town and Gown Club, Ithaca, N. Y. They were very robust specimens, and show the great distance between the upper and lower limb of the annulus. They are reproduced here real size.

A thin outer layer of the lower limb of the annulus is continuous below with the outer layer of the stem, and also with a very thin surface layer of the pileus. As the stem elongates at the time of the expansion of the plant, this outer layer of the stem lags behind and is thus torn into irregular patches shown very clearly in the two upper left-hand figures of Plate VII. The edges of these patches are frequently warped away from the stem, thus showing a tendency to exfoliation. This is especially marked in the case of the surface layer of the stem next the lower limb of the annulus. The warping upward of this layer, after it has been severed from its connection below, often gives the appearance of a double edge to the lower limb of the annulus, as shown in the lower right-hand figure of Plate VII., where the upper limb of the annulus has not yet broken away from the pileus margin.

The very thin layer on the pileus which is also continuous with a thin outer layer of the lower limb of the annulus often shows a tendency to exfoliation. This partial exfoliation of the stem and pileus surface is clearly marked where the basidiocarps are somewhat soiled by contact with particles of earth, as they are likely to be during the period of subterranean growth.

The outer portion of the lower limb of the annulus, as well as the corresponding thin, and partially exfoliating surface layer of the pileus and stem are derived from the outer layer of the blematogen. The blematogen layer, as I have interpreted it, is present in the genus *Agaricus* as well as in *Amanita*. In the species of *Amanita* thus far studied,[3] the blematogen at length is clearly separated from the pileus by a cleavage layer, arising from the gelatinization, or other kind of disintegration, of the external layer of the pileus primordium, thus

[3] Atkinson, Geo. F., "The Development of *Amanitopsis vaginata*," *Ann. Myc.*, 12, 369–392, pls. 17–19, 1914.

giving rise to the teleoblem, or finished volva. But in the genus *Agaricus*[4] no such cleavage layer is formed, and the surface of the pileus primordium becomes consolidated with the blematogen layer which here does not form a true volva, or teleoblem.

The lower limb of the annulus of *Agaricus rodmani* is not, therefore, strictly homologous with the volva of the *Amanitas,* not even including the thin layer of the stem and pileus which sometimes tends to peel off, since it does not comprise all of the blematogen layer, nor is it separated from the pileus by a distinct cleavage layer. If it were homologous with the volva of the *Amanitas,* then this species would represent a generic type distinct from *Agaricus* (*Psalliota*). In fact other species of *Agaricus* frequently show a similar condition of the annulus, *i. e.,* where the margin is "grooved," due to the inset of the pileus margin into the veil where the conditions for the robust development of the veil are favorable. In *Agaricus campestris* the annulus frequenlty presents a grooved margin, not only in the case of cultivated forms, but more rarely in the feral state. This condition is well shown in Plates 11 and 12 of my article on *Agaricus campestris.*[5] In Fig. 20 of that article the lower limb of the annulus has broken away from the outer surface of the incurved pileus margin, while the upper limb is still attached to the edge of the pileus. In Figs. 18 and 19 the upper limb has also become freed from the pileus margin and the grooved character of the edge of the annulus is very distinctly shown. In Fig. 15 of the same article, sections of the young basidiocarps show very clearly the position of the lower limb of the annulus extending over the outer (upper) side of the pileus margin. Fig. 20 also shows very clearly that the annulus as a whole is ripped off from the lower part of the stem, being an exaggerated case of the slight peeling up of the thin surface layer of the stem mentioned above in *Agaricus rodmani.* That the

[4] Atkinson, Geo. F., "The Development of *Agaricus arvensis* and *A. comtulus,*" *Am. Jour. Bot.,* 1, 3–22, pls. 1, 2, 1914.

Atkinson, Geo. F., "Homology of the Universal Veil in *Agaricus,*" *Myc. Centralb.,* 5, 13–19, pls. 1–3, 1914.

Atkinson, Geo. F., "The Development of *Lepiota clypeolaria, Ann. Myc.,* 12, 346–356, pls. 13–16, 1914.

[5] Atkinson, Geo. F., "The Development of *Agaricus campestris,*" *Bot. Gaz.,* 42: 241–264, pls. 7–12, 1906.

lower limb of the annulus in *A. rodmani* is merely a part of the marginal veil is clearly seen in the sectioned plants shown in the lower groups of Plate VII., where the connecting portion between the two limbs is clearly differentiated from the surface of the stem with which it is in contact, a situation very different from that in *Amanita* where the volva has no such relation to the annulus.

Comparison of Agaricus rodmani with other Species of Agaricus. —This extensive peeling, or ripping upward of the annulus from the lower part of the stem in *Agaricus campestris* is the cause of the more extensive, *i. e.,* broader, veil and annulus than is characteristic for *Agaricus rodmani.* Peck regards this species as intermediate between *Agaricus campestris* and *A. arvensis,*[6] resembling the former in size, shape and general appearance; the latter in the "whitish primary color of the lamellæ," in the occasional yellowish tints of the pileus, and the occasional rimose under surface of the annulus. The robust character of the annulus of *Agaricus rodmani* and the thick flesh of the pileus margin crowded by epinastic growth against the stem deepens and widens the groove on the edge of the annulus. This, together with the very short stem, in comparison with the longer stem of *Agaricus campestris* and *A. arvensis,* is, I think, largely responsible for certain differences in the character of the under surface of the annulus in the different species. In the species with the longer stem more stretching of the stem occurs and the annulus (or veil) is ripped upward from a greater extent of the stem surface. The radiately grooved character of the under surface of the annulus, in certain species (*A. arvensis* Schultz, *A. abruptibulbus* Pk., *A. placomyces* Pk., *A. hæmorrhoidarius* Schultz), or the coarsely floccose or scaly character in certain others (*Agaricus subrufescens* Pk., *A. augustus* Fr., or both features contained in some) is largely due to the fact that this part of the annulus is stripped from the stem and then brought under greater tension than the upper surface as the expansion of the pileus stretches the veil outward. All things considered *Agaricus rodmani* is much more closely related to *Agaricus campestris* than to any other of the species. It is very probably identical with *Agaricus campestris* var.

[6] N. Y. State Mus. Nat. Hist. Rept., 36, 45, 1885.

edulis Vitt.,[7] as I have elsewhere suggested[8] (1900, 1901, 1903, p. 20). Excellent figures of this variety are given by Vittadini (*l. c.*, pl. 6) and by Bresadola[9] (pl. 54).

II. Origin of the Hymenophore Primoridum

Primordium of the Basidiocarp.—The primordia of the basidiocarps are elliptical or oval in outline, and reach a diameter of 3 mm. or 4 mm. before there is any internal evidence of a differentiation of parts. The length is usually somewhat greater than the transverse diameter. In specimens not so well nourished differentiation may begin before the primordia have reached this size. The primordium, from the size of 2 mm. to 4 mm. in diameter, consists of a homogeneous interlacing of stout mycelial threads with rather thick walls. In primordia 3 mm. to 4 mm. in diameter the hyphae average about 5 μ to 7 μ in thickness, occasionally stouter ones are seen which measure up to 10 μ. More slender threads are also intermingled, but all sizes are so indiscriminately interwoven that no structural differentiation is perceptible. In smaller primordia the hyphæ average less in diameter. In most of the primordia examined, the sections are evenly stained throughout, but in a few a narrow zone a short distance from the surface stains more deeply than the external and internal tissue (Fig. 2). This suggested the possibility of a differentiation of an outer zone distinct from the bulk of the fruit body, which is sometimes present in *Agaricus campestris* and which I have called the *protoblem.*[10] A similar zone is found in some of the basidiocarps after the origin of the hymenophore fundament, but in the material which I have examined it is the exception rather than the rule, and I am inclined to the belief that it is due to some condition which affects the rate of growth or increase of cer-

[7] Vittadini, C., "Funghi Mangerecci," 44, 1835.

[8] Atkinson, Geo. F., "Studies of American Fungi; Mushrooms, Edible, Poisonous, etc.," 1st edition, I–VI., 1–275, 76 plates (223 figs.), Ithaca, N Y., 1900. *Idem,* 2d edition, I–VI., 1–322, 86 plates (250 figs.), Ithaca, N. Y. 1901. *Idem,* New York City, 1903.

[9] Bresadola, G., "Funghi Mangerecci e Velenosi," 1899.

[10] Atkinson, Geo. F., "The Development of *Agaricus arvensis* and *A. comtulus,*" *Am. Jour. Bot.,* 1, 3–22, pls. 1, 2, 1914. "Homology of the Universal Veil in *Agaricus,*" *Myc. Centralb.,* 5, 13–19, pls. 1–3, 1914.

tain individuals. A protoblem[11] is very likely present, but it is difficult to distinguish in primordia havng a subterranean origin because of the ease with which the delicate protoblem is removed while removing the soil, and especially in the forms and species of *Agaricus* with a white pileus. In those with a brown pileus, like *Agaricus campestris* var. *bohemia* of the commercial spawn growers, the delicate, white protoblem is very distinct.

Differentiation of an Internal Annular Hymenophore Primordium.—The first evidence of internal differentiation is the appearance of an internal annular zone of new growth in the region of the smaller end of the oval fruit body. This can be studied with advantage by means of serial, longitudinal sections. A median longitudinal section is shown in Fig. 3, while a "tangential" section, *i. e.*, parallel with the axis of the basidiocarp, but through one side of the annular zone of new growth is shown in Fig. 4. Diagrams 1 and 2 (in the text) show how the sections were made. Fig. 3 is from the region marked by the line 2, while Fig. 4 is from that marked by the lines 1 and 3. The darker staining areas in Figs. 3 and 4 mark the position of the zone of new growth. In the median

[11] The delicate, floccose, primary universal veil, or protoblem was observed by Fries on *Agaricus campestris* and a few other species, and called by him a subuniversal veil. Vittadini (in Fung. Mang., 147, pl. 18, fig. 2, 1835) describes and figures it in connection with his study of the development of his *Agaricus exquisitus*. But in this species he seems to confuse this delicate universal veil (protoblem) with what he terms the volva in several species of *Agaricus*. He also applies the term volva to the lower limb of the annulus in *Agaricus exquisitus* and in *Agaricus edulis*. He says (*l. c.*, 148) this delicate universal veil in *A. exquisitus* is perfectly similar to that which constitutes the veil of the "Tignose," *i. e.*, the scaly Amanitas like *A. muscaria*, etc. Vittadini also states (*l. c.* 147) that Trattinnick observed this delicate universal veil (protoblem) on *Agaricus edulis* (the species which Trattinnick describes as *A. edulis* is different from *A. campestris edulis* Vitt. or *A. rodmani* Pk.), but it appears that Vittadini misinterpreted Trattinnick's statment. The latter says, in order to prevent confusion one should avoid (*l. c.*, p. 73) taking for the edible one a mushroom (74), which may have also only the slightest trace of a membrane which in youth envelopes the entire mushroom, including pileus and stem, down to the roots. "Um Verwechslungen zu vermeiden, hüte man sich statt der Gugemuke einen Schwamm zu nehmen" (73), "(*d*) der auch nur die geringste Spur von einer Wulsthaut haben sollte, die in der Jugend den ganzen Schwamm mit sammt den Strunk und Hut bis auf die Wurzel verhüllet" (74 Die essbare Schwämme, 1830).

longitudinal section two such areas are seen, symmetrically situated on either side of the long axis and some distance from the surface of the fruit body. The annular zone is of quite limited extent as the

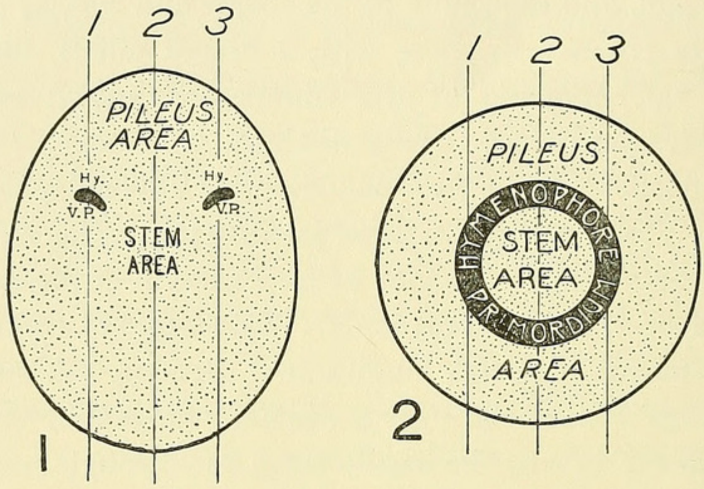

Diagram 1. Lateral view through young basidiocarp representing early stage of differentiation into the primordia of the four principal parts; pileus area, stem area, hymenophore fundament (*Hy*) and veil primordium (*V. P.*).

Diagram 2. Zenith view in young basidiocarp at same stage of fundaments, and annular hymenophore primordium. See text for details.

small area presented by its transection in Fig. 3 shows. The outline of this area in transection is somewhat elongated and rises at an oblique angle from the stem area, well shown in Fig. 3 and indicated in diagram 1. The area of the primordial hymenophore seen in the tangential section is much more extensive as shown in Fig. 4. The difference in the extent of these areas shown in median (Fig. 3) and tangential (Fig. 4) sections is clearly appreciated by reference to diagram 2.

Structure of the Young Hymenophore Primordium.—This internal annular zone of new growth arises by the origin of numerous. slender hyphal branches, rich in protoplasm, which are directed downward, or obliquely downward and outward. They have a more direct course than the hyphae of the basidiocarp primordium, the latter irregularly sinuous and interwoven, while the hyphae of the young hymenophore primordium are nearly or quite straight. Because of their small diameter and their slender, gradually tapering ends, they easily crowd their way through the rather open weft of hyphæ forming the ground tissue or fundamental plectenchyma. Fig. 9 is a highly magnified view of the hymenophore primordium shown in the section represented in Fig. 3, from the right-hand area. The dark area in Fig. 9 represents the mass of deeply stained hyphæ of the new growth zone. Because of the compactness of the tissue, very little detail is shown. But along the middle portion of the figure between the lighter, open mesh of the ground tissue below and to the right, and the dark area of the hymenophore primordium above and to the left, a number of hyphæ in advance of the others are shown extending into the loose mesh of the ground tissue. These are nearly parallel and their extremities are more or less distant, because they are in advance of the greater number of new branches present in the more deeply staining area. No annular gill cavity is present at this time.

Growth and Increase of the Hymenophore Primordium.—The growth and further organization of the hymenophore primordium is readily studied by the aid of similar serial sections of successively older stages of the basidiocarps. Sections of such stages are repre-

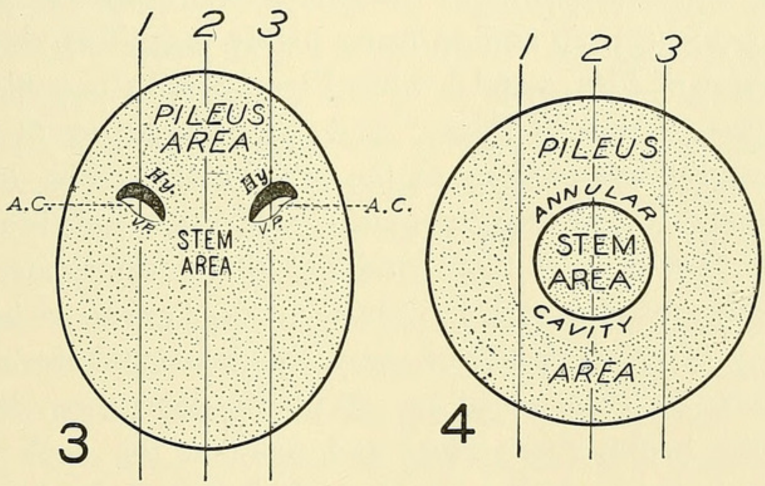

Diagram 3. Lateral view through young basidiocarp at a slightly later stage of development than in diagram 1. *Hy* = hymenophore; *A. C.* = annular cavity; *V. P.* = veil primordium.

Diagram 4. Zenith view in young basidiocarp at same stage of development. See text for details.

sented in Figs. 5–8 and 10–16. Diagrams 3 and 4 indicate how the sections were made. From the condition show in Figs. 3, 4 and 9, there is a rapid increase in the number of hyphæ in the zone of new growth, extending in the same direction, *i. e.*, downward and obliquely outward. During the increase in number the hyphæ become more crowded, are straighter and lie more nearly parallel. The upper outer portion of this new zone of growth, *i. e.*, the hymenophore primordium, represents the early stage of the organization of the pileus margin: in other words, the annular internal zone of new growth is to be interpreted as the young primordium of hymenophore and pileus margin, the latter including the area from which the new hyphal branches arise as well as the basal area of these branches. Not only is there interstitial growth in the increase of these hyphal branches, the new ones crowding in between the older ones forming a more compact zone, but there is also a centrifugal increase in the periphery of the annular zone. The centrifugal growth of the pileus margin and hymenophore primordium is very characteristic.

The position and direction of the hyphæ of the young hymenophore primordium, as well as the increasing density of this area, is well shown in Figs. 10–16. The stem axis of all the figures is parallel with the long axis of the Plate. Several of these figures are highly magnified views of the hymenophore primordium shown in Figs. 5–7; Figs. 10 and 15 being highly magnified views of the hymenophore of Figs. 5 and 6, while Figs. 12 and 16 are highly magnified views of that in Figs. 7 and 8. Figs. 10 to 14 are from median longitudinal sections of the basidiocarps. Fig. 10 is from the right-hand side of the stem axis, *i. e.*, the stem axis is at the left. Figs. 11–14 are from the left-hand side of the stem axis, the stem axis therefore being on the right-hand of the figures. The increasing density of the elements of the young hymenophore is progressively shown in Figs. 10 to 13. With the increasing density the ends of the hyphæ reach more and more to the same level and thus tend to form an even surface which forms the transition to the palisade layer.

Origin of the General Annular Gill Cavity.—A striking feature in all these radial transections of the hymenophore zone and pileus margin is the curved outline of the zone as seen in transection. This is remarkably strong in Figs. 11 and 12 because the young hymenophore primordium extends for a considerable distance down around the apex of the stem fundament. This arched form of the young annular hymenophore zone is the result of epinastic growth of the pileus margin, which is very marked even in this very early stage in the organization. The rapid increase in the number of the hyphæ in the young hymenophore, crowding in between the older ones, as well as their increase in diameter, produces a great pressure in this region. As a result of this increasing pressure within the arch a strong tension is exerted on the ground tissue below and adjacent to the arch. The ground tissue at this point is thus torn apart, forming a distinct opening, or cavity, beneath the young hymenophore, which is known as the annular gill cavity. The continuity as a general, annular, internal cavity can easily be determined by serial longitudinal sections through the young fruit body, the sections being made as indicated in diagrams 3 and 4, the knife travelling through the basidiocarp in the direction indicated by the lines 1, 2, 3. As the knife passes the region marked by the line 1, the sections will show a single cavity elongated transversely as shown in Figs. 6 and 8, 15 and 16. As the knife passes into the stem area the sections will show two cavities situated symmetrically as in Figs. 5 and 7 (or as in diagrams 3 and 4). Then as the knife passes out of the stem area, into the region indicated by the line 3, the sections will again show a single cavity elongated transversely.

The annular gill cavity[12] varies in strength in different individuals and at different stages of development. Sometimes it is very weak, at other times it is quite strong. The tearing apart of the ground tissue often leaves it with quite an open mesh, and the surface next the gill cavity is more or less frazzled. The gill cavity is stronger next the stem where the hymenophore is older, and is weaker toward the margin. Where the cavity is weak, isolated threads or irregular strands of the ground tissue are not completely torn away from the hymenophore, and the cavity is thus often traversed by lagging elements of the ground tissue. At a later stage, after the origin of the lamellæ, the annular cavity in some indi-

[12] In a recent paper, after describing the gills in *Coprinus micaceus*, Levine ("The Origin and Development of the Lamellæ in *Coprinus micaceus*," *Am. Jour. Bot.*, 1, 343–356, pls. 39, 40, 1914), makes the statement (p. 352) that "There is no general gill cavity as described by Hoffmann, deBary, Atkinson, and others." Since deBary ("Morphologie und Physiologie der Pilze, Flechten und Myxomyceten," 69, 1866) is the only person hitherto who has announced the presence of a general annular gill cavity in *Coprinus micaceus*, this statement by Levine can only be interpreted as a general denial of the presence of a general annular gill cavity in the species in which it has thus far been described, a rather rash statement which will be referred to again in the discussion of the origin of the lamellæ.

viduals may become nearly or quite closed by the increase in the elements of this ground tissue, which forms a portion of the marginal veil, but chiefly by the epinastic growth of the pileus margin which crowds this ground tissue up against the margin of the lamellæ, as shown in Figs. 32–38.

Organization of the Palisade Layer.—The level palisade layer of the hymenophore follows the primordial stage, immediately after the latter stage has become dense and compact by the increase in number and thickness of the parallel hyphal elements. The growing compactness of the primordial hymenophore zone is accompanied by the evening up of the hyphal ends into a plane surface. As the ends of the hyphæ broaden the free surface of the hymenophore becomes compact and smooth, or even. This is the level palisade stage of the hymenophore. It is a gradual, not abrupt, transition from the primordial stage. It begins next the stem, or in many cases on the outer surface of the upper part of the stem fundament as shown in Fig. 12. Here the palisade area, in radial section, rises upward at a strong oblique angle from the axis of the stem, and then grades into the primordial area toward the left. The palisade area progresses, like the primordial area and the pileus margin, in a centrifugal direction, the older portion lying next to, or on the upper part of the stem fundament.

The level palisade layer of the hymenophore, preceding the origin of the lamellæ, was first described by Hoffmann[13] in 1856, 1860, and 1861, in about a dozen species (see the later paragraph on the origin of the lamellæ for a list of species). DeBary[14] (1859, p. 386, 394) described the palisade layer of the young hymenophore in *Nyctalis asterophora* and *parasitica,* as having radial folds from its

[13] Hoffmann, H., "Die Pollinarien und Spermatien von Agaricus," *Bot. Zeit.,* 14: 137–148; 153–163, pl. 5, 1856. Beiträge zur Entwickelungsgeschichte und Anatomie der Agaricinen," *Bot. Zeit.,* 18: 389–395; 397–404, pls. 13, 14, 1860. Icones Analyticae Fungorum; Abbildungen und Beschreibungen von Pilzen mit besonderer Rucksicht auf Anatomie und Entwickelungsgeschichte," 1–105, pls. 1–24, 1861.

[14] DeBary, A., "Zur Kenntnis einer Agaricinen," *Bot. Zeit.,* 17: 385–388; 393–398; 401–404, pl. 13, 1859.

[15] DeBary; A., "Morphologie und Physiologie der Pilze, Flechten und Myxomyceten," Leipzig, 1866. "Vergleichende Morphologie und Biologie der Pilze, Mycetozoen und Bacterien," 1884. "Comparative Morphology and Biology of the Fungi, Mycetozoa and Bacteria," Oxford, 1887.

earliest appearance. But as this interpretation was shown by Hoffman (1860, p. 402) to be wrong, deBary[15] (1866, p. 63; 1884, p. 58, 312; 1887, p. 55, 289) studied a number of other forms and agreed with Hoffman that the earliest stage of the young palisade hymenophore was level, or smooth.

III. The Differentiation of Parts in the Primordial Ground Tissue.

There are four principal parts of the fruit body which are differentiated in the ground tissue of the basidiocarp primordium, the *hymenophore, pileus, stem* and *veil.* The primary differentiation in the ground tissue of *Agaricus rodmani* is the origin of the hymenophore primordium. As described above this arises as an internal annular zone of new growth, a little above the middle of the small oval primordial basidiocarp. It consists of numerous hyphal branches which extend downward and obliquely outward. These new hyphæ are nearly or quite parallel, are at first slender and taper very gradually to the free end. This form assists them in making their way through the mesh of the ground tissue. They are rich in protoplasm, become compacted by increase in number and diameter, and thus in sections, take on a deep color when stains are applied (see Figs. 3–16). The origin of this internal hymenophore zone differentiates at once the stem and pileus areas, or fundaments, but the organization of the stem and pileus occurs later.

In the early origin of the primordial hymenophore zone, *Agaricus rodmani* agrees with *Agaricus campestris*[16] as presented in a study of the commercial varieties, *alaska* and *bohemia.* In that paper I pointed out that we should not necessarily expect the first evidence of differentiation to be the appearance of the hymenophore primordium in plants not yet studied though it is probable that at least some of the other species of *Agaricus* (*Psalliota*) may show the same peculiarity. This suggestion is justified by the situation in *Agaricus rodmani.* The same situation exists in *Armillaria mellea.*[17]

[16] Atkinson, Geo. F., "The Development of *Agaricus compestris,*" *Bot.*
Universal Veil' in *Agaricus,*" *Myc. Centralb.*, 2, 13–19 pls. 1–3, 1914.
Gaz., 42: 241–264, pls. 7–12, 1906.

[17] Atkinson, Geo. F., "The Development of *Armillaria mellea,*" *Myc. Centralb.*, 4: 113–121, pls. 1, 2, 1914.

In the specimens of *Agaricus arvensis*[18] studied, the lagging behind of the ground tissue below the zone where the hymenophore primordium arises occurs before any differentiation of this zone is distinguishable, for a light area with a looser mesh occurs in an annular zone which marks the distinction between the stem and pileus areas. Or the lagging behind of the ground tissue may occur simultaneously with the appearance of the primordial hymenophore zone and the outline of the pileus area. In a number of forms studied by Fayod[19] the primordium of the pileus is organized, in the apex of the young homogeneous basidiocarp, as a new zone of growth, in the form of an inverted bowl, shown by the darker staining of the hyphæ rich in protoplasm, forming a pileus producing layer ("couche piléogène"). This method of differentiation he accepts as a general law for the Agariceæ, the only exception admitted by him being the coriaceous forms of *Lentinus. Agaricus rodmani,* the commercial varieties of *Agaricus campestris* (*columbia* and *alaska*) and *Stropharia ambigua* (Peck) Zeller,[20] also form exceptions to this rule. The primordium of the pileus in these forms may be regarded as diffuse within the upper part of the young basidiocarp, the differentiation and organization of the pileus margin beginning in conjunction with the organization of the primordial hymenophore zone, though in *Stropharia ambigua* the inverted bowl-shaped zone of new growth in the upper part of the pileus area is soon organized.[20] Other forms recently investigated which conform to the general law laid down by Fayod, are certain species of *Hypholoma* (Allen),[21] *Hypholoma fascicularis* and *Clitocybe laccata* by Beer,[22] *Lepiota*[23] *clypeolaria* and *Amanitopsis vaginata.*[24]

[18] Atkinson, Geo. F., "The Development of *Agaricus arvensis* and *A. comtulus*," *Am. Jour. Bot,* 1, 3–22, pls. 1, 2, 1914. "Homology of the 'Universal Veil' in *Agaricus*," *Myc. Centralbl.*, 2, 13–19 pls. 1–3, 1914.

[19] Fayod, V., "Prodrome d'une histoire naturelle des Agaricinées," *Ann. Sci. Nat. Bot.*, VII., 9, 181–411, pls. 6, 7, 1889.

[20] Zeller, S. M., "The Development of *Stropharia ambigua*," *Mycologia*, 6, 139–145: pls. 124, 125, 1914.

[21] Allen, Caroline L., "The Development of some Species of *Hypholoma*," *Ann. Myc.*, 4, 387–394, pls. 5–7, 1906.

[22] Beer, R., "Notes on the Development of the Carpophore in Some Agarincaceæ," *Ann. Bot.*, 25^2: 683–689, pl. 52, 1911.

[23] Atkinson, Geo. F., "The Development of *Lepiota clypeolaria*," *Ann. Myc.*, 12, 346–356, pls. 13–16, 1914.

Organization of the Pileus.—The organization of the pileus begins in connection with the primordial hymenophore zone. The upper part of this zone is very probably to be regarded as the primordium of the pileus margin which then increases by centrifugal growth. It is marked from an early period by strong epinastic growth, so the margin becomes strikingly involute, a feature also characteristic of *Agaricus campestris,*[25] *A. arvensis,*[26] *A. comtulus,* etc., as I have earlier described. The general relation of the hyphæ in the primordium of the pileus margin is a parallel one, and they become more and more strongly incurved as a result of epinasty. As the pileus primordium increases in width by marginal growth, it also increases in thickness, more perceptibly so farther back from the margin where the new growth is older. In this way the organization of the pileus advances more and more into the outer zone of the ground tissue, the blematogen, and becomes consolidated with it.[27]

Organization of the Stem.—The stem area is delimited at the same time as the pileus area by the origin of the young hymenophore zone, but its organization and differentiation from the ground tissue seems to lag behind the early stages of the organization of the pileus margin. While a general and more or less diffuse growth and expansion occurs for some time in the stem area, the first evidence of a differentiation from the ground tissue is seen in the organization of the stem surface. The outline of the stem may be compared to that of a broad, flat cone, since the stem at first is very short and

[24] Atkinson, Geo. F., "The Development of *Amanitopsis vaginata,*" *Ann. Myc.,* 12, 369–392, pls. 17–19, 1914.

[25] Atkinson, Geo. F., "The Development of *Agaricus campestris,*" *Bot. Gaz.,* 42: 241–264, pls. 7–12, 1906 (see figures 11 and 12).

[26] Atkinson, Geo. F., "The Development of *Agaricus arvensis* and *A. comtulus.*" *Am. Jour. Bot.,* 1: 3–22, pls. 1, 2, 1914.

[27] In *Agaricus campestris* var. *edulis,* Vittadini ("Fun. Mang.," 44, pl. 6, fig. 1, 1835) in a young oval fruit body, figures and describes the outline of the pileus within a stout volva, and states that, during the course of development, the volva is ruptured circularly, and the margin of the pileus as it emerges is held for a time against the stem by the lower limb of the annulus. His account of the release of the volva (blematogen) from the pileus does not seem clear, and his figures do not show the transition stage from *a* to *b* in figure 1 of his Plate VI In *Agaricus rodmani* nor in any other species of *Agaricus* (*Psalliota*) have I ever seen any indication of the clear cut outline of the pileus surface as distinct from the blematogen, such as Vittadini shows at *a,* fig. 1.

broad, and the surface slopes outward at a strong angle. The surface outline of the stem is quite clearly differentiated from the loose ground tissue forming the marginal veil, because of the deeper staining property of the stem shown in longitudinal sections (Fig. 32). Its differentiation and organization agrees entirely with that described for *Agaricus campestris*,[28] *Agaricus arvensis* and *A. comtulus*.[29]

Organization of the Marginal Veil.—The organization and limits of the marginal veil, or partial veil, as it is sometimes called, in *Agaricus arvensis, A. comtulus* and *A. campestris*, has been very fully discussed in previous papers[29] (13–15, 1914), briefly in another[30] (17, 1914). Its organization and composition in *Agaricus rodmani* is in the main similar, its different features being due to its more robust character, the stouter pileus and shorter stem. The fundament of the marginal veil is ground tissue in the angle between the primordial hymenophore zone and the stem fundament, including on its outer surface a narrow section of the blematogen layer. The ground tissue in this angle is indicated in *VP* (veil primordium) in diagram 3, and the corresponding areas in Figs. 3, 5, 7, 9–14 can readily be understood. There is considerable increase in this ground tissue by growth of the portion clothing the stem fundament. It is also added to by growth of the hyphæ at the margin of the pileus. The mass of the loose inner surface is often crowded up against the edges of the gills by the involute margin of the pileus pushing it upward, due to epinastic growth.

In such robust specimens usually presented by *Agaricus rodmani* the blematogen layer is comparatively thick but still forms a comparatively small portion of the marginal veil, and lies on the outer under surface of the lower limb of the annulus. By the incurving of the thick margin of the pileus its edge is crowded into the thick veil, and presses against the stem, thus separating the veil, which later becomes the annulus, into an upper and lower limb. As stated above, the fact that the short stem elongates but little in comparison

[28] Atkinson, Geo. F., "The Development of *Agaricus campestris*," *Bot. Gaz.*, 42: 241–264, pls. 7–12, 1906.

[29] Atkinson, Geo. F., "The Development of *Agaricus arvensis* and *A. comtulus*," *Am. Jour. Bot.*, 1. 3–22 pls. 1, 2, 1914.

[30] Atkinson, Geo. F., "Homology of the Universal Veil in *Agaricus*, *Myc. Cantralb.*, 5, 13–19, pls. 1–13, 1914.

with that of *Agaricus campestris, arvensis,* and a number of other species, the veil is usually not ripped up from the lower part of the stem as it is in the other species. A thin layer on the stem below the annulus is often cracked into distinct areas or patches, the margins of the areas sometimes being partially exfoliated. The partial exfoliation of the under part of the lower limb of the annulus frequently occurs, and then the lower limb itself has a double edge as described above, and as shown in several of the figures of Plate I. In *Agaricus campestris, arvensis, augustus, subrufescens, placomyces,* and others, the freeing of the lower part of the annulus from the stem is very extensive, since as the stem elongates the veil is ripped off for a considerable distance. In *Agaricus rodmani,* as the pileus expands, the lower limb of the veil clings to the stem, splitting off from the outer surface of the pileus margin as the latter is withdrawn. The inner or upper limb of the veil remains attached to the edge of the pileus margin for a longer time, but is eventually separated.

IV. Origin and Development of the Lamellæ.

Origin of the Gill Salients.—The development of the hymenophore is progressive and centrifugal. As described in the previous section, the primordial hymenophore zone originates in conjunction with the primordium of the pileus margin and lies in the angle separating the stem and pileus areas. The organization of the level palisade zone of the hymenophore from the primordial stage, begins in the older region, *i. e.,* next the stem. The margin of the pileus, primordial hymenophore and palisade zone all progress by growth in a centrifugal direction, the younger, later stages succeeding the earlier. The lamellæ succeed the level palisade zone and arise as downward growing salients of the same. These salients begin next the stem (or in some cases on it). They are regularly spaced and progress in a radial, centrifugal direction. The origin of the salients from the level palisade stage is well shown in Figs. 17–21.

In Figs. 18 and 20, different stages in the origin of the salients are shown. Three gill salients are seen in Fig. 20. At the left side of Fig. 20 is the level palisade. Next it to the right is a very low salient. Continuing to read toward the right, the second and third salients are successively stronger. While the hyphal structure is not very distinctly shown in in this figure, due to the difficulty of illumination which will produce on the photographic plate the same degree of resolution which can be detected by the eye, still the palisade character is evident. A similar situation is seen in Fig. 18, but the progression in the origin and growth of the salients is to be read from right to left. A somewhat later stage is shown in Fig. 19. Here the hyphal structure is well shown. The palisade character of the exposed surface of the hymenophore is very clearly shown. This figure gives us some suggestion of the factors operating in the formation of the gill salients. The elements of the palisade layer increase by interstitial growth, *i. e.*, by new branches which crowd in between the older ones. At the same time the elongate cells composing the palisade layer increase in diameter. In the primordial stage they passed from the terete tapering condition to the cylindrical form. Now they pass from the cylindrical to the clavate form, as well as increasing somewhat in diameter throughout. This produces a great pressure on the level palisade zone, which if continued, must result in throwing the level palisade layer into folds.

Another factor now comes into play which prevents the palisade layer from being thrown into a series of irregular folds. This is the downward growth, by elongation, of the subadjacent tramal hyphæ, along regularly spaced radial areas, beginning next the stem and proceeding in a centrifugal direction toward the margin of the pileus. These radial areas of subadjacent tramal hyphæ, elongating downwards, push the palisade area downward into corresponding radial salients. These salients are the first evidence of folds or ridges which appear in the young hymenophore. They are the gill salients, and by continued growth form the lamellæ themselves.

Fig. 19 presents another very interesting situation. This is the flaring, or fantailing, of the gill salients very soon after their emergence below the level of the general palisade surface. This is very clearly one of the first results of the release from the pressure to which the elongate cells were subject in the level palisade condition. Another still more interesting feature at this stage is the pressure to which the neutral portion of the level palisade is subjected as a result of this fantailing of the gill origins. The flanks of the young gill salients thus crowd against the intervening neutral palisade cells, more strongly against their free ends. This presses these intervening, neutral, radiating areas of the original level palisade into the form of ridges which thus alternate with the radiating gill salients. These intervening ridges between the young gill salients are very conspicuous in a corresponding stage of gill development in *Coprinus micaceus* as I have shown in another paper. This situation is a comparatively old stage in the development of the lamellæ and is one of the peculiar features presented by a number of the Agaricaceæ, which led Levine[31] to mistake these intervening ridges between comparatively old gill salients for the first ridges to appear in the hymenophore primordium of *Coprinus micaceus.* These ridges he thought were the first evidence of the gills. The gills were described as arising from the splitting of these first ridges and the union of approximate halves of adjacent ridges to form the gills between them. This matter will be referred to below when another peculiar situation is described which also assisted in leading this author astray.

Relation of the Different Phases of Hymenophore Development in the Young Basidiocarp.—Figs. 17–23 represent different phases of the organization and development of the hymenophore in a single basidiocarp, during an intermediate stage of its development. The relation of these different phases is determined by a study of longitudinal serial sections passing from near the stem to the margin of the pileus. With the exception of Fig. 20, Figs. 17–23 are all from the same plant, selected to represent the relation of different phases of the young hymenophore. The sections from which the photographs were taken were parallel with the axis of the stem, and thus were nearly or quite perpendicular to the hymenophore, or under surface of the pileus. The general plane of the hymenophore, or under surface of the pileus, is slightly arched, but for all practical purposes of this study, the plane is perpendicular to the stem axis, so that the sections are perpendicular to the general hymenophore surface, or plane. Fig. 17 is from a section near the stem, corresponding to line 4 in diagram 6 (diagram 6 is intended to illustrate the situation presented by the figures in Plate 5, but serves to illus-

[31] Levine, M., "The Origin and Development of the Lamellæ in *Coprinus micaceus*," *Am. Jour. Bot.*, 1, 343–356, pls. 39, 40, 1914.

trate also the relations now under consideration). An examination of the relation of line 4, in diagram 6, to the gill salients, the palisade and primordial areas, will assist in making the relation of the phases of the hymenophore presented in Fig. 17 very clear.

In the middle of the figure, or section, the gill salients are cut transversely. On either side of the middle they are cut obliquely, the more so the nearer the palisade area the salients are cut. But when the gill is so young, the structure of an oblique section at this angle is practically the same as in a transection. Since the hymenophore is older next the stem, and progressively younger toward the margin of the pileus, the gill salients are older next the stem, and younger next the palisade area, where they are very low and grade off insensibly into the level palisade zone. Toward the left and right from the middle of such a section as is represented by Fig. 17, the salients become less and less prominent until they grade insensibly into the level palisade zone on either side. In like manner the palisade zone grades to the left and right into the primordial zone, and this into the margin of the pileus, showing practically the same relation, so far as the palisade and primordial zones are concerned, as in a radial section.

Fig. 21 is from a section made near the outer ends of the middle salients, about in the region represented by line 7 in diagram 6. Only a few salients are shown, these are very low, and on either side soon grade insensibly into the palisade zone. Fig. 22 is from a section made in the region indicated by line 8 in diagram 6. Here there are no gill salients (nor any evidence of ridges in the hymenophore), a broad area in the middle is the palisade area, and this grades on either side insensibly into the primoridal area. Fig. 23 is from a section made in the region indicated by line 9 in diagram 6. It is entirely within the primordial zone, near the margin of the pileus. Knowing this relation of the different phases of the hymenophore, one can observe the transition of the primordial phase into the level palisade phase, and this into the phase of the salients. In other words, one can study the method of origin of the lamellæ by a study of the different phases of the gill salients in the area of transition from the palisade zone into the zone of the young gills.

Relation of the Hymenophore to the Stem.—One of the taxonomic characters employed for the genus *Agaricus* (*Psalliota*) is the free condition of the gills from the stem. In *Agaricus campestris,* while the gills are usually free, they are close to the stem, and in some cases are even adnexed to the stem. The same is true of *Agaricus rodmani.* Peck[32] says of the lamellæ,—" free, reaching nearly or quite to the stem. It is possible that in some examples the gills may be broadly attached to the stem fundament at the time of their origin, but become free at maturity by changes in the relation and tensions of the parts during expansion of the plant. That the young lamellæ are sometimes broadly attached around the upper end of the stem fundament has been observed in a number of examples during this study of development. In some examples the attachment of the stem is very broad, in others slight, and in still others the lamellæ are free from the time of their origin.

Deceptive Appearance of Sections near the Stem when the Young Lamellæ are Attached.—In studying the origin of the lamellæ in plants where the hymenophore, from its earliest appearance, is entirely free from the stem, little difficulty is experienced in the interpretation of the situation presented, in case there is a fairly well formed annular cavity prior to the origin of the gill salients. Longitudinal sections next the stem then present the simple situation shown in Fig. 17. But in those cases where the hymenophore primordium extends downward on the outer surface of the stem apex, as shown in Figs. 11 and 12, sections passing from the stem through this portion of the hymenophore, after the origin of the gill salients, present a complicated structure, which may be very confusing unless all the features of the situation are taken into consideration. As stated above the stem axis of the sections from which Figs. 11 and 12 were made is parallel with the longitudinal direction of the plate. In very young basidiocarps; as already described, the stem surface slopes outward at a very strong angle as shown in Fig. 32.

Now, when the gill salients begin to form by downward, or outward, extension of the level palisade, in those cases where the hymenophore primordium extends down on the surface of the stem,

[32] Peck, C. H., N. Y. State Mus. Nat. Hist Rept., 36, 45, 1885.

the salients first appear over this portion of the hymenophore, because it is the older. The older portion of the salients, therefore, extend outward perpendicular to the stem surface. Since their progression is centrifugal, the salients gradually extend over the angle between stem and pileus where their growth is downward. Since the growth in width of the salients is perpendicular to the surface of the level hymenophore at any point, there are formed, in the cases

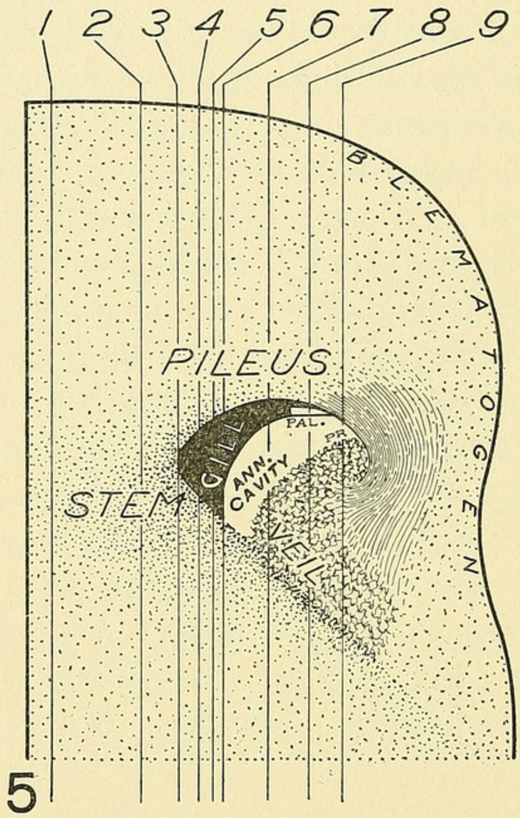

DIAGRAM 5. Lateral view through one half of a basidiocarp in an intermediate stage of development, showing (1) the strongly sloping surface of the stem; (2) the partly organized pileus margin which is becoming in volute because of eipnastic growth; (3) the hymenophore presenting three stages of development, (*a*) the oldest portion, the gill area extending on the under side of the pileus and far down on the surface of the stem (adnate at this stage), (*b*) the palisade area (*PAL*) distal to the gill area on under side of pileus, and (*c*) the primordial area (*PR*) near margin of pileus; (4) annular cavity; (5) the loose ground tissue of the marginal veil; and (6) the blematogen layer. See text.

under consideration, a series of little stalls, or pigeon holes, around the stem apex, between the young gills in the angle between the stem and pileus. This situation is illustrated in Figs. 24–31, from selected serial sections of the same basidiocarp. The sections were parallel with the long axis of the stem. Diagrams 5 and 6 illustrate the situation in this basidiocarp and show exactly how the scetions were made.

Fig. 24 is from a nearly median longitudinal section, made in the region indicated by line 1 of diagrams 5 and 6, which presents a situation practically the same as a median section. The outline of the narrow young gill salient is well shown in Fig. 24, with the distinct annular cavity. The gill salients are strongly curved and in the form of crescents, the lower limb of the crescent extending far down on the outwardly sloping stem surface; the upper limb reaching out on the under surface of the pileus, where it grades into the level palisade zone, and the latter into the primordial zone. The relation of parts is clearly represented by diagram 5. It is quite easy to form a mental picture of the series of little stalls, or pigeon holes, around the upper part of the stem between these crescentic salients.

Fig. 25 is from a section in the region indicated by line 2 of diagrams 5 and 6. The line 2 in diagram 6 shows how the section passes through the side of the stem and obliquely across a few of the young gills, then on either side passing through the level palisade and primordial zones. These features are clearly seen in Fig. 25. Fig. 26 is from the region indicated by line 3: Fig. 27 that of line 4; Fig. 28 that of line 5; Fig. 29 that of line 6; and Fig. 30 that of line 7, of diagrams 5 and 6 (figures of sections in the region indicated by lines 8 and 9 are not shown from this basidiocarp, but there is nothing essentially different in them from figures 22 and 23 from another plant). Fig. 31 is a more highly magnified view of the middle portion of Fig. 27.

Figs. 26–29 and 31 present a very interesting situation. They show transections of the stalls, or pigeon holes, mentioned above. Unless caution is observed this situation would be very misleading. The gill salients are attached above to the under side of the pileus and below to the surface of the stem, and this attachment above and below existed from the time of the origin of the salients. However, the attachment below is not that of the margin of the gills, but of their origin from the stem, since the salients grew outward from the level palisade organized in this region over the upper surface of the stem.

Similar sections of *Coprinus micaceus*[33] through the region of the attached gills was one of the features contributing to the incorrect interpretation, by Levine, of the origin of the lamellæ in this plant, as shown by his Figs. 13 and 14. The palisade cells on the sides and in the upper angle of these pigeon holes could easily give the impression that the gills had their origin from isolated radial areas of new growth of palisade cells, these areas, or "ridges" of

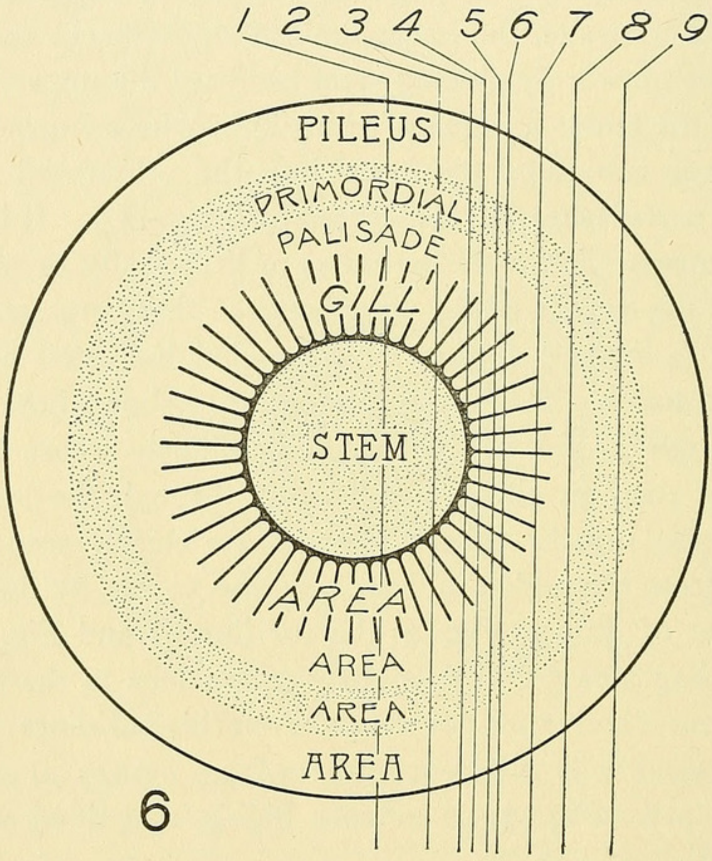

Diagram 6. Zenith view in a basidiocarp of the same age as that represented in diagram 5. See text for details not marked in the diagram.

palisade cells parting as they increase, forming a lining over the ground tissue or partitions of these little stalls, and thus enclosing "the notch between the gills."

Relation of the Gills to the Involute Margin of the Pileus.—There are other peculiar situations presented in the development of

[33] Levine, M., "The Origin and Development of *Coprinus micaceus*," *Am. Jour. Bot.*, 1, 343–356, pls. 124, 125, 1914.

Agaricus rodmani (and other species) which may lead to serious misinterpretation unless great caution is observed. This is the relation of the gills to the involute margin of the pileus and to the marginal veil, shown in a series of longitudinal, "tangential" sections of basidiocarps at an age when the gill salients, by centrifugal progression, have nearly or quite reached the margin of the pileus. The various features of this situation are presented in Figs. 32–42. The figures are photographs of selected serial sections from a single basidiocarp. Diagrams 7 and 8 illustrate the situation in this basidiocarp and the lines show the regions in which the sections were made.

In Fig. 32, from a nearly median longitudinal section (in the region of line 1), the involute margin of the pileus is shown. An indefinite portion of the outer, lighter stained area is the blematogen. The margin of the pileus is so strongly involute that the edge is curved upward toward the gills and has crowded the mass of the ground tissue constituting the inner portion of the veil up against the middle zone of the lamellæ. The attachment of this ground tissue to the margin of the gills is not very firm, though there is some adherence of the hyphæ. The attachment has occurred after the ground tissue was crowded against the margins of the gills by the strongly upturned, involute pileus margin. The strongly involute margin of the pileus is well shown also in several of the figures in Plate VII. The position of the upturned edge of the involute pileus margin is such that the loose ground tissue of the inner portion of the veil is lifted up against the middle area of the lamellæ, while the edges of the gills near the stem and also near the margin of the pileus are free. This is very clearly shown in Fig. 33, from a section in the region of line 2 in diagrams 7 and 8.

Figs. 34 and 35 are from sections in the region of lines 3 and 4 just passing through the surface of the stem in the angle at the junction of the pileus and stem. The hymenophore extends a short distance down on the upper surface of the stem, but the gills are only "adnexed," not extending so far down on the stem fundament as in the basidiocarp represented on Plate XII. and in diagrams 5 and 6. In the middle area of Fig. 35, the nearly solid block of tissue in the same level with the gills on either side, is hymenophore tissue from the surface of the stem, and a portion of the same area in Fig. 34 also belongs to the hymenophore. The hymenophore, as interpreted here, and in all of my recent papers, includes not only all parts of the lamellæ and the palisade cells between adjacent lamellæ, but also a thin, often indefinite zone of the subadjacent tissue corresponding to the subhymenial tissue of the palisade between the gill origins. As figure 35 shows, the "stalls," or "pigeon holes," in the angle of pileus and stem are quite small because the gill origins extend but

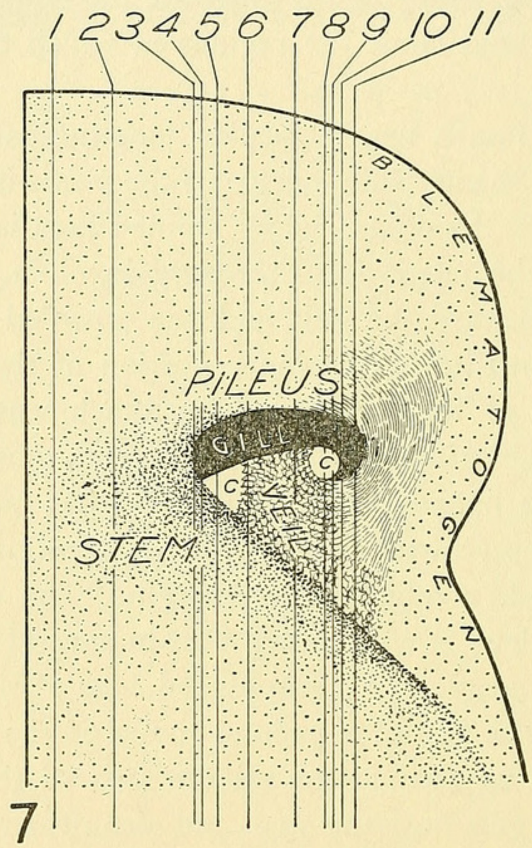

Diagram 7. Lateral view through one half of a basidiocarp in an older stage than that represented in diagrams 5 and 6. The hymenophore has all passed over into the gill stage. The gill area does not extend so far down on the stem as in diagram 5. The margin of the pileus is more strongly involute and the veil tissue has been crowded up against the middle portion of the gills. *C* = the portion of the annular cavity not filled. See text for other details not marked here.

a short distance down on the upper surface of the stem. The abrupt ending of this hymenophore tissue below is even with the margins of the gills on either side, and the lower edge is free from the ground tissue clothing the stem fundament, as shown by the clear line between the two. This indicates that the portion of the hymenophore on the upper surface of the stem projected by growth slightly above the level of the stem surface, or above that of the ground tissue. In Fig. 34 the distinct boundary line of the more compact tissue shows, but it is in contact with the ground issue below since this section did not pass outside of the junction of stem and pileus fundaments. In Fig. 35 a few of the gills on either side of the middle are free from the ground tissue below. Outside of this on either side (the middle zone between stem and pileus margin) a number of the gills are attached to the ground tissue pressed up against them by the involute pileus margin. On either side of these areas, *i. e.*, near the margin of the pileus, the gills are free.

Fig. 36 is from a section in the region indicated by line 5 in diagram 7. The middle of the section, according to line 5, would pass through the space of the annular cavity near the stem which has not been filled by the upward crowding of the ground tissue. The margin of the gills here should therefore be free from the ground tissue below. This is shown to be the case in Fig. 36, for the gills over the middle portion of the figure (which are near the stem). On either side of this area, however, the section passes through the zone where the ground tissue is crowded up against the gills, while toward the margin of the pileus the gills are again free from the ground tissue.

Figs. 37 and 38 are from sections in the region of lines 6 and 7 respectively, of diagram 7. Both sections are thus "tangents" through the region where the ground tissue in contact with the middle zone of the gills would be continuous and of considerable extent, but the area in the region of line 6 would be of greater extent than that in the region of line 7. This corresponds with the situation shown in Figs. 37 and 38, while toward the margin of the pileus on either side the gills are free. Figs. 39 and 40 are from the region of lines 8 and 9. These pass through the portion of the annular cavity between the margin of the pileus and the ground tissue crowded up against the middle region of the hymenophore. The gills therefore would not be in contact with the ground tissue below. In Figs. 39 and 40, however, it is clear that on either side the gills are attached below as well as above. The attachment below is not the margin of these gills, but their point of origin from the inner surface of the involute pileus margin. This will be clearly understood from a study of Figs. 41 and 42.

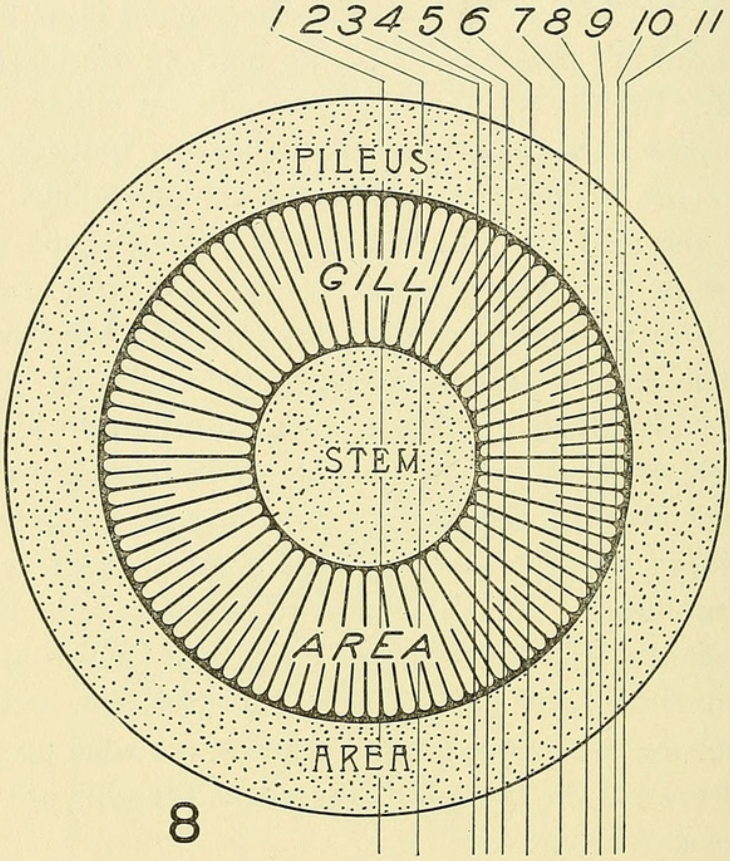

DIAGRAM 8. Zenith view into a basidiocarp of the same age. See text for details not marked.

Figs. 41 and 42 are from sections in the region of lines 10 and 11 in diagrams 7 and 8. The gills are attached above and below. But it is very clear here that the attachment below, as well as above, is to the pileus. Since the gills are downward growths of the level palisade, formed on the under surface of the pileus (*i. e.,* perpendicular to the level palisade), the attachment below in these figures, as well as that above, is at the point of origin of the gills, and must not be interpeted as an attachment of the gill margin to the stem.

The First Ridges, or Salients, of the Hymenophore are the Fundaments of the Lamellæ Themselves.—The question of the origin of the lamellæ is of renewed interest since it has recently been stated that one of the problems yet to be worked out in the Agaricaceæ is the origin of the lamellæ.[34] The evidence presented in support of this sweeping, and rather surprising statement, is made, so far as we can judge, on the basis of an investigation of *Coprinus micaceus.* It carries with it the implied charge that all of the observations and statements in regard to the origin of the gills, covering a period of more than half a century, are incorrect. In the case of my own work on *Agaricus campestris,*[35] *Armillaria mellea,*[36] *Lepiota clypeolaria,*[37] *Agaricus arvensis*[38] and *A. comtulus* it can be most positively reaffirmed that the lamellæ originate as described, as downward, radial growths of the level palisade portion of the hymenophore. The evidence was so clear in these examples that at the time of the study it did not seem desirable to present full series of "tangential" sections of the different stages in the origin of the gills, particularly as the method of origin agreed in all respects with that described in more than a dozen different species in earlier works. The present study of *Agaricus rodmani* was undertaken, not only for the purpose of examining into the significance of the double annulus, but also for the purpose of examining the different stages in the organization of the hymenophore primordium, the level palisade stage, and the origin of the gills, in a species closely related to *Agaricus campestris.* It is very clear that the present study has fully confirmed the earlier statements with reference to the origin of the lamellæ. Material has also been grown, and the young stages obtained for sectioning in the following commercial forms of *Agaricus: A. campestris* varieties *bohemia* and *alaska,* and *A. "villaticus."*

[34] Levine, M., "The Origin and Development of the Lamellæ in *Coprinus micaceus,*" *Am. Jour. Bot.,* 1, 343–356, pls. 39, 40, 1914.

[35] Atkinson, Geo. F., The Development of *Agaricus compestris,*" *Bot. Gaz.,* 42, 241–264, pls. 7–12, 1906.

[36] Atkinson, Geo. F., "The Development of *Armillaria mellea,*" *Myc. Centralb.,* 4, 113–121, pls. 1, 2, 1914.

[37] Atkinson, Geo. F., "The Development of *Lepiota clypeolaria,*" *Ann. Myc.,* 12, 346–356, pls. 13–16, 1914.

[38] Atkinson, Geo. F., "The Development of *Agaricus arvensis* and *A. comtulus,*" *Am. Jour. Bot.,* 1, 3–22, pls. 1, 2, 1914. "Homology of the Universal Veil in *Agaricus,*" *Myc. Centralb.,* 5, 13–19, pls. 1–3, 1914.

The situation in certain species of *Coprinus,* where the margins of the gills are attached to the stem before maturity, and break away during the expansion of the plants, has for a long time interested me, and I have intended to investigate certain of the species for the purpose of comparing the situation in this genus with that described in *Amanita rubescens*[39] by deBary, *A. muscaria*[40] by Brefeld and in *Amanitopsis vaginata*[41] by myself, where there is no general prelamellar cavity, and the first evidence of the lamellæ is the differentiation of a series of radial trabeculæ in the hymenophore primordium, continuous with the stem and trama of the pileus. This investigation was delayed, however, until the autumn of 1914. Material of three species, *Coprinus comatus, atramentarius* and *micaceus,* was studied, and the results will be published in another paper. This much may he said here, that these three species do not belong to the *Amanita* type but to the *Agaricus* type. There is a strong, annular, prelamellar cavity in *Coprinus comatus,* a weak one in *C. atramentarius* and *micaceus,* but in all three the lamellæ originate as downward-growing salients of a level palisade zone, exactly as described here for *Agaricus rodmani,* the only difference being in those specific features relating to the structure of the lamellæ. Levine based his interpretation of the origin of the lamellæ in *Coprinus micaceus* on complicated and rather well advanced stages of their development. Had the origin of these complicated structures been sought it is probable that the origin of the lamellæ would have been found.

Of the plants thus far studied the following species may be mentioned as examples of the *Agaricus* type in which the origin of the lamellæ has been clearly and correctly described, those by Hoffmann more than half a century ago. *Agaricus carneotomentosus* (*Panus torulosus*) by Hoffmann[42] (1856, p. 145); *Cantharellus*

[39] De Bary, A., "Morphologie und Physiologie der Pilze, Flechten und Myxomyceten," Leipzig, 1866. "Vergleichende Morphologie and Biologie der Pilze, Mycetozoen und Bacterien," 1884. "Comparative Morphology and Biology of the Fungi, Mycetozoa and Bacteria," Oxford, 1887.

[40] Brefeld, O., "Botanische Untersuchungen über Schimmelpilze," 3, Basidiomyceten, I., I.–IV., 1–226; pls. 6–11, 1887.

[41] Atkinson, Geo. F., "The Development of *Amanitopsis vaginata*," *Ann. Myc.*, 12, 369–392, pls. 17–19, 1914.

[42] Hoffmann, H., "Die Pollinarien und Spermatien von Agaricus," *Bot. Zeit.*, 14: 137–148; 153–163, pls. 5, 1856.

tubaeformis, C. aurantiacus, Panus stipticus, Pleurotus tremulus, Omphalia umbellifera, O. pyxidata, Marasmius epiphyllus by Hoffmann[43] (1860); *Collybia velutipes, C. fusipes, Hygrophorus chlorophanus, Galera mycenopsis, Hebeloma mesophaeus, Coprinus fimitarius, Paxillus involutus, Entoloma sericeum,* and others by Hoffmann[44] (1861); *Mycena vulgaris, Collybia dryophila, Nyctalis parasitica, Clitocybe cyathiformis,* and *Cantharellus infundibuliformis* by deBary[45] (1866, 1884, 1887) the latter two in conjunction with Woronin; *Coprinus lagopus* by Brefeld[46] (1877, p. 127); *Agaricus campestris* by Atkinson[47] (1906); *Hypholoma* by Miss Allen[48] (1906) and by Beer[49] (1911); *Stropharia ambigua*[50] by Zeller (1914); *Agaricus arvensis* and *comtulus,*[51] and *Armillaria mellea*[52] by Atkinson (1914).

Summary.

1. The lower limb of the double annulus of *Agaricus rodmani* is not a true volva like that of the Amanitas thus far studied. It is composed of a short segment of the blematogen plus some of the inner tissue of the marginal veil. The greater portion of the blematogen remains "concrete" with or consolidated with the surface of

[43] "Beiträge zur Entwickelungsgeschichte und Anatomie der Agaricinen," *Bot. Zeit.,* 18: 389–395; 397–404, pls. 13, 14, 1860.

[44] Hoffmann, H., "Icones Analyticæ Fungorum; Abbildungen und Bescreibungen von Pilzen mit besonderer Rucksicht auf Anatomie und Entwickelungsgeschichte, 1–105, pls. 1–24, 1861.

[45] DeBary, A., "Morphologie und Physiologie der Pilze, Flechten und Mycetozoen," Leipzig, 1866. "Vergleichende Morphologie und Biologie der Pilze, Mycetozoen und Bacterien," 1884. "Comparative Morphology and Biology of the Fungi, Mycetezoa and Bacteria," Oxford, 1887.

[46] Brefeld, O., Botanische Untersuchungen über Schimmelpilze," 3, Basidiomyceten, I., I.–IV., 1–226; pls. 6–11, 1887.

[47] Atkinson, Geo. F., "The Development of *Agaricus campestris,*" *Bot.* Gaz., 42: 241–264, pls. 7–12, 1906.

[48] Allen, Caroline L., "The Development of Some Species of *Hypholoma,*" *Ann. Myc.,* 4: 387–394, pls. 5–7, 1906.

[49] Beer, R., "Notes on the Development of the Carpophore in Some Agaricaceæ," *Ann. Bot.,* 25^2: 683–689, pl. 52, 1911.

[50] Zeller, S. M., "The Development of *Stropharia ambigua,*" *Mycologia,* 6: 139–145, pls. 124, 125, 1914.

[51] Atkinson, Geo. F., "The Development of *Agaricus arvensis* and *A. comtulus,*" *Am. Jour. Bot.,* 1: 3–22, pls. 1, 2, 1914.

[52] Atkinson, Geo. F., "The Development of *Armillaria mellea,*" *Myc. Centralb.,* 4: 113–121, pls. 1, 2, 1914.

the pileus, while in *Amanita* the blematogen is finally delimited from the surface of the pileus by a cleavage layer. A double annulus homologous with that of *Agaricus rodmani* is often present in certain other species of *Agaricus*.

2. The primordium of the basidiocarp is oval in form, and homogeneous in structure, consisting of intricately interwoven hyphæ.

3. The four primary parts of the basidiocarp, pileus, stem, marginal veil and hymenophore, are first differentiated by the origin of the hymenophore fundament.

4. The hymenophore primordium arises as an internal, annular zone of new growth toward the upper part of the young basidiocarp. It consists of slender hyphæ rich in protoplasm, parallel, and directed obliquely downward. The lower outer surface is at first more or less open and uneven, presenting a frayed or fimbriate appearance. By continued growth and multiplication of these hyphæ the hymenophore primordium becomes more compact and the under surface becomes even, forming a level palisade zone. Growth of the hymenophore proceeds in a centrifugal direction, the older portions being next the stem fundament. By the epinastic growth of the pileus margin the hymenophore takes on the form of an annular arch.

5. The increase in number and diameter of the elements of the hymenophore fundament produce a tension upon the ground tissue beneath, which lags behind in growth and is torn away from the under surface of the hymenophore, thus forming an annular, prelamellar cavity. This cavity may later be nearly filled by the ground tissue of the inner portion of the veil which increases in bulk, and is often crowded up against the young gills by the involute margin of the pileus.

6. The lamellæ originate as downward growing radial salients of the level palisade zone, beginning next, or on the stem, according as the hymenophore primordium is free from or extends down on the upper portion of the stem fundament. They progress in a centrifugal direction. In an intermediate stage of development of the basidiocarp, all three stages of the hymenophore may be present, the zone of gill salients next the stem, then the level palisade zone, and beyond this the primordial zone.

7. The first ridges, or salients, which appear in connection with the hymenophore are the fundaments of the lamellæ themselves, and the palisade layer is continuous over their edges as well as in the notch between adjacent salients.

DESCRIPTION OF PLATES VII.–XIII.

PLATE VII.

Mature and nearly mature plants of *Agaricus rodmani* showing the double nature of the annulus with its edge grooved; forming an upper and lower limb; the short stem, involute margin of the pileus, etc. $\times$ 2/3 diameter. For details see text.

PLATE VIII.

Mature and very robust plants from parking between sidewalk and street. Real size. See text.

PLATES IX.–XIII.

The magnifications of the photomicrographs are as follows: Figs. 3–8; $\times$ 9 diameters. Fig. 33; $\times$ 10 diameters. Figs. 1, 2; $\times$ 12 diameters. Fig. 32; $\times$ 13 diameters. Figs. 34–36; $\times$ 20 diameters. Fig. 17; $\times$ 23 diameters. Figs. 15, 16; $\times$ 28 diameters. Figs. 21–30, 37–42; $\times$ 30 diameters. Fig. 31; $\times$ 100 diameters. Fig. 12; $\times$ 110 diameters. Fig. 13; $\times$ 155 diameters. Figs. 10, 11; $\times$ 160 diameters Fig. 18; $\times$ 170 diameters. Figs. 9–14; $\times$ 225 diameters. Figs. 19, 20; $\times$ 250 diameters.

PLATE IX.

FIG. 1. (No. 18.) Young stage of basidiocarp primordium.

FIG. 2. (No. 20.) Somewhat older stage of basidiocarp primordium, but still in the undifferentiated stage.

FIG. 3. (No. 27/1.) Earliest stage of differentiation in the young basidiocarp, median longitunial section showing a transection of the internal annular hymenophore fundament, the general prelamellar cavity not yet formed. Pileus fundament is above, stem fundament below, and veil fundament underneath the hymenophore primordium (see Fig. 9).

FIG. 4. (No. 27/4.) Longitudinal section of the same basidiocarp, "tangential" to the hymenophore primordium, which is shown as a transverse deeply staining area.

FIG. 5. (No. 23/1.) Median longitudinal section through a basidiocarp just after the formation of the general, annular, prelamellar cavity. The hymenophore is still in the primordial condition (see Fig. 10) but does not extend down on the surface of the upper part of the stem fundament.

FIG. 6. (No. 23/3.) Longitudinal section of the same basidiocarp, "tangential" to the hymenophore and annular cavity (see Fig. 13).

FIG. 7. (No. 12/2.) Median longitudinal section of a basidiocarp just after the formation of the general, annular, prelamellar cavity. The

hymenophore is still entirely in the primordial stage (see Fig. 11) and extends for a considerable distance down on the surface of the upper part of the stem fundament.

Fig. 8. (No. 12/7.) Longitudinal section of the same basidiocarp, "tangential" to the hymenophore and annular cavity (see Fig. 16).

PLATE X.

Fig. 9. (No. 27/7.) More highly magnified view of the transection of the hymenophore primordium shown in Fig. 3; stem axis at the left. In the darker area (hymenophore primordium) the hyphae extend downward and obliquely outward toward, and some projecting into, the veil fundament below, which consists of a loose mesh of interwoven hyphae.

Fig. 10. (No. 23/1.) More highly magnified view of the transection of the hymenophore primordium and annular cavity shown in Fig. 5 (axis of stem at the left).

Fig. 11. (No. 12/2.) More highly magnified view of the transection of the hymenophore primordium and annular cavity shown in Fig. 7 (stem axis at right). The hymenophore primordium extends down over the upper part of the stem outer surface. Veil fundament in the angle below, the ground tissue tearing apart and separting from the fimbriate under surface of the hymenophore

Fig. 12. (No. 3/3.) Transection of hymenophore and annular cavity, showing same view as Fig. 11 (stem axis at right) but in another basidiocarp and slightly older stage; the portion of the hymenophore primordium on the upper part of the stem fundament has become transformed into the level palisade stage.

Figs. 13 and 14. (No. 2/2.) Section of another basidiocarp showing the hymenophore and annular cavity in same stage as in Fig. 10, at different magnifications (stem axis at right). Hymenophore primordium with fimbriate edge. Ground tissue below (veil fundament) breaking away from the fimbriate surface of the hymenophore as a result of the tension produced by the rapid increase in number and size of the elements of the hymenophore and the lagging behind of the ground tissue below, thus forming the annular cavity. These sections are radial and parallel with the direction of the later lamellæ. The elements of the hymenophore here are somewhat clustered, the slender ends of the hyphæ clinging in groups as the lower surface of the hymenophore is loosened by the tension of the increase above.

Fig. 15. (No. 23/3.) "Tangential" section of the hymenophore primordium, more highly magnified view of the hymenophore and general, annular, prelamellar cavity shown in Fig. 6. Note the fimbriate lower surface of the hymenophore primordium, and the loose ground tissue (primordium of veil) below separating from it and forming the annular cavity. The structure of the hymenophore primordium is homogeneous, there is not the slightest evidence of gill salients, or of ridges of any sort, which precede or have any relation to the lamellæ which are to arise later.

Fig. 16. (No. 12/7.) "Tangential" section of hymenophore primordium, annular cavity and veil fundament, a more highly magnified view of this part of the basidiocarp shown in Fig. 8. Details as in Fig. 15.

PLATE XI.

Figs. 17–19 and 21–23, all from a single basidiocarp (No. 5/2), from selected serial sections parallel with the axis of the stem and "tangential" in the pileus. Fig. 17 is from near the stem, and shows the three stages of the developing hymenophore, primordial zone, level palisade zone, and the zone of gill salients (transected) with different stages in the origin of the latter from the level palisade condition (see text for details). The general annular cavity is well shown.

Fig. 18. More highly magnified view of portion of the same section in the region of the origin of the gill salients from the level palisade stage.

Fig. 19. More highly magnified view of the young gill salients, showing how they flare, or fantail, when released from the pressure to which the elements are subjected in the level palisade zone, also showing how this flaring of the young gill salients crowds the intervening palisade cells of the original level into "ridges," these ridges of palisade in the notch between two lamellæ being formed later than the gill salients, and as a result of the lateral pressure of the flaring salients. For details see the text.

Fig. 20. (No. 1/2.) Section from another basidiocarp showing transition from the level palisade stage to the gill salients.

Fig. 21. Section nearer the margin of the pileus than that shown in Fig. 17. In the middle area the gill salients are cut near their distal end where they are very low (see text for details). Transition to level palisade and primordial zone on either side.

Fig. 22. Section still nearer the margin of the pileus showing the level palisade zone in the center, and the primordial zone on either side.

Fig. 23. Section still nearer the margin of the pileus, entirely through the primordial zone.

PLATE XII.

Figs. 24–31. Selected serial sections from a single basidiocarp (No. 1/3), parallel with the stem axis and from nearly median in the stem to midway from stem surface to the margin of the pileus. Here the hymenophore extends for some distance down on the outward sloping surface of the stem fundament, and there are little "stalls" or pigeon holes between them in the angle at junction of pileus and stem. See text for details.

PLATE XIII.

Figs. 32–42. Selected serial sections from a single basidiocarp (No. 11), parallel with the axis of the stem and from median in the stem to "tangential" in the margin of the pileus. See text for details.