Bacillen sind weiß, eine ist fluorescierend und verflüssigend, die andere nicht verflüssigend. Colonien der Coccen sind gelb und orangegelb.

Die fäulniserregende Bacterienart ist dem *Bacterium fluorescens* (Flügge) Lehm. et Neum. sehr ähnlich, sie verflüssigt Gelatine, Milch wird peptonisiert. Bei *Micrococcus sulfureus* Zimm.? findet man unter der gesunden Schale kleine gelbliche Colonien. Dieser Micrococcus ist kein Fäulniserreger.

Tafelerklärung.

Fig. 1. Erkrankte Zwiebel. — Fig. 2. Blattstück der erkrankten Zwiebelpflanzen. — Fig. 3. Erstes Stadium der Erkrankung. — Fig. 4. Eine Pflanze mit erkrankten und gesunden Zwiebeln. — Fig. 5. Zwiebel mit Sclerotien. — Fig. 6. Erkranktes Blattstück.

Homology of the "universal veil" in *Agaricus*.

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(With 3 plates.)

Confusion in the use of the term „universal veil".

In his Systema Mycologicum Fries[1]) used the term "universal veil" only in the diagnosis of the sections *Amanita*, and *Lepiota*. It appears quite evident that his interpretation of this structure was that of an external zone, present even in the young fruit body, discrete from the pileus in *Amanita* (p. 13) and forming a volva, but concrete with the pileus in *Lepiota* (p. 19) and forming an annulus. It may be open to question whether or not Fries actually understood the real nature of the situation in regard to this external zone in *Amanita* and *Lepiota*. I am inclined to believe that he did not, except as it applied to the later stages of development in *Amanita*, and to certain species of *Lepiota*. This, however, is not surprising, since the true homology of these structures can only be determined by careful studies of development from the earliest stages of differentiation of the sporophore or basidiocarp. During Fries' time it was quite impossible to do this with the degree of accuracy which is now obtainable.

A number of later students have made a wider application of the term ("universal veil"), extending it to other genera, among which is the genus *Agaricus* (*Psalliota* Fries). In the diagnosis of *Psalliota* Cooke[2]) uses the term in the same sense as Fries did in *Lepiota*, where he says, "Veil universal, concrete with the cuticle of the pileus, and fixed to the stem, forming a ring". Smith[3]) employs almost the same words in his characterization of *Psalliota*, "Veil universal, concrete with the cuticle

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1) Fries, E., Syst. Myc. **1**, 9, 13. 19, 1821.
2) Cooke, M. C., Handbook of British Fungi **1**, 136, 137, 1871.
3) Smith, W. G., Synopsis Brit. Basid. 170, 1908.

of the pileus and forming an annulus on the stem". In his figure of the morphology of *Agaricus campestris* (l. c. fig. 42) he shows a universal veil *(U. V.)* extending from the base of the stem over the entire fruit body. During the expansion of the plant this universal veil is ruptured and the lower part is shown as a small ring at the base of the stem. But the interpretation of his concept of universal veil and annulus is made difficult by the illustration of an additional structure, the inner, or partial veil which appears higher up on the stem and is marked annulus *(AN)*. In his description of the family *Agaricaceae* (l. c. p. 11) he clearly distinguishes between the "primary" or "universal veil" which forms the volva and fragments on the pileus, and the partial veil by the statement, "In some species a secondary or partial veil is also present in the earlier stages spreading from the upper part of the stem to the edge of the pileus. This veil is finally ruptured and partly persists as a ring or annulus *(A)* encircling the stem".

Such an interpretation of the morphology of *Agaricus campestris* is certainly far from lucid. One of the very confusing features in all systematic works on the *Agaricaceae* is the use of the term veil, and "universal veil". I must confess that I have never been quite able to form a satisfactory concept of the use of these terms, and have always met with difficulty in attempting an explanation of them to my students. But after a study of the development of several species of *Agaricus*, of *Amanitopsis vaginata* and *Lepiota clypeolaria*, I believe it is possible to obtain a clearer insight into the homologies of these structures than we have had heretofore. But caution should be used in attempting to apply these interpretations to all of the *Agaricaceae*. We need careful studies of development in all of the genera to determine the origin and differentiation of the "universal veils", and other sections of the genus *Lepiota* than that to which *L. clypeolaria* belongs should be studied.

"Universal veil" in *Lepiota clypeolaria*.

In *Lepiota clypeolaria* there is a well formed external layer surrounding the very young fruit body before there is any internal differentiation of the fundamental parts of the fruit body in the center of the primordium. This may well be regarded as a "universal veil", for at later stages it envelops the stem, is continuous over the pileus and remains concrete with it. The development of *Lepiota clypeolaria* will be described in another paper. A similar "universal veil" is present in the very young stages of *Armillaria mellea*[4]), but its inner zone is not quite so well organized as in that of *Lepiota clypeolaria*.

Differentiation of the primordia in *Agaricus arvensis*.

I have recently described the development of *Agaricus arvensis* and *A. comtulus*[5]) from material collected in the forests of the Jura Mountains, near Pontarlier, France, in 1905. Different stages of the very young

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4) Atkinson, Geo. F., The development of *Armillaria mellea*. Myc. Centralbl. 4, 113—121, 1914.

5) Atkinson, Geo. F., The development of *Agaricus arvensis* and *A. comtulus*. Am. Journ. Bot. 1, 3—22; pls. 1, 2, 1914.

sporophore[6]) of *Agaricus arvensis* are shown in figs. 1—3. The first evidence of the internal annular gill cavity is shown in fig. 1 and slightly later stages are presented in figs. 2 and 3. The primordium of the hymenophore lies just above the gill cavity, and is differentiated by the darker color of the tissue in figs. 2 and 3. The hymenophore is therefore not only endogenous in origin, but originates deep within the fruit body. The primordium of the pileus margin lies just above the outer angle of the gill cavity and is merged with the hymenophore primordium at this early stage. External to this is a broad zone of looser tissue with thick walled hyphae which envelops the young fruit body. Fig. 8 is a more highly magnified photomicrograph showing the very young primordium of the pileus margin at the junction of lines perpendicular to *a*, *a*. The general course of the hyphae is outward and downward. The loose meshed tissue below is the first evidence of the gill cavity, the threads lagging behind in growth are torn appart. The hyphae in the gill cavity and those of the hymenophore and pileus primordium are thin walled.

The loose meshed tissue at the right of the pileus margin in the same figure (fig. 8) belongs to the external zone which envelops the entire fruit body at this and somewhat later stages. The thick walled hyphae of this zone are readily distinguished from the thinner walled more compact ones of the pileus and hymenophore primordia, and from those of the loose meshed tissue below the hymenophore which is separating to form the gill cavity. In fig. 9 an older stage is represented, a more highly magnified illustration of a portion of fig. 3. The margin of the pileus here is at the junction of lines perpendicular from *b*, *b*.

Comparison with *Agaricus comtulus*.

A similar zone of loose-meshed tissue of thick walled hyphae forming an enveloping zone around the pileus and stem fundaments is present in *Agaricus comtulus* and shown in fig. 7. The hymenophore primordium here appears as two symmetrically disposed dark areas in the longitudinal section, the dark area between them and forming a convex area within the upper part of the sporophore is the pileus primordium. The dark area below which broadens downward is the stem fundament.

Union of the pileus and the external zone.

Older stages of this external zone of loose meshed tissue, with thick walled hyphae, are shown in figs. 5, 6 and 10. The elements of the pileus primordium become more active from the margin upward toward the center and extending outward (the hyphae, toward the margin being more strongly epinastic) grow into the inner portion of this external zone, binding it to the surface of the pileus.

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6) In my article: The development of *Agaricus arvensis* and *A. comtulus* Am. Journ. Bot. **1**, 3—22; pls. 1, 2, 1914 I used in several places the term "carpophore", for the fruit body. GARNSEY and BALFOUR, in the English Edition of DE BARY's Comparative morphology and biology of the Fungi, Mycetozoa and Bacteria, Oxford 1887 define carpophore (p. 493) as a "stalk of a sporocarp". It is perhaps, therefore not an apt term for the fruit body (Fruchtkörper), or basidiocarp of the basidiomycetes.

Comparison with the *Amanitae*.

In *Amanitopsis vaginata* a similar external zone of loose-meshed tissue is present from the early stages of the primordium of the fruit body, which completely envelops the pileus and stem primordia. The margin and surface of the pileus primordium in a similar way grows out toward this enveloping zone, the hyphae of the surface being epinastic, strongly so at the margin. There is no clear cut border between the mature pileus primordium surface and this outer zone, but many of the surface hyphae of the former tie into the inner surface of the latter. The relation of the mature pileus primordium to the enveloping zone is exactly the same in *Amanitopsis vaginata* und *Agaricus*. The enveloping zones in *Amanitopsis* and *Agaricus* are homologous structures, the "universal veil" of Fries in its primordial condition. From this point, however, the course of development is different in the two geners. In *Amanitopsis*[7]) a cleavage layer is formed which separates the fundament of the "universal veil", or blematogen[8]), from the pileus, forming a complete or finished veil, the volva, or teleoblema[9]). In *Agaricus* the "universal veil", or blematogen, remains concrete with the surface of the pileus, no cleavage layer being formed.

Comparison with *Agaricus campestris*.

This interpretation of the "universal veil" is different from that given by me in the case of *Agaricus campestris* in 1906 and I must confess that in the interpretation there given, I also have contributed to the confusion of the subject of the "universal veil", or rather have assisted in preserving it. The very delicate, floccose weft of mycelium enveloping the sporophore primordium in *Agaricus campestris*[10]) I formerly interpreted as the "universal veil". It is a universal veil, but is not homologous with the stouter "universal veil", present also in *Agaricus campestris* and homologous with the blematogen as here described. The outer delicate, floccose layer described in *Agaricus campestris* is a primary "universal veil", or protoblema[11]). In fig. 12 this protoblem is well shown enveloping the young fruit bodies. The older fruit bodies show that it is being torn into loose floccose scales which are often quite distinct on the surface of the mature pileus as shown in fig. 13. This is perhaps what Fries refers to as "subuniversal veil" which he says

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7) A full account of the development of *Amanitopsis vaginata* will be published in another paper.

8) Blematogen, or blematogen layer (*βλημα* = cover; *γενής* = producing), term proposed for the external zone of tissue in the fruit bodies of the *Amanitae* which later becomes separated from the pileus by a cleavage layer, and for the homologous layer in *Agaricus* and other genera where it remains concrete with the pileus. See p. 13, Atkinson, Geo. F., The development of *Agaricus arvensis* and *A. comtulus*. Am. Journ. Bot. **1**, 3—22; pls. 1, 2, 1914.

9) Teleoblema, or teleoblem (*τελειος* = complete or finished; *βλημα* = cover), term proposed for the complete or finished veil in the *Amanitas* formed through the separation of the blematogen from the pileus by a cleavage layer (see p. 17, Atkinson, l. c.).

10) See pl. 10 and pl. 12, fig. 18, in Atkinson, Geo. F., The development of *Agaricus campestris*. Bot. Gaz. **42**, 241—264; pls. 7—12, 1906.

11) Protoblema or protoblem (*πρῶτος* = first; *βλημα* = cover). See p. 13 in Atkinson, Geo. F., The development of *Agaricus arvensis* and *A. comtulus*. Am. Journ. Bot. **1**, 3—22; pls. 1, 2, 1914.

occurs as a rudiment in certain species of *Agaricus*[12]), among which is *A. campestris*. A protoblem may be present in *A. arvensis*, as suggested by the situation in figs. 6 and 9, but as these fruit bodies originated underneath the forest mold, the protoblem, if present, was largely removed in collecting the plants and preparing them for sectioning.

The partial, or marginal veil.

The partial veil, or marginal veil, as it is frequently termed, extends from the margin of the pileus to the stem, and when freed from the pileus margin forms the ring or annulus on the stem. FAYOD[13]) states that it is merely a section of the "universal veil". If it were entirely composed of the tissue external to the gill cavity at the time of the origin of the latter it would be merely a section of the blematogen. But it is a much more bulky structure. It is very largely composed of tissue resulting from growth of the thinwalled hyphae next the stem and by growth of hyphae from the margin of the pileus primordium. The latter growth forms the upper or inner more compact zone of the annulus, while the former gives rise to the looser, open-meshed lower zone. This forms a duplex veil or annulus which is so conspicuous a feature of the annulus of *Agaricus arvensis* and some other species, the lower looser portion usually separating into characteristic patches. It is well shown in figs. 5, 6 and 11. There is a section of the blematogen or "universal veil", external to the partial veil, which may remain adherent to the margin of the annulus, or be largely sloughed off at a rather early stage. But the great bulk of the partial veil is formed by new growth. The marginal veil is therefore properly to be regarded as a structure sui generis.

Summary.

1. In the early primordium of *Agaricus arvensis*, *A. campestris* and *A. comtulus*, there is an external thick zone of tissue distinguished from the internal fundamental tissue, but not separated from it, by a more open mesh of interwoven hyphae. The hypha walls of this enveloping zone are thick walled in strong contrast to the thinner walled hyphae, richer in protoplasm, of the interior.

2. The primordia of the principal parts of the fruit body, pileus, hymenophore and stem, are endogenous, and are differentiated within the central portion. The enveloping zone of loose-meshed tissue with stout hypha walls is the "universal veil", or blematogen, homologous with a similar layer in *Amanitopsis vaginata*. As organization of the pileus proceeds the surface hyphae of the mature pileus primordium become tied to the inner portion of the blematogen layer, so that the latter becomes concrete with the surface of the pileus, no cleavage layer being formed to separate the blematogen and form the complete or finished "universal veil" (the teleoblem) as in the genus *Amanita*.

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12) FRIES, E., Syst. Myc. **1**, 280, 1821.

13) FAYOD, V., Prodrome d'une histoire naturelle des *Agaricinés*. Ann. Sci. Nat. Bot. VII, **9**, 181—411; pls. 6, 7, 1899.

3. The partial or marginal veil in the above species of *Agaricus* is not merely a sector of the "universal veil". It is largely a structure sui generis, the upper and inner portion being formed by the downward and inward growth of the margin of the pileus primordium; the lower portion being formed by increased growth of the hyphae on the surface of the pileus; there is but a slight external contingent which is derived from the thick walled hyphae of the blematogen layer at this point, which may be largely or completely sloughed off or only remain as scattered portions on the margin of the annulus.

4. In some species of *Agaricus*, for example in the early stages of *Agaricus campestris*, there is an additional "universal veil", the protoblem, which lies outside of the blematogen, and consists of a delicate floccose, loose layer, soon becoming torn into floccose patches, sometimes present after the complete expansion of the plant.

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Description of Plates.

The photomicrographs were made as follows: **Figures 1—6** with an extension camera and Zeiss lenses, × 15 diameters. **Figures 8—11** were made with a Zeiss microscope, the object being 370 mm from the sensitive plate. **Figs. 7, 10** and **16** with ocular ⅄ 4 and objective ⅄ 16 mm. **Fig. 8** with ocular ⅄ 8 and objective ⅄ 3 mm; **fig. 9** with ocular ⅄ 12 and objective ⅄ 16 mm.

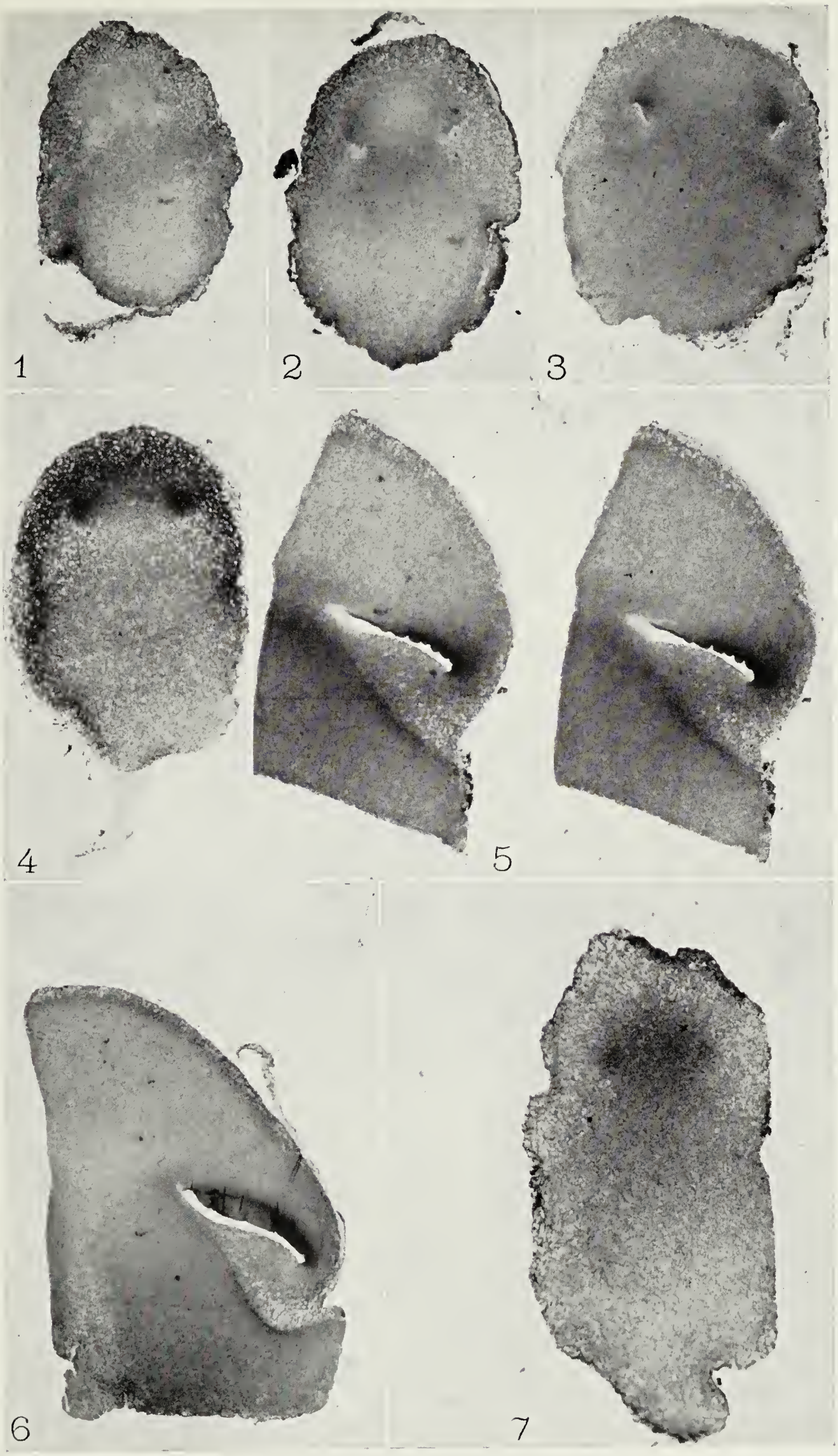
Fig. 1. Longitudinal section of very young basidiocarp of *Ag. arvensis* showing earliest origin of gill cavity as two symmetrically disposed light spots, separating pileus fundament above from the stem fundament below, indicating a constriction between them. External to the fundament of the pileus and stem is the fundament of the "universal veil", or the blematogen layer. It is easily recognized in this figure by the more open mesh of its tissue compared with the denser tissue of the pileus and stem fundaments, and stains darker because the thick walls of the hyphae take up the stain readily. The base of the young basidiocarp is lighter colored than the stem fundament indicating that growth is more active in the latter. The rhizomorph is attached to the base.

Fig. 2. Same in a little older stage, the gill cavity is evident, the hymenophore primordium is well organized as also the primordium of the pileus margin shown by the deeper stain over the gill cavity. Note the oblique position of the gill cavity rising outward and upward, also shown in fig. 3.

Fig. 3. Same in a still more advanced stage. The pileus margin is more definite and the inner limit of the blematogen layer is more distinct. The outline of the stem is more distinct showing its present form to be shorter than broad. In figs. 2 and 3 there is shown the exfoliation of a very thin layer from the basidiocarp. This may represent the primary universal veil, or protoblem, present sometimes on young basidiocarps of *Ag. campestris* in addition to the blematogen, or it may represent merely a dead outer layer of the blematogen which was in contact with the substratum; it is difficult to determine this point on basidiocarps developed in the substratum. A similar exfoliating layer is shown in figs. 6 and 10.

Fig. 4 is a section of a young basidiocarp of *Ag. arvensis* or a closely related species, collected in the edge of the forests south of Pontarlier in 1905. If it is not *Ag. arvensis* it is probably *Ag. flavescens* as young basidiocarps of this species were collected, but the number became detached. It differs from fig. 1 chiefly in the very deep stain of the hymenophore primordium, and shows also a dome-shaped primordium of the pileus connecting with the primordium of the hymenophore and pileus margin. though not so deeply stained. The blematogen layer is very deeply stained due to the absorption of the stain by the thickened hypha walls. The section was not decolorised to the extent of that of fig. 1, but if it were the primordium of the hymenophore would stand out strongly as compared to that in fig. 1. The reactions here are more like those in specimens of *Ag. campestris* studied.

Fig. 5. Sections of an older stage of *Ag. arvensis* than shown in fig. 3. The position of the gill cavity is now reversed, sloping downward. The fundaments of the



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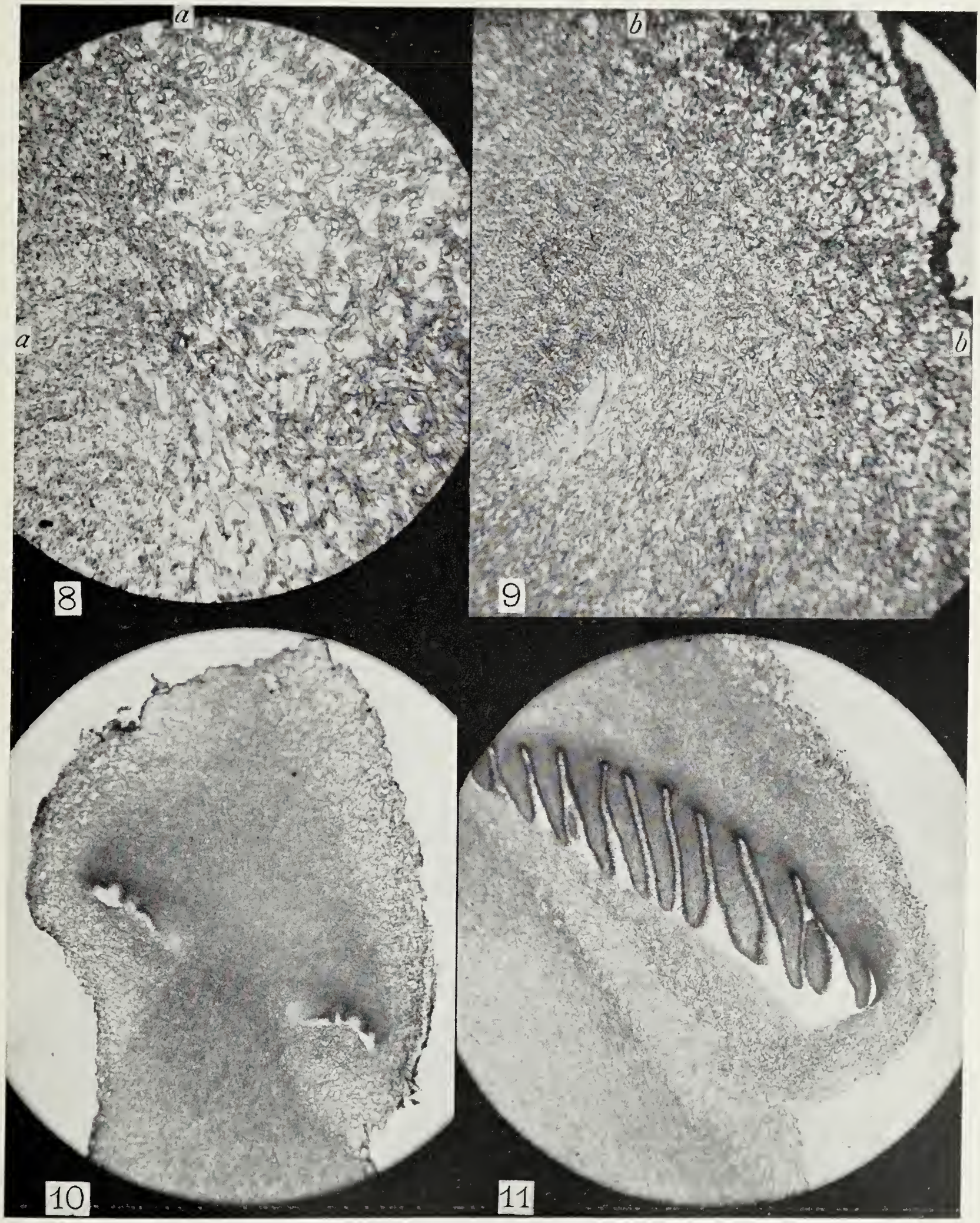

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lamellae are beginning to show as low folds. The outline of the surface of the stem is very distinct as a downward and outward sloping dark area below the partial veil. The surface of the primordial pileus is nearly organized, its elements interlacing with the inner layer of the "universal veil", or blematogen which still shows the coarser mesh. The partial or marginal veil shows a section of the blematogen or "universal veil", as its outer surface, but the bulk of it is formed by the growth of threads from the margin of the primordial pileus and increase of its own elements. The duplex character is beginning to show, the lower portion showing a more open mesh, increase having come chiefly from growth of fundamental tissue between the blematogen and stem surface.

Fig. 6. Section of a somewhat older basidiocarp of *Ag. arvensis*, the gill cavity slopes downward still more due to continued epinasty of the pileus margin and the elongation of the stem; the duplex character of the veil is more distinct; the bulb of the basidiocarp has broadened greatly but has not elongated appreciably so that the stem surface here is horizontal while the main part of the stem is elongating which brings the surface nearer a perpendicular position. The open mesh character of the medulla is beginning to show due to a lagging behind in growth. The primordial surface of the pileus has become concrete with the inner zone of the blematogen, or "universal veil", so that its outer zone really becomes the surface of the mature pileus.

Fig. 7. Section of a young basidiocarp of *Ag. comtulus* showing in the upper portion the roundish primordial area of the pileus, on either side the more densely staining primordium of the hymenophore and pileus margin; below the nascent primordium of the stem. Enveloping stem and pileus fundaments is the coarse meshed blematogen, or "universal veil".

Fig. 8. *Ag. arvensis*, highly magnified portion of fig. 1 showing details of structure and differentiation in the region of the early primordium of the hymenophore and pileus margin. This is located at the intersection of lines perpendicular to *a*, *a*. At the right note the coarse meshed tissue of the blematogen with its thick walled hyphae, in strong contrast with the dense area at the left with thin walled hyphae. At the angle of this tissue (intersection of lines from *a*, *a*) note curving downward of the elements of this primordium. The open meshed tissue beneath is the beginning of the gill cavity, and the threads of this tissue form the primordium of the inner portion of the partial veil, the hyphae are thin walled and distinct from those of the blematogen lying outside.

Fig. 9. *Ag. arvensis.* Highly magnified portion of a section from the same basidiocarp as fig. 2, showing young gill cavity, the hymenophore primordium just above; the primordium of the pileus margin above and slightly to the right, at intersection of perpendicular lines from *b*, *b*; on the right, the open meshed tissue of the blematogen, or "universal veil", below the margin of the pileus and the gill cavity is the now more abundant tissue of the partial veil of finer texture than that of the blematogen.

Fig. 10. *Ag. comtulus.* Section of well advanced basidiocarp, showing the hymenophore primordium with nascent lamellae; the distinct primordial margin of the pileus, the less differentiated area of the pileus primordium above; the loose meshed blematogen, or "universal veil", the well advanced partial veil of duplex structure below the gill cavity covered externally by a section of the blematogen; the conical primordium of the stem below.

Fig. 11. *Ag. comtulus.* Section of a nearly mature basidiocarp, slightly tangential, showing nearly mature lamellae; duplex partial veil; surface of stem; and pileus surface "concrete" with the "universal veil", or blematogen; a section of the latter forms one-third to one-half the thickness of the portion of the partial veil extending from margin of pileus to its junction with the lower portion.

Fig. 12. From photograph of young cluster of basidiocarps of *Ag. campestris*, showing on the older specimens the tearing apart of the delicate floccose protoblem on the surface of the blematogen.

Fig. 13. From photograph of a cluster of mature individuals of *Ag. campestris.* showing white patches of the protoblem on the surface of the pileus.