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Hunt Institute was dedicated in 1961 as the Rachel McMasters Miller Hunt Botanical Library, an international center for bibliographical research and service in the interests of botany and horticulture, as well as a center for the study of all aspects of the history of the plant sciences. By 1971 the Library's activities had so diversified that the name was changed to Hunt Institute for Botanical Documentation. Growth in collections and research projects led to the establishment of four programmatic departments: Archives, Art, Bibliography and the Library.

Notes on the Development of the Carpophore of
some Agaricaceae.

BY

RUDOLF BEER, B.Sc., F.L.S.

With Plate LII.

THE exact order and manner in which the different parts of the carpophore develop is still uncertain in a large number of Agaricaceae. In his earlier work De Bary (1) attributed an internal origin to the hymenium of *Agaricus (Psalliota) campestris* and some other Agarics which he had studied. In 1874, however, Robert Hartig (3) described the development of the carpophore of *Agaricus (Armillaria) melleus*, and he found that the pileus arises through a superficial annular furrow which in the beginning is completely open to the outside, and that later, through growth of the marginal hyphae of the pileus and of the stem, the annular furrow becomes covered over with a hyphal layer, the veil.

In his 'Comparative Morphology and Biology of the Fungi, &c.', published in 1884, De Bary (2) renounces his former opinion and accepts that of R. Hartig. He now believes that in *Agaricus campestris*, as in *A. melleus*, the primordium of the hymenium is first exposed in the open annular furrow which marks off the rudimentary pileus from the stem, and that only subsequently it becomes enclosed by hyphae, which grow towards one another from the edges of the furrow and form the marginal veil.

Fayod (4) studied a very large number of Agaricaceae, and he concluded that the primordium of the pileus was always the first to be differentiated within the rudiment of the carpophore. It arises as a definite layer, the 'couche piléogène,' which has the form of a shallow inverted bowl, convex above and concave below. This is surrounded externally by a thin layer which he calls the 'cuticule primordiale'. Fayod divides the Agaricaceae into angiocarpous, subangiocarpous, gymnocarpous, and endocarpous forms, and he attempts to trace his 'cuticule primordiale' in all of them. He very obviously, however, brings together several very different structures under the one name. For seventeen years after the publication of Fayod's work

no additions were made to our knowledge of the development of the fruit-bodies of these Fungi. In 1906, however, the long silence was broken, and Professor G. F. Atkinson (5) published an admirable account of the development of the carpophore of the mushroom.

He found that the young homogeneous fruit-body, in its earliest stage, shows no differentiation into parts (except the rudimentary universal veil), and is to be considered as the primordium of the carpophore. The first differentiation consists in the appearance of a ring of deeply staining hyphae near the upper end of the young fruit-body and some distance below the surface. This is the primordium of the hymenium, and it marks the differentiation of the primordium of the fruit-body into the primordium of the pileus and that of the stem and marginal veil, the latter being the tissue of the young fruit-body external to the hymenial primordium and continuous with what is to be the margin of the pileus above and with the undifferentiated stem surface below.

Soon after the hymenial primordium has been formed the tissue of the pileus primordium becomes definitely organized, and appears as a deeply staining area lying some depth below the surface.

The three salient facts which Professor Atkinson demonstrated in *Agaricus campestris* were:—

1. The hymenial primordium was the first structure to become differentiated in the homogeneous fruit-body.
2. This hymenial primordium arises endogenously and the marginal veil is not an aftergrowth.
3. The tissue of the pileus (the 'couche pileogène' of Fayod) arises in this plant after the appearance of the hymenial ring.

A few years later C. C. E. Fischer (6) published an account of his study of the development of the carpophore of *Armillaria mucida*. He finds that this does not at all agree with the description given by Robert Hartig in the case of *A. mellea*.

No open furrow is formed round the young fruit-body which subsequently becomes closed by the aftergrowth of a marginal veil. On the contrary, Fischer finds the development of this plant to resemble that of the mushroom, as given by Atkinson, in so far as, in both species, the hymenium originates endogenously and is separated from the exterior from the first by a layer of neutral tissue which constitutes the marginal veil.

If I read his account correctly, however, *Armillaria mucida* differs from *Agaricus campestris* in that in the former plant the pileus ('couche pileogène' of Fayod) precedes the appearance of the hymenial rudiment.

Fischer states that the hyphae near the apex of the young fruit-body show a tendency to radiate towards the periphery and form a subcuticular palisade layer of tissue. This palisade layer defines the rudiment of the

pileus. Later the palisade tissue spreads inwards to form the primordium of the hymenium.

Some time ago I collected material of a number of Agarics in order to determine their mode of development. A few of these have now been sectioned, and in the present note I have brought together the photographs of these sections and have added a few words of description.

The great difficulty in studying the development of the carpophore of these Fungi, when growing in the open, usually lies in obtaining sufficiently young stages. In the case of *Hypholoma fascicularis* (Huds.), however, no trouble is experienced in finding all stages of development from the youngest rudiment to the mature fruit-body.

In the earliest stage the primordium of the carpophore consists of a mass of narrow, closely packed, much interwoven hyphae, which for the most part take a clearly marked longitudinal course. Over the surface the hyphae are broader in diameter and more loosely arranged. This layer of superficial hyphae constitutes the universal veil. In Fig. 1, Pl. LII, three young fruit-bodies at this stage are seen developing side by side.

Fig. 2 represents a slightly older carpophore rudiment. It will be noticed that the body has elongated considerably and that it now shows the first signs of a differentiation of its parts. Near the apex a cup-shaped layer of hyphae has become conspicuous in consequence of the deeper stain which it takes. This layer constitutes the primordium of the pileus, the 'couche pileogène' of Fayod. The hyphae which compose it appear to be richer in protoplasm than their neighbours; they do not assume, in this fungus, a palisade arrangement such as Fischer described in *Armillaria mucida*, but on the contrary they tend rather to run transversely, so that their course is parallel with the surface of the 'cup' which they form.

The layer of deeply staining hyphae increases in thickness and then spreads inwards, so that the edges of the 'cup' become incurved towards the centre of the young carpophore. This incurved and somewhat thickened area of the deeply staining layer of hyphae forms the rudiment of the hymenium (Fig. 3). In the next figure (Fig. 4) a slightly older stage is represented.

In the section of the fruit-body here represented there are to be seen the first signs of the loosening of the tissue just below the primordium of the hymenium. The hyphae in this locality cease to keep pace with the growth of the rest of the carpophore. In consequence there is first a loosening of the tissue below the hymenial rudiment, and a little later an actual cavity is formed there. This cavity is the gill cavity. An early stage in its formation is shown in Fig. 5. In this photograph we can distinguish the different parts of the carpophore: the universal veil, the pileus, the stipe, the hymenium, the gill cavity, and the marginal veil. In slightly older fruit-bodies we find that the whole structure, and more particularly the pileus, is broadening

out laterally. This can be seen by comparing Fig. 6 with Fig. 5, Pl. LII. At this period of the development the hymenial layer is composed of a large number of narrow hyphae, densely filled with deeply staining protoplasm, and arranged very regularly and closely together side by side over the whole hymenial surface. The marginal veil can now be very clearly distinguished, and it will be seen that it is composed of the neutral tissue lying just outside the gill cavity and within the universal veil. About this time or slightly later the stipe shows a differentiation into medullary and cortical regions. The former is composed of loosely arranged hyphae which stain very lightly, whilst in the cortical area the hyphae are more closely arranged and stain more deeply. The gill cavity continues to enlarge as the carpophore grows and the hymenial surface increases in area (Fig. 7). The gills are next developed as a series of down-growths from the hymenial surface (Fig. 8).

The further history of the fruit-body is largely that of the expansion of its parts. The increased growth of the lower surface of the pileus and of the gills at length leads to the rupture of the marginal veil, which is left in the older carpophore as a fringe to the edge of the pileus and a darkened area upon the stipe. The stipe has in the meanwhile become hollow.

Another Agaric which I have examined is *Clitocybe laccatus* (Scop.).

Here also the first differentiation of the carpophore primordium consists in the demarcation of the pileus (Fig. 9). Just below the surface in the upper part of the elongated carpophore primordium a cup-shaped aggregate of closely interwoven hyphae appears and marks the rudiment of the pileus. Soon the rim or edge of the 'cup' grows inwards, and this internal extension of the closely arranged hyphae forms the rudiment of the hymenial layer. It will be noticed in Fig. 10, which represents this stage, that both pileus and hymenium have originated below the surface of the fruit-body, and that this is completely surrounded by a rather poorly developed, but still quite distinct, universal veil. The pileus now grows laterally, and in doing so soon ruptures the feebly developed universal veil (Fig. 11). The rest of the development of the hymenium takes place whilst this is exposed to the air and uncovered by any universal or marginal veil (Fig. 12).

I have also cut a series of sections of the young fruit-bodies of *Armillaria mellea* (Vahl). These preparations do not bear out the account given of the development of this carpophore by R. Hartig; they are, on the contrary, in general agreement with the description given by Atkinson of the mushroom and that given by Fischer of *Armillaria mucida*.

The first differentiation of the previously homogeneous fruit-body consists in the appearance (in longitudinal sections) of two darkly stained patches lying a little way below the surface and near the upper end of the carpophore (Fig. 13). These darkly coloured patches in the longitudinal

sections naturally correspond to a ring-shaped area in the entire carpophore, and they represent the primordium of the hymenium. Very soon afterwards the differentiation of a cup-shaped layer of deeply staining hyphae takes place, which extends upwards from the primordium of the hymenium over the summit of the carpophore, but always some distance below its surface (Fig. 14). This cup-shaped layer forms the primordium of the pileus. A little later a gill cavity is formed just below the hymenial primordium by the cessation in growth of the hyphae at that spot (Fig. 15). The gill cavity increases in size and the differentiation of the various parts of the fruit-body becomes more distinct (Fig. 16). The marginal veil, formed of neutral tissue present from the first, covers in the gill cavity. The universal veil, which is well developed over the summit of the young pileus, can only with difficulty be traced in the neighbourhood of the marginal veil as a distinct structure from this. The whole development of the hymenium and the formation of the gills takes place within the cavity which is curtailed off from the exterior by the marginal veil (Fig. 17).

Not until a late stage does the growth of the pileus rupture the marginal veil along its margin and leave this structure as the 'annulus' upon the stipe. The chief facts which result from my observations upon *Armillaria mellea* are that the primordium of the hymenium is the first part of the carpophore to be differentiated in this plant, and that this differentiation takes place endogenously. Fischer found that a palisade layer, marking off the pileus, was the first area to differentiate in *Armillaria mucida*. It is not unlikely that there may be some variation in the exact spot in which the differentiation commences; in any case, my preparations of *A. mellea* show that the differentiation of the pileus follows rapidly upon that of the hymenium, and it is quite possible that under certain circumstances the differentiation of pileus and hymenium may be practically simultaneous, or that the 'couche piléogène' may even be distinguished before the hymenium.

On the other hand, however, the order of differentiation may be constantly distinct in the fruit-bodies of *Armillaria mellea* and *A. mucida*. Further observations can alone decide this. However this may be, the particular set of plants which I have examined correspond in this respect more closely with Atkinson's observations upon *Agaricus campestris*, in which he found the primordium of the hymenium to be the first part to differentiate in the young carpophore. I am in complete agreement with both Atkinson and Fischer with regard to the endogenous origin of the hymenial primordium, and in finding the marginal veil to be present from the first and not formed as an aftergrowth as Hartig believed.

In conclusion, I should like to express my thanks to the staff of the department of Cryptogamic Botany at the British Museum (Natural History) for their kind assistance in identifying the Fungi described above.

SUMMARY.

A. *Hypholoma fascicularis* (Huds.).

1. The very young carpophore consists of a mass of densely interwoven hyphae enveloped in a layer of looser hyphae.

2. The first differentiation of parts in this carpophore consists in the appearance of a cup-shaped layer of deeply staining hyphae a little way below the surface at the upper end of the young fruit-body. This marks the primordium of the pileus, which is thus the first part to differentiate in *Hypholoma*.

3. The inward extension of the edge of this cup defines the hymenial layer.

4. Below this primordium of the hymenium an air-space—the gill cavity—is formed. A marginal veil can now be clearly distinguished. It is derived from the neutral tissue just outside and below the hymenial layer; it is present from the first and is not an aftergrowth.

5. The stipe differentiates into a cortical and a medullary region. It later becomes hollow.

B. *Clitocybe laccatus* (Scop.).

6. In this plant also the first differentiation of the carpophore consists in the demarcation of the pileus. It appears as a cup-shaped layer of hyphae lying a little way below the surface at the upper end of the elongated carpophore primordium.

7. The rim or edge of the 'cup' grows inward to form the rudiment of the hymenial layer.

8. A poorly-developed universal veil surrounds the whole carpophore at first. At an early stage, however, the lateral growth of the pileus ruptures this universal veil, and the whole of the rest of the development of the hymenium takes place whilst this is exposed to the air and unprotected by either a marginal or universal veil.

C. *Armillaria mellea* (Vahl).

9. The primordium of the hymenium is the first part to become differentiated in the plants which I have examined. It has an endogenous origin.

10. The pileus becomes differentiated soon after the hymenium has been marked off.

11. The hymenium is never exposed in an open furrow. On the contrary, the marginal veil is present from the first, and is never an aftergrowth as Hartig supposed.

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6. FISCHER, C. C. E.: On the Development of the Fructification of *Armillaria mucida* (Schrad.). Ann. Bot., vol. xxiii, July 1909.

EXPLANATION OF FIGURES IN PLATE LII.

Illustrating Mr. Beer's paper on the Carpophore of some Agaricaceae.

All the figures are from untouched photographs taken by the author.

Figs. 1-8 represent *Hypholoma fascicularis* (Huds.).

- Fig. 1. Three very young carpophores with tissues still undifferentiated. × 41.
 Fig. 2. Differentiation of rudiment of pileus. × 41.
 Fig. 3. Further differentiation of pileus and commencement of differentiation of hymenial rudiment. × 46.
 Fig. 4. Loosening of hyphae below the hymenial rudiment to form gill cavity. × 44.
 Fig. 5. Early stage in development of gill cavity. × 45.
 Fig. 6. Broadening of pileus and further development of gill cavity. × 45.
 Fig. 7. Gill cavity further enlarged. Universal and marginal veils shown clearly. × 42.
 Fig. 8. Later stage of development. Formation of gills. × 44.

Figs. 9-12 represent *Clitocybe laccatus* (Scop.).

- Fig. 9. Differentiation of pileus. × 45.
 Fig. 10. Differentiation of hymenial rudiment. × 45.
 Fig. 11. Hymenial layer exposed by lateral expansion of the pileus. × 43.
 Fig. 12. Older stage. × 43.

Figs. 13-17 represent *Armillaria mellea* (Vahl).

- Fig. 13. Differentiation of hymenial rudiment. × 41.
 Fig. 14. Differentiation of pileus. × 41.
 Fig. 15. First indication of formation of gill cavity. × 41.
 Fig. 16. Older stage. × 41.
 Fig. 17. Development of gills. × 43.



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BEER—AGARICACEAE.

Booth, coll.

Notes on the development of the Carpophore of
Some Agaricaceae

By Rudolf Beer D.S. F.L.S.
The exact order & manner in which the different parts of the carpophore develops is still uncertain in a large number of Agaricaceae. In his earlier work De Bary⁽¹⁾ attributed an internal origin to the hyphenium of Agaricus (Psalliota) campestris & some other Agarics which he had studied. In 1874, however, Robert Hartig⁽³⁾ described the development of the carpophore of Agaricus (Armillaria) melleus & he found that the pileus arises through ~~the~~ a superficial annular furrow which in the beginning is completely open to the outside, & that later through growth of the marginal hyphae of the pileus & of the stem the annular furrow becomes covered over with a hyphal layer, the veil*.

In his ~~Comparative Morphology~~ "Comparative Morphology & Biology of the Fungi etc"

published in 1884 De Bary⁽²⁾ renounces
his former opinion & accepts that of
R. Hartig. He now believes that in
Agaricus campestris, as in A. melleus,
the primordium of the hymenium is first
exposed in the open annular furrow
which delimitates the rudimentary pileus
from the stem & that ~~is~~ only subsequently
it becomes enclosed by hyphae which grow
towards one another from the edges of the
furrows & form the marginal veil.

Fayod⁽⁴⁾ studied a very large number of
~~from~~ Agariceae & he concluded that
the primordium of the pileus^{was} always the
first to be differentiated within the rudiment
of the carpophore. It arises as ^{the} a definite layer
"couche pileogène", which ^{has} the form of
a shallow inverted bowl, convex above
& concave below. This ^{is} surrounded
externally by a thin layer which he calls

the "cuticle primordiale".

Fagol divides the Agaricaceae into ~~the~~
~~three great division~~ groups angiocarpous,
Subangiocarpous, gymnocarpous +
Endocarpous forms + he ~~seeks~~ ^{attempts} to
trace his "cuticle primordiale" in all of
them. He very obviously, however, brings
~~many structures~~ ^{together} several very different
structures ~~together~~ under the one name.

For seventeen years after the publication of
Fagol's work no additions were made
to our knowledge of the development of the
fruit-bodies of these Fungi. In 1906,
however, the long silence was broken +
Prof G. F. Atkinson (5) published an admirable
account of the development of the carpophore
of the mushroom.

He found that the young homogeneous
fruit body, in its earliest stage, shows
no differentiation into parts (except the
rudimentary universal ~~veil~~ veil) + is to be
considered as the primordium of the carpophore.

The first differentiation consists of in the appearance of a ring of deeply staining hyphae near the upper end of the young fruit body & some distance below the surface. This is the primordium of the hymenium & it marks the differentiation of the primordium of the fruit body into the primordium of the pileus & that of the stem & ~~the~~ marginal veil, the latter being the tissue of the young fruit body external to the hymenial primordium & continuous with what is to be the margin of the pileus above & with the undifferentiated stem surface below. ~~Soon, by unequal growth, a gill cavity is formed below the hymenial primordium~~

Soon after the hymenial primordium has been formed the tissue of the pileus primordium becomes definitely organised & appears as a deeply staining area lying some

depth below the surface.
The ~~three~~ ^{three} ^{salient} ^{facts} ~~most important~~ facts which
Prof. Atkinson demonstrated ~~in Agaricus~~ in Agaricus

campestris were: (1) The hymenial primordium
was the first structure to become differentiated
in the homogeneous fruit body.

(2) This hymenial primordium arises
endogenously + ~~the~~ the marginal
veil is not an aftergrowth

(3) The tissue of the pileus (the "concha
pileosine" of Fayod) arises in this
plant after the appearance of the
hymenial ring.

A few years later C. C. Z. Fischer (6)
published an account of his study of
the development of the carpophore of
Armillaria mucida. He finds that
this does not at all ~~fully~~ agree with
the description given by Robert Hartig.
The No open furrow is formed round
the young fruit body which subsequently
becomes closed by the aftergrowth of a

Marginal Veil. ^{On the contrary} Fischer finds the ^(development of the) plant ^(resemble that) to ~~agree with~~
~~the development of the mushroom~~ as
given by Atkinson, in ^{in both species} so far as the
hymenium originates endogenously &
is separated from the exterior from the
first by a layer of neutral tissue
which constitutes the marginal veil.

If I read his account correctly, however,
Armillaria mucedo differs from Agaricus
campestris in the fact that in the
former plant the pileus ("couche
pileogène" of Fayod) precedes the
appearance of the hymenial rudiment.
The Fischer states that the hyphae near the
apex of young fruit body show a tendency
to radiate towards the periphery & form a
subcuticular palisade layer of tissue.
This palisade layer defines the rudiment of
the pileus. Later the palisade tissue

spreads inwards to form the primordium
of the hymenium.

Some time ago I collected material of
a number of Agarics in order to
determine their mode of development.

A few of these have now been sectioned
& ~~I thought it might be worth~~
~~while~~ & in the present note I have
brought together the photographs of
these sections & have added a few
words of description.

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The great difficulty in studying the develop-
-ment of the carpophore of these fungi,
~~is usually~~ ^{when} growing in the open,
usually lies in obtaining sufficiently young
stages. In the case of Hypopholoma
fascicularis ^(Huds.), however, no trouble is
experienced in finding all stages of
development from the youngest rudiment
to the mature fruit-body. ~~This renders~~

In the earliest stage the primordium of the carpophore consists of a mass of narrow, closely packed, much interwoven hyphae which for the most part ~~run~~ take a clearly marked longitudinal course.

Over the surface the hyphae are broader ^{in diameter} & more loosely arranged. This ~~is~~ layer of superficial hyphae constitutes the universal veil. In Fig 1 ~~are~~ ^{three}

young fruit-bodies at this stage of ~~development~~ are seen ~~lying side by side~~ developing side by side.

Fig 2 represents a slightly older carpophore rudiment. It will be noticed that the body has elongated considerably & that it now shows the first signs of ~~the~~ ^a differentiation of its parts.

Near the ^a apex a cup shaped layer of hyphae has become conspicuous in consequence of the deeper stain which

it takes. This layer constitutes the primordium of the pileus, the ^{of Fagad.} couche pileogène. The hyphae which compose it appear to be richer in protoplasm than their ^{neighbours} ~~neighbours~~; they do not assume, ~~a palisade~~ in this fungus, a palisade arrangement such as Fischer described in Armillaria mucida but quite on the contrary they tend rather to run transversely so that ~~they~~ their course is parallel with the surface of the "cup" which they form.

The layer of deeply staining hyphae increases in thickness + then spreads inward so that the edges of the "cup" become ~~triple~~ incurved towards the centre of the young carpophore. This incurved & somewhat thickened area of the deeply staining layer of hyphae forms ~~so~~ the rudiment of the hymenium. (Fig 3) In the next figure (Fig 4)

a slightly older stage is represented.

~~At this~~ In the sections of this fruit body there are to be seen the first signs of the loosening of the tissue just below the primordium of the hymenium.

The hyphae in this locality cease to grow ~~so that at first the~~ at the same

~~rate~~ keeps pace with the growth of the rest of the carpophore. In consequence

there is first a loosening of the tissue

below the hymenial rudiment & a little later an actual cavity is formed there.

This cavity is the gill cavity. An early stage in its formation is shown in Fig 5. In this section photograph we can clearly distinguish the different parts of the carpophore: the universal veil, the pileus, the stipe, the hymenium, the ~~marginal veil~~ gill cavity & the marginal veil. In slightly older ~~fruit~~

fruit bodies we find that the ~~pilae~~
whole structure + more particularly the pileus
is broadening out laterally. This can
be seen by comparing Fig 6 with Fig 5.

At this period of the development the
hymenial layer is composed of a large
number of narrow hyphae, ~~and~~ densely
filled with deeply staining protoplasm, +
arranged very regularly + closely together side by
side over the whole hymenial surface.

The marginal veil can now be very clearly
distinguished ~~as the~~ ~~it~~

will be seen that it is composed of the
neutral tissue lying just ^{outside} ~~below~~ the
gill cavity + within the universal veil.

About this time or slightly later the
stipe shows a differentiation into a
medullary + ~~the~~ cortical regions. The
former is composed of ~~about empty~~
loosely arranged hyphae which stain
very lightly whilst in the cortical

area the hyphae are more closely arranged & stain more deeply.

The gill cavity continues to enlarge as the carpophore ~~expands~~ grows & the hymenial surface ~~extends~~ increases in area (Fig 7). The gills are next developed as a series of downgrowths from the hymenial surface (Fig 8).

The further history of the fruit body is largely that of the expansion of its parts.

The ~~growth~~ increased growth of the lower surface of the pileus & of the gills at length leads to the rupture of the marginal veil which is left in the older carpophore as a fringe to the edge of the pileus & a darkened area upon the stipe. The stipe has in the meanwhile become hollow. ~~Basidia~~ ^{which} Basidia, each bearing four basidiospores, have developed over the surface of the lamellae.

Another Agaric which I have examined is Clitocyba laevis (Scop.)

Here also the first differentiation of the carpophore - primordium consists in the delimitation of the pileus (Fig 9)

Just below the surface in the upper part of the elongated carpophore - primordium a cup-shaped aggregate of closely interwoven hyphae appears & marks the rudiment of the pileus.

Soon the rim or edge of the "cup" grows inwards & this ~~inward~~ internal extension of the closely arranged hyphae forms the rudiment of the hymenial layer. (Fig 10) It will be noticed in Fig 10, which represents this stage, that both pileus & hymenium have originated below the surface of the fruit-body & that this is completely ~~surrounded by~~ ^{surrounded by} ~~enveloped~~ in a rather poorly developed,

^ ^

but still quite distinct, universal veil.

The pileus now grows laterally & in doing so soon ruptures the feebly developed universal veil (Fig 11) The rest of the development of the hymenium takes place whilst this is exposed to the air & uncovered by any universal or marginal veil (Fig 12)

~~This represents the development of the gills.~~

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I have also cut a series of sections of the young fruit bodies of Armillaria mellea (Vahl)

~~Here, contrary to the account given of this plant by Hartig, the~~

These preparations do not bear out the description account given of the development of this ~~the~~ carpophore by R. Hartig; they are, on the contrary, in ^{general} agreement with the general description given by Atkinson of the mushroom + Fischer of Armillaria mucida

The first differentiation of the previously homogeneous fruit body consists in the appearance ^(in longitudinal sections) of two darkly stained patches lying a little way below the surface & near the upper end of the carpophore ^(Fig 13).

These darkly coloured patches ~~are~~ in the longitudinal sections naturally correspond to a ring-shaped area in the ~~entire~~ ^{entire} ~~surface~~ ^{surface} of the carpophore & ~~very soon~~ they represent the primordium of the hymenium.

Very soon afterwards the differentiation of a cup-shaped layer of deeply staining ^{take place} hyphae ^{which extends} ~~extends~~ ^{extends} upwards from the primordium of the hymenium over the summit of the carpophore but always some distance below ^{its} the surface ^(Fig 14). This cup-shaped layer forms the primordium of the pileus.

A little later a gill cavity is formed just below the hymenial primordium by the cessation ⁱⁿ of growth of

the hyphae at ~~these~~ that spot (Fig 15)
The gill cavity increases in size + the
differentiation of the ^{various} ~~different~~ parts of the
fruit body becomes more distinct (Fig 16).
The marginal veil, formed of neutral
tissue present from the first, ~~covers in~~
the gill cavity. The universal veil,
which is ~~very distinct~~ + well developed
over the summit of the young pileus,
can only with difficulty be ~~traced~~
~~in the neighbourhood~~ traced in the
neighbourhood of the marginal veil as a
distinct structure from this. ~~In the~~
~~hyphae of both marginal + universal~~
~~veils are very similar to one another in~~
~~this part + both are loosely arranged.~~
The whole ~~future~~ development of the
hymenium + the formation of the gills
takes place within the cavity which is
contained off from the exterior by the
marginal veil. (Fig 17).

Not until

^{does}
1 July ~~at~~ a late stage, the growth of
the pileus ruptures the marginal veil ~~at~~
along its margin & leaves this structure
as the "annulus" upon the stipe.

The chief facts which ~~appear~~ ^{result} ~~from~~
~~appear~~ from my observations upon
Armillaria mellea are ~~that~~ ^{that} the
primordium of the hymenium is the first
part of the carpophore to be differentiated

^{plants}
in this ~~that~~ the differentiation takes place
endogenously. Fischer found that

a palisade layer, delimiting the
pileus, was the first area to
differentiate in Armillaria mucida.

It is not unlikely that there may be some
variation in the exact spot in which
the differentiation commences, in any case

my preparations ^{of A. mellea} show that the ~~first~~
differentiation of the pileus follows ~~very~~ rapidly
upon that of the hymenium & it is quite

possible that under certain circumstances the differentiation of pileus & hymenium may be practically simultaneous or that the "couche pileogène" may even ~~be~~ be delimited before the hymenium.

On the other hand, however, the order of differentiation may be constantly distinct in the fruit bodies of Armillaria mellea & A. mucedo. Further observations can alone decide this.

However this may be the particular set of plants which I have examined correspond in this respect more closely with Atkinson's observations upon Agaricus campestris in which he found the primordium of the hymenium to be the first part to differentiate in the young carpophore. I am in complete agreement with both Atkinson & Fischer with regard to the endogenous origin of the hymenial primordium & in finding the marginal veil to be present from the first & not formed as an aftergrowth as Hartig believed.

Summary

A. Hypopholoma fascicularis (Huds.)

- (1) The very young carpophore consists of a mass of densely interwoven hyphae enveloped in a layer of looser hyphae.
- (2) The first differentiation of parts in the carpophore consists in the appearance of a cup-shaped layer of deeply staining hyphae a little way below the surface ^{at} the upper end of the young fruit body. This marks the primordium of the pileus which is thus the first part to differentiate in Hypopholoma.
- (3) The inward extension of the edge of this cup defines the hymenial layer.
- (4) Below this primordium of the hymenium an air-space - the gill cavity - is formed. A marginal veil

can now be clearly distinguished.
It is derived from the neutral tissue
just outside ~~below~~ ^{or below} the hymenial
layer; it is present from the
first & is not an aftergrowth.

- (5) The stipe differentiates into a
cortical & a medullary region.
It later becomes hollow.

B. Clitocybe laccatus (Scop.)

(6) In this plant also the first
differentiation of the carpophore
consists in the delimitation of
the pileus. It appears as ~~little~~
~~way below the surface~~ a cup-shaped
layer of hyphae lying a little way
below the surface at the upper end of
the elongated carpophore primordium.

- (7) The rim or edge of the cup grows
inward to form the rudiment of
the hymenial layer.

(8) A poorly developed universal veil surrounds the whole carpophore at first. At an early stage, however, the lateral growth of the pileus ruptures this universal veil + the whole of the rest of the development of the hymenium takes place whilst this is exposed to the air & unprotected by either a marginal or universal veil.

C. Armillaria mellea (Vahl.)

(9) The primordium of the hymenium is the first part to become differentiated in the plants which I have examined. It has an endogenous origin.

(10) The pileus becomes differentiated soon after the hymenium has been delimited.

(11) The hymenium is never exposed in an open furrow. On the contrary, the marginal veil is present from the first & is never an aftergrowth as Hartig supposed.

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Explanation of Figures in Plates A + B.

All the figures are from ^{untouched} photographs taken
by the author. ~~from the sections.~~

Plate A

~~Fig 1~~ All the figures on this plate are of
Hypholoma fascicularis (Huds.).

Fig 1 Three very young carpophores ~~still~~
~~undifferentiated~~ with tissues still ~~undifferentiated~~
undifferentiated. X 41

Fig 2 Differentiation of rudiment of pileus
X 41

Fig 3 Further differentiation of pileus +
commencement of differentiation
of hymenial rudiment X 46

Fig 4 Loosening of hyphae below the
hymenial rudiment to form gill cavity
X 44

Fig 5 Early stage in development of gill
cavity X 45

- Fig 6 . Broadening of pileus +
 further development of gill cavity.
 X 45
- Fig 7. Gill cavity further enlarged.
 Universal + marginal Veils
 Shown clearly X 42
- Fig 8 Later stage of development. Formation
 of gills. X 44.

Plate B.

Figs 9 - 12 represent Clitocybe laccatus (Scop)

~~Figs 13 - 17 represent Armillaria mellea (Vahl)~~

- Fig 9 Differentiation of ^{pileus} ~~hymenial rudiment~~
 X 45
- Fig 10 Differentiation of ^(hymenial rudiment) ~~pileus~~ X 45
- Fig 11 Hymenial layer exposed by ^{lateral} expansion
 of the pileus X 43
- Fig 12 Older stage X 43

Figs 13 - 17 represent Armillaria mellea (Vahl)

- 251
- Fig 13. Differentiation of hymenial rudiment
X 41
- Fig 14 Differentiation of pileus X 41
- Fig 15 First indication of formation of
gill cavity X 41
- Fig 16 Older stage X 41
- Fig 17 Development of gills X 43