PERSOONIA
Published by the Rijksherbarium, Leiden
Volume 9, Part 3, pp. 329–362 (1977)

THE HISTOGENESIS OF BULB AND TRAMA TISSUE OF THE HIGHER BASIDIOMYCETES AND ITS PHYLOGENETIC IMPLICATIONS

A. F. M. REIJNDERS
Amersfoort, Netherlands

(With two Text-figures, one Table, and Plates 32–37)

At the base of the stipe in Agaricales basal plectenchyma is found which may enlarge to form a bulb. This tissue is not homogeneous. It is characterized by peculiar configurations: free tips of branches, sinuous hyphae, loops, spirals and rings (sometimes enclosing another hypha) and hyphal knots. The hyphal knots present themselves as bundles of hyphae, which may or may not be the centre of cell division, or as agglomerations of cells surrounded by coiled hyphae. The latter structure, present in many species of Agaricales, is found in its perfect form in the trama of the Amanitaceae, which recalls the trama of the Russulaceae. The young pileus trama of many species shows the same characteristics; these also occur in the trunk of *Ramaria*, in young bulbs of Gasteromycetes, and in various veils. The diverse kinds of cell formation in the primordia of Agaricales are treated at some length, the conception meristemoid is defined, and a comparison with the development of some of the true Aphyllophorales is made. The heteromerous trama of the Asterosporales and the trama of the Amanitaceae, characterized by acrophysalides, are considered to be derived from the young trama of other Agaricales. The tissue of the bulbs of the strains 59b and 59c of *Agaricus bisporus* is analyzed. Strain 59b is homologous with the bulb tissue of a normal fruitbody of *Agaricus bisporus*. In agreement with G. Fritsche the conclusion is drawn that 59c is a gigas-form. Watling's carpophoroids of *Psilocybe merdaria* are considered.

The fundamental differences between the development of true Aphyllophorales and that of cantharelloid fungi, Agaricales, and Gasteromycetes are emphasized. As for the evolution within the Asterosporales, it is concluded that the degradation of certain characters in the gasteromycetoid forms (Heim, Malençon) need not contradict the arguments advanced by R. Singer and A. H. Smith.

CONTENTS

INTRODUCTION

This study was undertaken as the result of two previous studies; the first on ontogenetic investigation of the bulbs of the strains '59b' and '59c' of *Agaricus bisporus*, 'the cultivated mushroom', obtained by Fritsche & von Sengbusch (*1963*) as spontaneous mutations in single spore cultures; the second on an investigation into the origin of the atypical trama in *Lactarius* and *Russula* (Reijnders, *1976*).

The first investigation showed that bulbs of the strains 59b and 59c have a characteristic structure. It follows that the next step was to compare these with the tissue of normal bulbs of *Agaricus bisporus* (Lange) Imbach. The investigation was subsequently extended to bulbs of other Agaricaceae, both in the primordial and the more mature states. Some of these structures, in particular the hyphal knots, also occur in the remaining trama of the fruitbody so that it was necessary to observe these in a wide variety of species. The comparison was facilitated by the fact that it was possible to examine a large number of microtome sections from previous work (e.g. Reijnders, *1963*). At the same time it also seemed advisable to investigate fresh and living material, especially that of bulbs so that the study was extended to include all the Agaricales; it was not possible to exclude the bulbs of a few Gasteromycetes or the trunk of some Clavariaceae. It will become apparent that in all these examples structures are formed showing marked similarity. In the younger stages of the real Aphyllophorales (Corticiaceae, Stereaceae, Steccherinaceae, and Polyporoideae) these structures do not occur. The development from the point of initiation has not been adequately investigated in the Aphyllophorales but it appears to be entirely stereotypic (see below).

By basal plectenchyma a tissue is indicated that differentiates from the protenchyma as soon as the primordium has been formed. The term protenchyma is used for the generative tissue which makes up all the parts of the carpophore. In the Aphyllophorales (Corner, *1950*) generative hyphae are spoken of. Although this term is also applicable to the Agaricales and the Gasteromycetes, it seems proper to continue to use the terms protenchymatic and protenchyma because here in many cases the generative hyphae form complexes which serve to form certain structures that function as a unit. The basal plectenchyma soon differentiates from the primary protenchyma at the base of the primordium, becoming distinguishable by its special structure. Inflation of the cells takes place forthwith. The basal plectenchyma is probably universal in the Agaricales, though its extent can vary widely. The exten-

sion of the basal plectenchyma is limited in families like the Pleurotaceae, Hygrophoraceae, and Tricholomataceae (approximately in the circumscription of Kühner & Romagnesi, *1953*), that is in such species as show a dominant stipitocarpous type of development.

Previously we discussed the fact that the bulb at the base of the stipe in many species is homologous to the basal plectenchyma (Reijnders, *1974*). This is not quite true, however, because for example in such species as are pileocarpous or hymenocarpous from the beginning a certain amount of undifferentiated protenchyma remains in the bulb so that species with a strongly developed bulb have a large basal plectenchyma completely enveloping the remaining primary protenchyma. In later stages this remaining plectenchyma can for example be found in the volva (namely in those species which are termed bulbangiocarpous, e. g. *Volvariella*). Some remaining basal plectenchyma can also be found in the centre of the cap trama, that is when the stipe is initiated inside the bulb. In that case the upper stipe, characterized by parallel longitudinal hyphae, may have a zone of primary protenchyma which forms a part of the cap trama. Subsequently in many species the cap trama will increase in volume through the formation of cells in a proximal direction by the hyphal bundles of the cap margin. It is thus necessary that both the structure of the cap trama and that of the base of the stipe be studied. Before describing the results considerations should be given to the manner in which the cell formation of the primordium takes place.

In many cases basal plectenchyma is also found in what Corner (*1950*) assembled as clavarioid fungi. In many places in his extensive monograph he depicted the basal plectenchyma (see for example figs. 40, 43, 51, 170, 173, 222, etc.). It is interesting to verify to what degree the sclerotium, as in *Typhula*, can be considered homologous to the basal plectenchyma; this could not be ascertained from the description given by Berthier (*1973*: 45). For this a drawing by Corner (*1950*: fig. 51, *Typhula sclerotioides*) is of importance.

THE INITIATION OF CELLS IN THE PRIMORDIUM.—The initiation of the primordium normally consists of a ball of interwoven hyphae. The first differentiation usually gives rise to the basal plectenchyma and also to the velum (if present). When a bundle of parallel hyphae forms quickly at the upper part of the ball and lengthens the species is referred to as stipitocarpous. Corner (*1950*) gives many fine drawings of such bundles in his monograph (e. g. figs. 7, 34, 39, 40, 42, 43, 65, 74, 170, 173, 200).

When cell formation in the bundle is followed immediately by cell inflation, that is if the zone of inflation is situated at the proximal end of the bundle, Corner (*1929*: 282) terms this 'direct development'. When there is some alteration in the time factor in the 'growing point' he terms the development 'indirect'. It is not quite true that there is merely an alteration in the time factor because, as will be shown below, inflation also occurs in tissues not formed by such a 'growing point'. In our opinion it is not correct to state in this connection that the direct method always

takes place in 'clavarioid' fungi, the tissue in the trunk of *Ramaria* comparing more closely to a basal plectenchyma.

In the Agaricales the cells are formed by the cooperation of the protenchyma, which remains plectenchymatic, and the bundles. For this reason we do not agree with Corner that the development of the Agaricales and the Gasteromycetes should be regarded as the sum of alterations in individual hyphae. We referred to this earlier (Reijnders, *1963*: 277). In this the development of the Gasteromycetes and Agaricales differs from true Aphyllophorales.

An apical sheaf like that above is found in the Agaricales: *Cantharellula umbonata*, *Clitocybe clavipes*, etc. When the balls of primordial hyphae have become serried a longitudinal orientation arising in the centre or a little way beneath the apex is often visible. In that case a remnant of the original plectenchyma remains in the upper part of the primordium, where typical plectenchymal structures (hyphal knots) can be recognized; these will form the centre of the cap trama. In more concentrated forms (Reijnders, *1963*: 221 onwards) hyphae may also be longitudinal from the beginning but at the upper end of the hyphae, that is just beneath the veil, a zone of cell division may be found which deposits cells mostly downwards (*Coprinus*). In principle we speak of a pileo-stipitocarpous development in both cases but we fear that, especially in the first case of a remnant of an original protenchyma, we have often called such a primordium stipitocarpous (especially because of the long shaft). It is difficult to draw distinctions but there are many clear cases in which a large part of the cap trama is made up of originally plectenchymatic protenchyma (e. g. *Marasmius ramealis*).

There are two ways in which cells are initiated in the primordium: ramification of the hyphae and cell division. Ramification takes place in bundles of parallel hyphae as well as in plectenchyma. The bundled hyphae in the cap margin form hyphae inwards that join the hymenophore, and hyphae outwards that strengthen the cap trama or the veil. The first palisade hyphae of the hymenophore often originate in the plectenchyma of the cap trama and grow downwards (Reijnders, *1948*: pl. 7 fig. 28, *Leucocoprinus*). Many hyphae also originate by ramification at the surface of the primordium to strengthen the veil (Reijnders, l.c.: pl. 22 figs. 130–133, *Strobilomyces*).

In addition to this striking phenomenon of cell increase by ramification and individual septation of hyphae so formed there exist many places with coordinated cell division, as though these were meristems. The term meristemoids is proposed for these tissues.[1] Both the apical hyphal bundles in clavarioid fungi and the bundles in the cap margin of the Agaricales are therefore meristemoids in which the cell division (and growth) is coordinated. A zone in the upper part of the stipe in which rapid cell division takes place falls equally into this category (Pls. 36A, B, *Coprinus*

[1] Some authors refer to pseudo-tissues in fungi because these originate from hyphae. Pseudomeristems or parameristems could also be used but meristemoid has not been applied to fungi in the past and indicates clearly what is meant.

macrorhizus (Pers. ex Fr.) Rea). At the same time, however, in other parts of the primordium are to be found layers of cells which are so close to one another and where cell increase is so rapid, that it is also possible to speak of meristemoids. Such a zone often occurs at the periphery of the cap trama; this layer then forms the veil, or a marked part thereof, and concurrently or subsequently the pileipellis (Pl. 35C, *Psathyrella candolleana* (Fr.) Maire; Pl. 35D, *Coprinus macrocephalus* Berk.; Pl. 35B, *Cortinarius limonius* (Fr. ex Fr.) Fr.). In the lower part of the cap trama or just above the hymenophore or belonging to this area there is normally a layer of radial, parallel hyphae growing partly downwards and then strongly ramifying. Just above this layer a dense tissue with marked cell formation is present. In the trama of the lamellae ramification in divergent hyphae (in most cases the structure of the young lamellae is divergent) is dominant, but the subhymenium can again be a layer with a cellular structure in which divisions take place to form those elements of the hymenium which push themselves between the previously formed palisade tissue (intercalary growth). In that case because of the richly coordinated cell divisions occuring in that layer it would also be correct to speak of a meristemoid.

The basal plectenchyma and the bulb tissue are not homogeneous; this also applies to other plectenchymatic tissue in primordia and tissue in mature fruitbodies. In microtome sections of those parts where the tissue is compact there are not infrequently visible sectioned groups of round elements (that at first might be regarded as cells but that could also be hyphae), surrounded by curved, coiled or spiral hyphae. In between these a framework of less numerous hyphae which pass straight through are sometimes discernible. In looser parts (compact tissue also becomes looser in later stages) we often find places where the hyphae adhere to one another in entangled bundles; other places show many short side branches or else the hyphae are divided into many short cells (or hyphal knots); also interposed places where the tissue is looser and the hyphae are more separate are present. Particular attention will be paid to these hyphal knots in the description of the histological structure of the above mentioned material. In addition many free hyphal ends and typical structures like loops and rings are also encountered.

To conclude this introduction another phenomenon should be mentioned. In previous work (Reijnders, *1963*: 269, 276) we noted the structural consistency of the primordia and the proportional growth of all the parts in relation to one another and referred to cell inflation. This does not initiate everywhere at the same time but in very young primordia proceeds in such a manner that the globular shape may be preserved and all the parts remain in their same positions. Later the so-called period of rapid elongation takes place.

The formation of new cells has the same consistency as the cell inflation. Just enough cells are formed by hyphal branching and by cell division in meristemoid tissue to give rise to a well proportioned fruitbody.

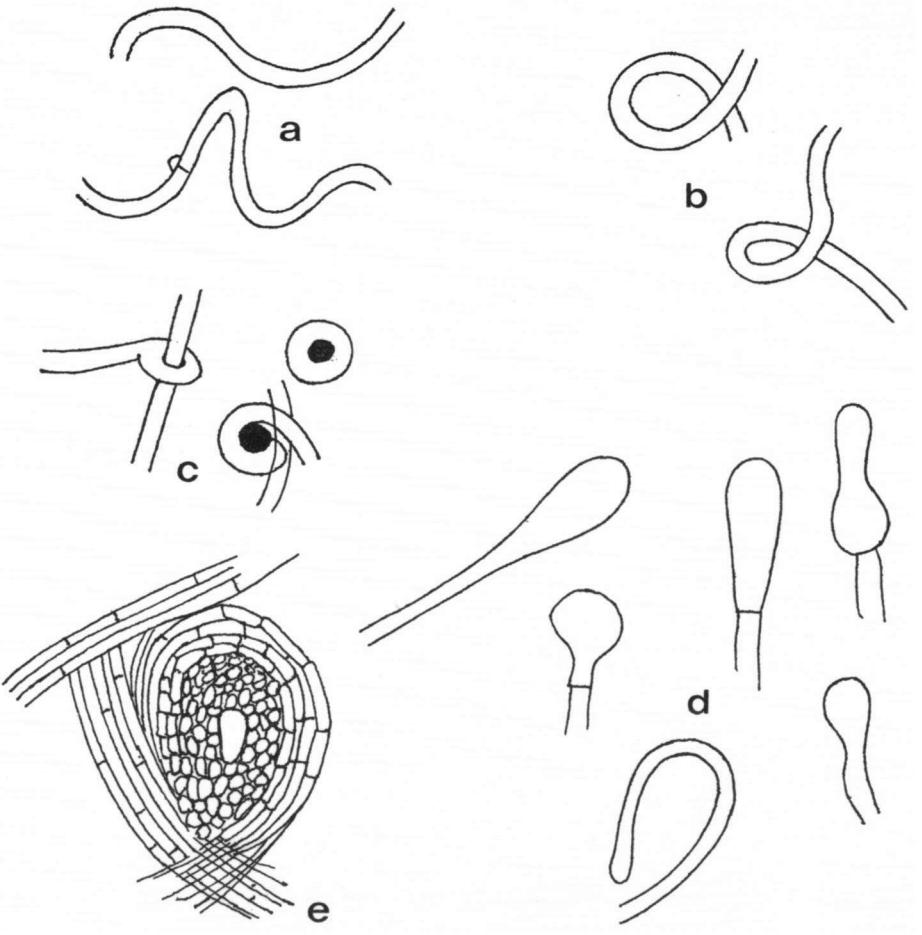


Fig. 1. Hyphal configurations in plectenchymatic tissues in Agaricales. — a. Sinuous hyphae. — b. Loops. — c. Spiral hypha enclosing an other hypha, and rings. — d. Free ends of branches, with or without inflated terminal cells. — e. Coiled hyphae, surrounding a group of isodiametric cells, with the inflated tip in the centre.

OBSERVATIONS

THE ELEMENTS.—Authors disagree about the use of the term plectenchyma. Some apply this term to all tissues or pseudo-tissues which are formed by hyphae. The one speaks of prosoplectenchyma when the tissue clearly consists of interwoven hyphae, and of paraplectenchyma or pseudo-parenchyma when the tissue appears to consist of cells. Other authors restrict the term plectenchyma to the first case, where the tissue clearly consists of interwoven hyphae, and use pseudoparenchyma

for the second type, in which the tissue appears to consist of cells; it is to this interpretation that we will confirm. (Yet others reserve the term plectenchyma for a more specialized structure, viz. when the elements adhere to one another through an intercalary substance and are difficult to separate; but this application of the term is very rare.)

We ourselves apply the term plectenchyma to any fungal tissue in which the characteristics of hyphae are recognizable. Such plectenchyma is seldom homogeneous in either mature fruitbodies or in primordia. In places the tissue is denser and looser. We termed the places where the hyphae adhere in bundles hyphal knots. Occasionally only hyphal bundles can be seen in such places but in many cases the hyphae appear to be divided into short cells. This phenomenon will be dealt with below (see chapter on hyphal knots and meristemoids). At first it must be considered whether it is in fact a question of a deceptive structure. All our observations had to be made with only two dimensional sections so that what appears to be a cell may in fact be a hyphal cross section. As a result in dense tissue many 'cells' may appear to be adjacent to one another. These circles are usually empty, making them more easily recognizable. Where the hyphae cross the section obliquely the hyphal walls may be visible as short ellipses. There is another optical illusion when hyphal bundles cross one another in the section and once more apparent 'cells' are seen. The section is often thick enough (10 μm on the average) to make this possible. We have often wondered to what extent such optical illusions are responsible for the conclusion that they are short cells. There are places in the hyphal knots, however, where so many adjacent cells are visible that optical illusion could not be the explanation. The hyphae following the direction of the section for some distance (i. e. are recognizable as hyphae) should be closely examined to find out whether they have many septa. Rows of cells are indeed often to be seen in these hyphae. Furthermore counting these longer length of hyphae around the knots makes it possible to calculate the number of sections one can expect to see. Also often perceptible are bunches of grape-like figures: one or more longer hyphae surrounded by rows of cells, or hyphae of a bundle locally divided into cells but it should not be assumed that another bundle passes through the first one. Comparison of the tissue of the primordia of *Russula* and *Lactarius* with that of other Agaricales may reveal the same structure of hyphal knots: coiled hyphae around large groups of cells. In the above genera, however, we are definitely dealing with cells; they are seen again as spherocysts in the mature tissue. Extensive comparison of both mature material and microtome sections of primordia led to the conclusion that cell division is often more marked in the hyphal knots than in the looser parts of the tissue in which the cells of the hyphae are longer. The significance of this phenomenon will be referred to below.

Some structures always present in the plectenchyma, especially when this is denser, are the very sinuous or undulating hyphae (Pls. 32G, 36 F, and Fig. 1a) and also the loops (Pl. 32G, and Fig. 1b). Where a loop encircles another hypha if the loop is viewed laterally (Pls. 33A, B, 34B, 36C, G, and Fig. 1c), in section an apparent ring or spiral may be seen. This configuration is frequently seen in dense tissues,

Table I

			hyphal knots		meristemoid	free tips	inflated intercalary elements	sinuous hyphae	loops spirals rings	system of straight hyphae	photo's
			merely an agglomeration of hyphae	with cell formation	coiled hyphae mostly around cells						
Cantharellus cibarius	m			p.tr. ±	p.tr. ±	p.tr.++					
Cantharellus tubaeformis	m		st.,p.tr.								
Paxillus involutus	m			b.pl.,p.tr.							
Chroogomphus rutilus	m			b.pl.,p.tr.							Pl. 33F
Gomphidius roseus	m,v			veil, ?							
Suillus aeruginascens	m,+v			p.tr., veil		p.tr.++,inf.			+		Pl. 33C
Suillus luteus	m,v			veil							
Xerocomus subtomentosus	m			b.pl.,p.tr.		p.tr.,bulb,inf.		+	+		Pl. 36C
Boletus edulis	f		?		bulb	+		+	+		Pl. 36E
Boletus satanas	f			bulb,sh.b.	±	+		+	+	+	Pl. 33D, E
Gyroporus cyanescens	m			b.pl.,p.tr.	veil			veil	veil		Pl. 35A
Pleurotus dryinus	m,v			veil	tr. ±			+	+		
Panellus serotinus	m			tr. ±	b.pl.						Pl. 34A
Hygrophorus hypothejus	m,+v			b.pl.	b.pl.,p.tr.±						
Hygrophorus chrysaspis	m			b.pl.,p.tr.	b.pl.,p.tr.						
Hygrophorus dichrous	m,v		- (veil)	- (veil)	- (veil)						
Armillaria luteovirens	m,v										
Armillariella mellea	m,v						m.l. veil				
Cathathelasma imperiale	f		b.pl. ±					+	+		
Galera marginata	m,v		veil ±								
Galera paludosa	m,v		- (veil)								
Alnicola melinoides	m,v		veil ±								
Kühneromyces mutabilis	m,v			veil ±							

Inocybe geophylla	f	b.pl.	b.pl.,s.c.h.				b.pl.	+	++		
Inocybe asterospora	m		b.pl.,p.tr., veil	b.pl.,p.tr.		+ t.c.			++		
Cortinarius calochrous	m		bulb			bulb					
Cortinarius praestans	f	b.pl.						+	++		
Cortinarius traganus	f		b.pl.			+		+	+		
Cortinarius limonius	m,v		veil		m.l. veil not serried			veil			Pl. 35B
Cortinarius acutus	m,v	— (veil)									
Dermocybe uliginosa	m,v		veil		m.l. veil not serried						
Leucocortinarius bulbiger	m		bulb	±					+	bulb	
Agrocybe aegerita	m,v	veil									
Conocybe hebelomatoides	m			p.tr.,bulb		bulb, acroph.	p.tr.				
Naematoloma udum	m,v	veil ±									
Naematoloma ericaeum	m,v	— (veil)									
Naematoloma radicosum	m,v	veil									
Psathyrella candolleana	m,v				m.l. veil						Pl. 35C
Psathyrella hydrophila	m,v				m.l. veil	+					
Psathyrella nolitangere	m,v				m.l. veil						
Psathyrella velutina	m,v				m.l. veil ±						
Coprinus fimetarius	m,v				m.l. veil						
Coprinus macrocephalus	m,v				m.l. veil						Pl. 35D
Coprinus macrorhizus	m,+v				m.l. veil						Pl. 36A,B
Coprinus radians	m,v				m.l. veil						
Coprinus auricomus	m,v		b.pl.		m.l. veil						
Cystoderma carcharias	m,v				m.l. veil not serried						
Phaeolepiota aurea	m,v				m.l.not well developed						
Lepiota aspera	f	bulb	±			++, inf.	+	+	++		
Lepiota mastoidea	f		bulb, sh.b.			++			+		

Table I (continued)

			hyphal knots			meristemoid	free tips	inflated intercalary elements	sinuous hyphae	loops spirals rings	system of straight hyphae	photo's
			merely an agglomeration of hyphae	with cell formation	coiled hyphae mostly around cells							
Macrolepiota rhacodes	f		bulb	±			++	+	+	+	+	
Macrolepiota procera	f		bulb	±			++, t.c.	+	+	+		
Leucocoprinus cepaestipes	m,v			± veil					veil			
Leucocoprinus denudatus	m,v		veil	±								
Leucoagaricus naucinus	m			bulb, veil		m.l. veil not serried	++					
Agaricus bisporus	f,m		+	bulb, ah.b.			++, inf.	+	+	++	+	Pl. 32G,H
Agaricus bisporus strain 59b	f,m		+	±	++, s.c.h.		++, inf.		+	++	+	Pl. 32A,B,C,E
Agaricus bisporus strain 59c	f,m		+	+	+, s.c.h.		++, inf.		+	+	+	Pl. 32D,F;33A,B
Agaricus osecanus	f			bulb			++, t.c.	+	±	+	+	Pl. 36H
Volvariella speciosa var. gloiocephala	f,m						acroph.	+				
Volvariella bombycina	m			bulb,p.tr., volva	+		+	+		+	+	Pl. 35E
Volvariella surrecta	m			bulb	bulb,volva						+	
Volvariella pusilla	m											
Pluteus atricapillus	f,m			b.pl.,p.tr.	+		+, t.c.		+	+		
Pluteus salicinus	f			bulb			+					
Limacella guttata	f,m			bulb	++, s.c.h.		bulb, p.tr., acroph.			+	+	Pl. 34B
Amanita solitaria	m			bulb,p.tr.	++, s.c.h.		bulb, p.tr., acroph.				+	Pl. 34C

Amanita rubescens	m		bulb, p.tr.	++, s.c.h.		bulb, p.tr., acroph.				+	Pl. 34D
Lycoperdon pyriforme	f	+	young bulb, ±			++		+	+		Pl. 36F,G
Chamonixia caespitosa	m		columella	++		++, inf.				+	Pl. 34E
Scleroderma aurantium	m		young bulb, veil								Pl. 34F;35F
Geastrum triplex	m		young bulb, veil								
Ramaria aurea	f	+	±			++	+	+	++		Pl. 36D
Ramaria formosa	f	+	+, sh.b.	±		++, inf.		+	++		
Ramaria mairei	f	+	±	±		++, inf.		+	++		

The following indications have been used:

acroph. = acrophysalides
b.pl. = present in basal plectenchyma
bulb = present in bulb
f. = freehand section of mature material
inf. = inflated
m. = microtome section
m.l. = matrix layer
p.tr. = pileus trama
s.c.h. = sometimes central hypha
sh.b. = short branches
st. = present in stem
t.c. = terminal cell
v. = the veil has mainly been examined
veil = present in veil
\+ = present in either basal plectenchyma, bulb or pileus trama or in both, not specified
++ = numerous
± = present, not numerous
— = definitely missing

Nomenclature according to Singer (1975).

in both primordia and maturer froms. An actual ring in the hypha can be formed by anastomosis of the loop (Pls. 32A, 33B, and Fig. 1c). Tips of hyphal branches are found nearly everywhere. These free tips of the penetrating hyphae are characteristic of the basal plectenchyma and the young cap trama, whereas they are seen much less or not at all in mature tissues. Where they are seen they are regarded as a peculiarity of the tissue (Amanitaceae). Occasionally the tip of the branch consists of a terminal cell; the tips are often club-shaped (Pls. 32D, E, H, 33D, 36E, H, and Fig. 1d). Besides inflated terminal cells there are also in many cases intercalary elements in the hyphae which have suddenly become much broader. A further complication in these tissues, which may occur in the most varied tissues (but by no means always), is formed by a system of straight hyphae forming a type of framework through the undulating hyphae; these straight hyphae may be somewhat wider.

We have summarized our results on 73 species in Table I; this was the only way to avoid very lengthy descriptions, with many repetitions. The nature of our comparisons in many species was such that sometimes little attention was paid to certain parts. An empty space, therefore, may mean that these structures were not studied but not necessarily that they were absent. In a number of species we studied only the veil.

HYPHAL KNOTS AND MERISTEMOIDS.—In simple form a hyphal knot is a bundle of hyphae which continue to adhere to one another during the expansion of the tissue, while the rest becomes looser.

The knots usually consist of many short cells, so that it can be assumed that cell division is more marked here than in the surrounding tissue. How did these agglomerations of hyphae initiate? Could they have been formed by interweaving of the growing hyphae? Frequently there appear twisted hyphae in the hyphal knots, e. g. in the veil (Pl. 35A, *Pleurotus dryinus* (Pers. ex Fr.) Kummer; Pl. 35F, *Scleroderma aurantium* L. ex Pers., exoperidium; *Gomphidius roseus* (Fr.) Karst.; *Suillus aeruginascens* (Secr.) Snell, etc.) or in the lipsanenchyma. In many cases the latter tissue is strengthened by hyphae growing out of the edge of the cap or the stipe (even out of the edge of the gills). In cases where the mature fruitbody has a luxuriant ring the lipsanenchyma shows marked growth, e.g. *Agaricus* sp., *Macrolepiota* sp., *Limacella*, etc. Cell formation must then take place in the lipsanenchyma; this may be concentrated in hyphal knots. Sometimes, however, it is evident that the cells continue to divide in the whole lipsanenchyma.

In most cases the hyphal knots are initiated by the loosening of an originally compact tissue. In a very young primordium the tissue can be very dense. In these interwoven hyphae, active cell formation commonly takes place. Such tissues are subsequently pushed apart, either because they are stretched or because some cells inflate. Cell division continues in the hyphal knots and these alternate with places where hyphae have much longer cells (Pl. 33F, basal plectenchyma of *Chroogomphus rutilus* (Schaeff. ex Fr.) Lundell). The hyphal knots may also occur in places where cell formation is even more serried so that it is not incorrect to speak of a meriste-

moid. For example the matrix layers, found in the cap are forced apart by the lengthening hyphae. In this manner the hyphal knots present in the veil are formed (Pl. 35B, *Cortinarius*, veil on the cap). In a very young primordium of *Agaricus bisporus*, for example, a closed tissue completely made up of cells is present; later hyphal knots can be distinguished.

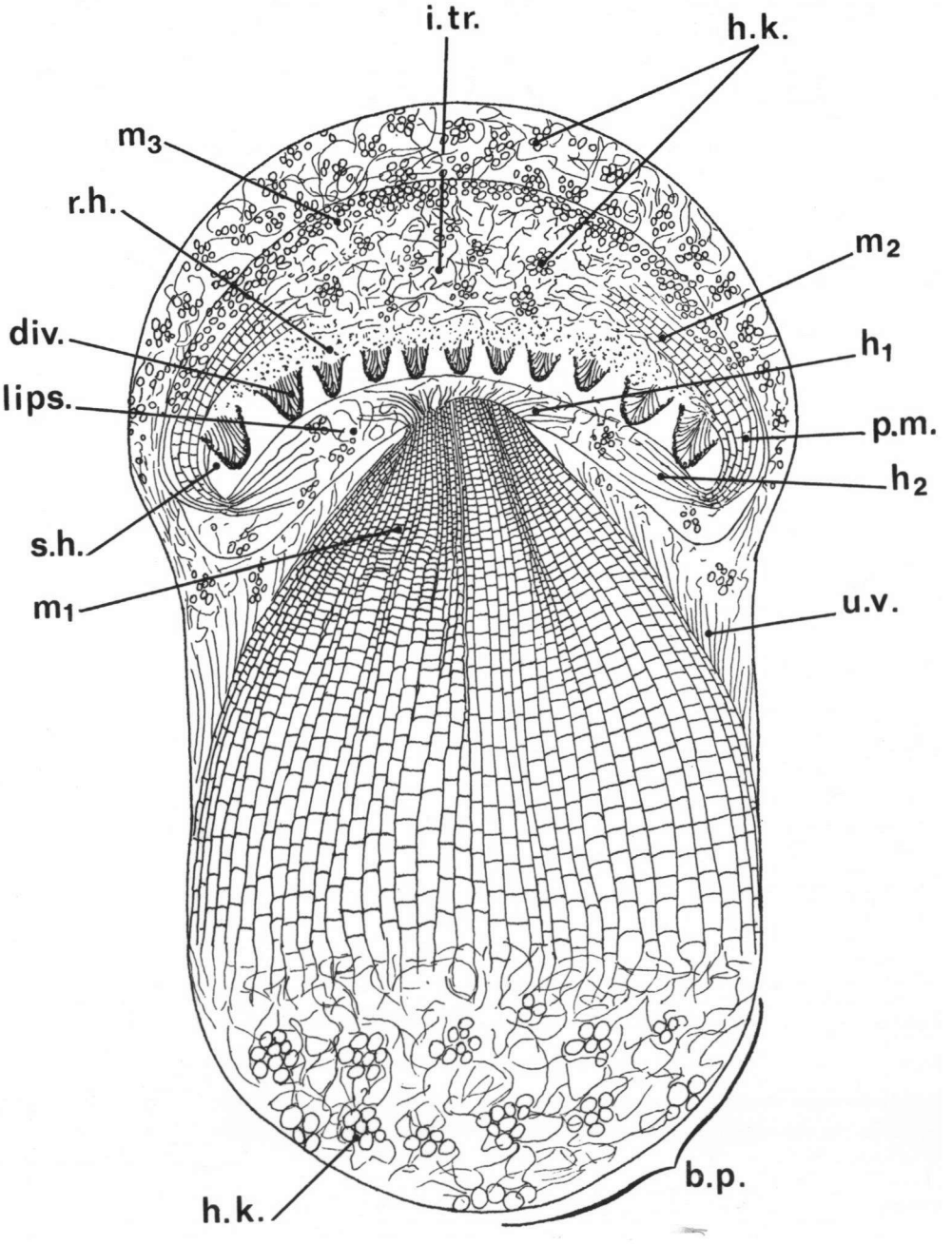
In the hyphal knots there are commonly twisted or spiral-like hyphae which wind themselves between the other hyphae. In many cases such coiled hyphae are to be found around the knot as well as around the bundles of hyphae. A very characteristic configuration may then be seen: the bundle of twisted hyphae around a group of cells (Fig. 1e). As shown in Table I, this typical structure in the original primordial tissue (basal plectenchyma and pileus trama) is to be found in various species throughout the system. It is especially well developed in the strains 59b and 59c of *Agaricus bisporus*, more particularly in genera like *Amanita* and *Limacella*. Here the bundles of curled hyphae and the alternating cell complexes are just as clearly marked as in the trama of *Russula* (Reijnders, *1963*: pl. 8 figs. 4–6). Compare these figures to those of Plates 32B, 34C and D.

Whether a central hypha can be distinguished in the centre of the cell group of such complexes or not is important. In *Russula* and *Lactarius* the development of these complexes starts as primary rosettes around an induction hypha (Reijnders, *1976*). In these genera the cell groups sometimes appear to arrange themselves around the hyphal tips (l.c.: pls. 13E, 14A). In general, however, cell formation takes place along the whole hypha. In other species as well it appeared that sometimes, but by no means always, a club-shaped tip of a hypha is visible in the centre of a cell group of such a hyphal knot. (No new names are applied to these twisted complexes because it was assumed that they develop from simpler hyphal knots or are connected to them in some way.) For example this was the case in *Agaricus bisporus* strain 59b (Pl. 32E), *Limacella guttata* (Pl. 34B), *Gyroporus cyanescens* (Pl. 33E). In *Amanita rubescens* this peculiarity turned up so often that mere chance was unlikely. Here the tissue of the trama of the young stipe and cap has a system of long, broadened, club-shaped, usually somewhat curved hyphae. These are the tips regularly found in the centre of cell groups which are surrounded by bundles of coiled hyphae. (The later formed acrophysalides are short and pear-shaped in *Amanita rubescens*.) These observations are nevertheless too few to warrant that this is caused by induction.

It is, of course, quite possible that the hyphae in all the hyphal knots have an induction effect on one another that advances cell division. Here again there is insufficient evidence.

We have already described meristemoids as a close tissue in which coordinated cell division takes place. Such parts may be found in various places in the primordium. At some points it would appear that they consist wholly of cells with no thin hyphae included (Pl. 35D, *Coprinus macrocephalus*, matrix layer of the veil; Pl. 36B, *C. macrorhizus*, the same type of stipe). This would also be true in tissues formed by such meristemoids, i.e. here the 'hyphes connectives' of Fayod, the undifferentiated generative hyphae, would be absent. Probably this is not entirely true.

These meristemoids closely resemble the meristems of the Phanerogams; sometimes


i.tr.
h.k.
m3
r.h.
m2
div.
h1
lips.
p.m.
h2
s.h.
m1
u.v.
b.p.
h.k.

they are referred to as such. This is not correct because the meristemoids initiate from hyphae which together form a simple tissue; cell division, therefore, can only take place in one direction and the cell walls between the cells of different hyphae are double.

Many phases between individual hyphae and a neatly closed meristemoid can be distinguished. At the proximal end, behind the hyphal bundle of the cap edge, there may be a closed meristemoid but individual hyphae undergoing much cell division may also be found there.

The presence of a meristemoid would appear to be a progressive characteristic. The neatly arranged adjacent cells resembling a tissue of higher plants are often seen in the stipe or cap of more highly developed groups; in many instances such a texture occurs where there is considerable inflation (e.g. Pl. 36B, *Coprinus macrorhizus*; compare also Reijnders, *1963*: pl. 21 figs. 3–5, *Marasmius*; pl. 26 fig. 5, pl. 27 figs. 2, 3, *Mycena*; pl. 39 figs. 1–4, *Conocybe*, etc.). The veil of connected cells (Pl. 35D, *Coprinus macrocephalus*) and the spherocyst veil are usually also formed by a meristemoid as a specially evolved form of the veil.

It is difficult to say whether, and if so to what extent, these cells formed by the meristemoid undergo secondary septation, but as they soon differentiate by inflation this is highly unlikely.

The different types of cell formation which can occur in a primordium of an agaric are illustrated in a schematic diagram (Fig. 2).

HYPHAL KNOTS IN VEILS

It is desirable to establish whether hyphal knots occur in parts of the carpophore other than the bulbus and the trama. Hyphal knots were found in certain veils. It is important to distinguish between innate and emanated veils among the veils of the Agaricales (Reijnders, *1963*: 224–227). An innate veil is initiated when the differentiation of the cap and the stipe of a young primordium is embedded rather than superficial. If this is the case some protenchyma (the first undifferentiated tissue of the primordium) remains at the periphery. Occasionally some changes had taken place earlier at the periphery but hyphae were never added. An emanated veil is formed by the growth of hyphae out of the surface of the young primordium. Frequently it is difficult to demarcate the two types of veils precisely because the two processes, differentiation of cap and stipe surface and the outgrowth of hyphae, may begin at almost exactly the same time (Reijnders, *1963*: 227–230).

An innate veil which shows little further growth will, of course, soon begin to

Fig. 2. Scheme of cell formation in an advanced primordium of an agaric (as shown in a slightly tangential section).

ABBREVIATIONS USED. — b. p., basal plectenchyma; div., divergent trama of the young folds of the lamellae; h_1, hyphae that grow from the stipe into the lipsanenchyma; h_2, hyphae growing from the pileus margin into the lipsanen chyma; h. k., hyphal knots; i. tr., initial pileus trama; lips., lipsanenchyma; m_1, meristemoid of the stipe tissue; m_2, meristemoid of the pileus margin; m_3, matrix layer of the veil; p. m., sheaf of parallel hyphae in the pileus margin; r. h., radiating hyphae over the hymenophore (belonging to it); s. h., subhymenium and palisade of the hymenium; u. v., hyphae growing from the stipe into the universal veil.

tear as the primordium enlarges, and the knots will be absent, like for example, in *Galera paludosa* (Fr.) Kühn.; or will be rare, like in *Galera marginata* (Batsch ex Fr.) Kühn., *Hypholoma udum* (Pers. ex Fr.) Kühn., and *H. ericaceum* (Pers. ex Fr.) Kühn.

The parts showing the most marked growth would have to be investigated to reveal any hyphal knots. This may also be true in an innate veil because where there is concentrated development the veil is strengthened by a number of hyphae growing out from the surface.

Some good examples of hyphal knots were found in the universal veil of *Cortinarius limonius* (Fr. ex Fr.) Fr. (Pl. 35B) and to a lesser extent in that of *C. uliginosus* (Berk.) Moser. In the extending velum *sui generis* it is not just a question of the strengthening of the innate veil; there are also good examples, e.g. in young stages of *Pleurotus dryinus* (Pers. ex Fr.) Kummer (Pl. 35A) in which an emanated universal veil is present, and in *Suillus luteus* (L. ex Fr.) S. F. Gray. In the last species examination showed that the veil is made up of hyphae from the upper cap layer which grow downward and meet hyphae which grow out of the stipe surface (between the elements of the hymenium). In this veil a good deal of cell formation resembling hyphal knots exists. The hyphae in such rapidly growing veils are often grouped in convoluted bundles. Here again the hyphal knots are not always well demarcated; the hyphal bundles show some areas with short cells where cell formation seems to take place. Hyphal knots are also present in the young volva of *Volvariella* (e.g. *Volvariella bombycina* (Schaeff. ex Fr.) Sing., Pl. 35E). This is not surprising because the volva in the bulbangiocarpous species is only a part of the bulb.

The spherocysts veil may be derived from the above type of veils with localized cell formation. The spherocysts usually arise from a sort of matrix layer at the surface of the primordium, where much cell division takes place. Through the repeated formation of numerous septa in the same elements rows of cells are often formed which differentiate to progressively form spherocysts towards the outside (Pl. 35D, *Coprinus macrocephalus* Berk.; Pl. 35C, *Psathyrella candolleana* (Fr.) Maire). In the zone of transition to the veil in the uppermost layer of the cap trama there are for instance many complexes of small round cells which do not all adhere to one another (Pl. 35B). In the veil above these cells there are more separated hyphal knots arising from the groups of small cells of the cap trama. A layer of closely serried cells where much cell division occurs, i.e. a matrix layer of the spherocysts veil, could originate from the kind of feature found in *Cortinatius limonius* (Fr. ex Fr.) Fr.

Hyphal knots may also be found in certain parts of the peridium of the Gasteromycetes. Peridia are generally very heterogeneous in origin; they need not be homologous to the veils of the Agaricaceae (Reijnders, *1963*: 363–364), which are themselves not homologous. On the other hand there is no need to doubt the homology of the exoperidia of, for example, *Scleroderma* or *Geastrum*; these consist of outwardly growing and entwining hyphae; as established, the original bulbus of the Agaricales may be compared to that of the Gasteromycetes (i.e. homologous). In the exoperidium of the above mentioned genera were found clear examples of hyphal knots; these occur again among twisted hyphae, loops, and hyphal bundles (Pl. 35F, *Scleroderma*, and *Geastrum triplex* Jungh.).

CORRESPONDING STRUCTURES

Can structures which correspond to those found in the plectenchyma of bulbus and trama also occur outside the carpophore, e.g. in the mycelium? Heim (*1967*: 177) illustrated a number of configurations of hyphae in the mycelium from cultures of *Psilocybe fagicola* Heim & Cailleux. Here there are obvious similarities to those structures found in the plectenchyma: spirals, curled hyphae, groups of approximately isodiametric cells at the ends of twisted hyphae, etc., but these structures do not always occur in the same places, as they do in the hyphal knots.

The similar initiation of sclerotia is of more importance. Townsend & Willetts (*1954*) differentiate among three developmental patterns of sclerotium formation. In *Rhizoctonia solani* a compact mass of cells is formed by localized branching and repeated septation in adjacent cells. In *Botrytis* these processes are accompanied by repeated dichotomous branching of hyphae over a restricted area. *Sclerotinia gladioli* represents a third strand type in which numerous lateral branches originate from a few parallel hyphae. Many cell divisions are initiated in the area by septation; through adhesion of the hyphae and through these processes a compact body is finally formed.

Adhesion in order to form bundles (locally by lateral hyphae) and the abundant cell division in adjacent hyphae are also typical of hyphal knots but the twisting and curling of the hyphae frequently encountered earlier appear less common in the initial stages of sclerotia. In the sclerotia moreover many cells are formed, so that a combination of the structures producing this phenomenon is understandable.

Like in some types of sclerotia corresponding structures in the developmental stages of papulaspores (Weresub & Le Clair, *1971*) are present.

A COMPARISON OF THE TISSUE FOUND IN THE BASAL PLECTENCHYMA AND THE BULB IN AGARICALES WITH THE TRAMA OF ASTEROSPORALES AND AMANITACEAE

Over such a large range as the trunk of *Ramaria*, the trama of *Cantharellus cibarius* Fr., the basal plectenchyma and the bulb of numerous Agaricales, and some younger stages of Gasteromycetes, were found a number of structures characteristic of these plectenchymatic tissues. These include free ends of hyphal side branches and hyphal knots, balls of adhering and interwoven hyphae not infrequently divided into short cells and eventually forming a close mass of spherocysts, commonly surrounded by coiled hyphae. From these structures the derivation of the different construction of the trama of the Asterosporales on the one hand and the Amanitaceae on the other hand should be shown. This ought to make it possible to solve a problem which has intrigued mycologists, especially systematic mycologists, for some time.

The heteromerous trama of the Russulaceae consists not only of spherocysts and connective hyphae but also of vascular hyphae. It was previously thought that these spherocysts were absent in the trama of the Agaricales, except in a few species

of *Amanita* in which subglobular cells can make up a large part of the trama but these cells proved to be really more or less pear-shaped and not quite round. In young fruitbodies and in *Russula* primordia hyphal knots in the trama were found consisting of short cells surrounded by curled hyphae. These structures are illustrated in our study of the development of some *Russula* species (Reijnders, *1963*: pl. 8 figs. 4–6). Moreover the same structures are visible in the trama of *Limacella guttata* (Fr.) Konr. & Maubl. (Pl. 34B), *Amanita solitaria* (Bull. ex Fr.)Mérat (Pl. 34C), *Amanita rubescens* (Pers. ex Fr.) S. F. Gray (Pl. 34D), etc. These structures do not differ from those which were repeatedly discerned in the bulb and sometimes in the cap trama of other Agaricales, though in a less perfect from. As a rule the homology of all these trama structures can be accepted.

In 1963 we were not yet aware that the complexes of spherocysts in *Russula*, like in *Lactarius*, develop around a central hypha indicating induction. Recently (Reijnders, *1976*) we investigated the origin of this heteromerous trama in some detail and found that such induction can also occur in those Asterosporales which have a gasteroid habitus (*Arcangeliella*, *Elasmomyces*). In the latter case the clumps of spherocysts were simpler and looked more like the ordinary type of hyphal knots, surrounded by coiled hyphae. Thus far we have been unable to prove with certainty any form of induction started by a central hypha. Apart from this phenomenon the structures are exactly alike, so that it is possible to speak of a homology. In *Lactarius* the spherocyst masses arrange themselves around the longitudinal, central hyphae, with the result that they are parallel to the axis of the primordium. Primary rosettes are formed which in cross section are seen to consist of a central hypha surrounded by a row of spherocysts; these are deposited by a hypha coiled spirally around the central hypha. In *Russula* more of these spherocyst cylinders, which form around a central hypha, often merge in larger complexes. The central hyphae degenerate rapidly.

The trama structure of the Amanitaceae is unusual in that short laterals form which finally become so numerous that they take up the major part of the trama. The peculiarities of these elements were discovered by Bonorden as early as 1858 (Reijnders, *1963*: 6). Bas (*1975*: 54) proposed that they be termed acrophysalides. These elements are not found only in the trama of the Amanitaceae; even there they are not always the same in shape. In *Amanita vittadinii* (Mor.) Vitt. they consist of a chain of markedly inflated cells (Reijnders, *1963*: pl. 54 fig. 1); in *Amanita rubescens* on the other hand they are short, pear-shaped elements (Reijnders, l.c.: pl. 55 fig. 6); in *Limacella guttata* (Fr.) Konr. & Maubl. they vary in shape (Reijnders, l.c.: 119, pl. 52 fig. 1). Similar elements are found in the bulb; in *Amanita rubescens* the bulb is mostly taken up by such pear-shaped, much inflated cells while there are still only a few in the developing fruitbody, their number decreasing upwards. In *Amanita rubescens* there are in addition other widened hyphae with free ends. It is clear that the acrophysalides of the stipe and cap trama in the Amanitaceae must be regarded as homologous to the similar elements in the bulb, and that these in turn are homologous to the free ends of hyphal ramifications in the bulbs of other species of Agaricales which may also have a club-shaped terminal cell (e.g. Pl. 36E, F, H).

It is thus apparent that the Amanitaceae have hyphal knots in the trama involved in the initiation of cells. They are clearest in a somewhat older primordium or in a young fruitbody because in a young primordium the tissue is often too compact, though the differentiation into hyphal knots and intercalary hyphae probably took place earlier. The cells of the hyphal knots grow out and lengthen so that in a more developed stage they will form hyphae; these in turn, produce side branches which form acrophysalides. This process does not differ from processes normal in other Agaricales.

The conclusion is warranted that the apparently atypical trama of the Asterosporales, like that of the Amanitaceae, may be traced back to the normal tissue at the base of the stipe (and also often in the trama) of other Agaricales and that the atypical character of these structures arose only from an accentuation of certain processes which are in principle normal (except possibly in the induction of one particular hypha) for the Agaricales in general and even for the clavarioid fungi and the Gasteromycetes.

ANOMALIES

(1) Histological analysis of the strains '59b' and '59c' of *Agaricus bisporus*. Fritsche & von Sengbusch (*1963*) obtained different forms of fruitbodies from single spore cultures and indicated these as 59a, 59b, and 59c. Form 59b was obtained from 59a, and 59c appeared spontaneously in 59b. All three forms (possibly mutants) deviate from the normal type of fruitbody in that they lack a stipe or cap and do not form lamellae. The fruitbodies are bulb-shaped and show some differences worth mentioning. Form 59a has a cavity in the lamellar position of normal specimens and is puff-ball shaped. Form 59b differs from 59a because of its smooth surface and the possibility that it will show a slight external stipe resulting from the narrowing of the undersurface. Strain 59c produces huge, irregular tubers which can weigh up to 825–1800 gram and usually have an irregular surface. Transitional forms of 59b and 59c may be obtained in pure culture; a reversion to the 59b form is often seen in culture. On one occasion a new form appeared in a culture of 59c: a gigantic tuber tapering apically to a much smaller stipe supporting a rudimentary cap (Fritsche, *1968*: fig. 9).

From the above phenomena and bearing in mind the separation of the bulb from the rest of the mushroom (Reijnders, *1974*), a morphologist will assume that here it is a question of hypertrophied bulbs initiated because the rest of the fruitbody was unable to develop. *Agaricus bisporus* (Lange) Imbach is hymenocarpous (Reijnders, *1963*: 202), i.e. the first differentiation of the fruitbody in the tuber is formed by the palisade hyphae of the hymenophore, which grow downwards in a ring perpendicular to the axis of the primordium, but we do not wish to suggest that at this stage there is no differentiation at all in the bulb itself.

To analyse the tissues of forms 59b and 59c we were able to use fresh material supplied by the 'Proefstation voor de Champignoncultuur', for which we would

like to thank Dr. G. Fritsche. We concentrated especially on a comparison of microtome sections of the fixed material of young fruitbodies of 59b and 59c with similarly prepared sections of normal primordia. Material was fixed with Bouin's fluid as usual and stained with Mayer's haemalum. Finally we studied the bulb tissue of mature specimens of some species of the genus *Agaricus*. The formation of the plectenchyma in the bulbs had the same appearance as in all the other species. This comparative investigation seemed to be needed because at first about either the presence or the function of the hyphal knots was uncertain.

Plate 32A shows the tissue of a young stage, a small bulb with a diameter of 950 μm. In many places the hyphae appear to form a ring around the transverse section of another hypha. Spirally coiled up hyphae are present as well as a system of straight hyphae, also groups of isodiametric cells. There are also numerous hyphae ending freely. We photographed coiled hyphae and round cells in a fairly advanced stage (diam. 1.8 mm, Pl. 32B). Occasionally these groups of isodiametric cells appear to be arranged around a central terminal end of a wider hypha (Pl. 32E, a more advanced stage of 59b: length *c.* 5.8 mm, width 3.2 mm).

The above structures may be found in bulbs of strain 59b. To supplement the data we made a microtome section of a bulb of strain 59c with a diameter of a few centimeters. As these bulbs become much larger than those of 59b the measurements of the elements of this tissue can be compared with those of the more advanced stage of 59b above. In that case the structures seem to be the same in 59c but the diameter of the elements is larger. This applies to a high degree to the free hyphal ends, which have a width of up to 19 μm (usually *c.* 10 μm) in the 59b stage, and may even be 49 μm wide in the 59c stage; 20–40 μm being more normal. There also exists a difference in the diameters of the short cells: in 59b 6–11 μm (average *c.* 8 μm), in 59c (6.5–)8–15 μm. The width of the straight hyphae (6–8 μm) is much the same as the former 5–15 μm (usually *c.* 7 μm). On comparison with a smaller stage of the normal *Agaricus bisporus* (width *c.* 1.4 cm) smaller measurements were found: free hyphal ends 5–8 μm, round cells 3–6.5 μm (average *c.* 5 μm), straight hyphae 3–8 μm (average *c.* 5 μm). The unusual width of 59c will be considered below. Further the measurements of a young, living specimen of *Agaricus bisporus* (cap width *c.* 1 cm) do not compare to those of relatively small bulbs of 59c: free hyphal ends up to 16 μm, hyphae 6.5–10 μm. Cross sections of the lower part of this living bulb show a plectenchyma with markedly coiled hyphae having undulations and loops. It is noticeable that some cells in the chain of a hypha are much broader than the rest (up to 16 μm). Free hyphal ends are numerous, as are knots of coiled hyphae with short ramifying branches (fewer short cells).

Comparison of this material, fixed or unfixed, led to the deduction that the bulbs of 59b and 59c are identical with those of normal specimens of *Agaricus bisporus* and with the Agaricales in general. This may well be used to support the idea that the bulbs of 59b and 59c are actually hypertrophic bulbs in which further development and differentiation into a fruitbody are not genetically possible. There is only one morphological difference between 59b and 59c on the one hand and the normal

bulb of *Agaricus bisporus* on the other. In the first two we find a more differentiated rind of thinner, periclinal, loosely woven hyphae (diam. 2–3 μm) packed more closely together at the periphery (Pl. 32c). This layer is absent in normal primordia, which are surrounded by a universal veil only slightly differentiated from the lower or adjacent trama; the looser lipsanenchyma is left out of consideration.

Fritsche (*1972*) also investigated the cytology of strain 59c. She came to the conclusion that 59c has more nuclei in the cells than 59b; furthermore that the nuclei of 59c are statistically larger than those of 59b. Superficially the primordia of 59b have the normal form of primordia; the measurements may also be compared to those of *Agaricus bisporus*; the mature fruitbodies are, however, slightly smaller than normal fruitbodies. By contrast strain 59c is a gigas form (Sinnott, *1960*: 438). Gigas forms often depend on the number of chromosomes (polyploidy). Polyploidy is very common in Phanerogams and also occurs in fungi (see, e.g. Esser & Kuenen, *1965*: 326–330). We conclude that the bulbs of 59c are hypertrophied bulbs of the normal *Agaricus bisporus* formed by a delay in the development of the normal fruitbodies and that they are probably examples of polyploidy. The fruitbody forms of strains 59b and 59c are like those which Singer (*1975*: 18–19) termed carpophoroids. It would be useful to investigate whether in other cases of such monstrosities there is also a very marked development of the bulb.

(2) Watling's aberrant forms of *Psilocybe merdaria*. Ascertainment of whether forms 59b and 59c should be classed among the carpophoroids depends on what is understood by carpophoroids. According to the definition used by Singer (*1949*: 25), the carpophoroids are completely sterile bodies which formed in place of those bearing basidia. In agreement with this, forms 59b and 59c belong in the carpophoroids. The gasteromycete-like forms of *Psilocybe merdaria* described by Watling (*1971*) have superficial cavities along whose walls a hymenium is formed. Besides these gasteromycete-like types Watling obtained a whole series of monstrosities where especially the cyphelloid and the pleurotoid, *Melanotus*-like forms (with lateral stipes) occur.

It is unfortunate that because descriptions have been macroscopic rather than histological we know so little about the hyphal development inside these structures. We believe that the teratoid forms of *Psilocybe merdaria* are not homologous to the fruitbodies of 59b and 59c, which actually represent bulbs. Here it would be fitting to go into the causes of the initiation of *Psilocybe* abnormalities.

At first sight it is surprising that gasteroid and cyphelloid forms should develop together, though their growth patterns are seemingly contradictory. The gasteroid form appears to be very concentrated; strongly developing parts are scarcely present. In pleurotoid and cyphelloid forms the growing margin of the cap plays a more important role, the development of these forms falling under the diffuse type (Reijnders, *1963*). If the phenomenon is an atavism part of the monstrosities would indicate a gasteromycetic origin and the other part a relationship to, e.g., *Pleurotus* (Polyporaceae sensu Singer). It is not really necessary to go that far. Sporulation

continues in the bovist-like bodies of *Psilocybe merdaria*. Watling's descriptions make it clear that in many of these teratoid forms the hymenophore does not develop normally (there is also a *Weraroa* type). In the cyphelloid type abnormal lamellae are also formed. Both in this type and in the gasteroids the stipe is poorly developed; at least it is never long and robust; in gasteroid forms the stipe is often comparable to a columella.

In our book on the development of fruitbodies in Agaricales (Reijnders, *1963*) we attempted to emphasize the significance of the order of succession of which the parts of the fruitbody developed in the primordium. The hyphae that are to form the hymenophore appear first among undifferentiated generative tissue, which we termed protenchyma, in a hymenocarpous primordium. Like most of the closely investigated species of *Stropharia Agaricus bisporus* is hymenocarpous but in *Psilocybe* this structure does not appear (or is less apparent) before the stipe rudiments. (We referred to *Psilocybe merdaria* as isocarpous.) The studies made by Urayama, Hagimoto, Konishi, and Gruen have indicated that substances produced in the lamellae can influence the growth of the stipe. This is related to the inflation of the stipe cells, though the longitudinal arrangement of the stipe cells might also be influenced; this orientation of the hyphae shows that a stipe is being formed. In strains 59b and 59c of *Agaricus bisporus* no hymenophore is formed, and later no stipe. In *Psilocybe merdaria* the deficiency in the developmental mechanism of the hymenophore could thus cause abnormal stipe formation. If the stipe remains small and short the fruitbody inside the bivelangiocarpous primordium stays covered and a gasteroid form results. It is thus conceivable that cyphelloid aberrations are also initiated when the fruitbody does open but that the rudimentary stipe is unable to support the body. Cyphelloids with different attachments may develop via pleurotoids (Reijnders, *1963*: 252–256).

Observations on the development of the Aphyllophorales

Few studies have been published on the development of the Aphyllophorales. The histological differentiation of this group is, as far as is known, more marked than in the Agaricales. Corner's distinction of hyphal types in the Polyporaceae etc. and that of Maas Geesteranus (*1962*) in spine fungi promoted investigation of the origin of these elements. Studies like those of Kennedy & Larcade (*1971*) on the development of *Bjerkandera adusta* lead to the conclusion that innumerable details of the origin of the fruitbodies are still unknown.

When the youngest stages of certain common species of Aphyllophorales are described it is to ascertain whether they have a basal plectenchyma and also to see how they grow. It was possible to collect young forms of *Hyphodontia quercinum* (Fr.) J. Erikss., *Stereum sanguinolentum* (Fr.) Fr., *Irpex lacteus* Fr., *Coriolus versicolor* (L. ex Fr.) Quél., *Hirschioporus abietinus* (Dicks. ex Fr.) Donk, *Gloeophyllum abietinum* (Bull. ex Fr.) Karst., and *Gloeophyllum odoratum* (Wulf. ex Fr.) Imazeki. Since in the

absence of a rapidly increasing elongation there is no demarcation of stages it is not really correct to speak here of primordia.

HYPHODONTIA QUERCINUM (Fr.) J. Erikss.—We made median sections through effused fruitbodies of 3–5.5 mm in diam. lying on the rind. The fruitbodies are made up of two layers; one layer has entangled or horizontal hyphae which advance over the substrate, and the other layer has erect hyphae on which parallel bundles can develop which are to form the teeth. The first layer incorporates much substrate and may be 200 μm wide, while the second layer may be 300–650 μm wide. Only one kind of hypha exists (diameter up to 1.0–1.5 μm) which has the same appearance as the mycelial hyphae on the cork layer, i.e. the generative hyphae. These are oriented parallel to one another at the margin of the young fruitbody. They often extrude through a fissure in the bark, where they are still much intertwined.

STEREUM SANGUINOLENTUM (Fr.) Fr.—The youngest stage of this species forms a small cushion with an arched upper surface which may be about 1850 μm broad and 650 μm high (Pl. 37A). The structure rests on the substrate but is only basally and centrally attached, at which point a zone of much intertwined hyphae (1.5–2 μm in diam.) is present. From this point the hyphae extend in all directions and form a dome. The central height is about 400 μm. At the edge of the dome the hyphae are mostly parallel but not close together (Pl. 37B); they grow outwards. The extending hyphae are also generative hyphae. Between the outwardly growing hyphae more coloured hyphae are also visible; these are initially much broader than the generative hyphae; they widen towards the periphery (diameter up to 5 μm) and often show club-shaped extremities. These hyphae are probably vascular hyphae which may eventually end in a cystidium. Skeletal hyphae are either absent or not clear at this stage; they become visible at a more advanced stage (3.5 μm in diam.). They are thin but thicker-walled than the generative hyphae (diameter *c.* 2.5 μm).

IRPEX LACTEUS Fr.—The young stage (Pl. 37C), of which we made median sections, also presses against the substrate and is only attached at the centre (width 2150 μm, height 820 μm). The hyphae extrude through a lenticel and are much entangled at their bases. From this point deeply coloured, thin hyphae extend outwards, being thus generative hyphae (Pl. 37C). More towards the periphery the colouring lessens, giving rise to faintly coloured, wider hyphae (diameter up to 3 μm) with thicker walls. These are skeletal hyphae. The typical form and colouring of the generative hyphae can be seen most distinctly at the periphery and the edge of the dome. However, there seem to be a number of gradations between the generative and skeletal hyphae. The generative hyphae lose their coloured contents and if they also thicken it becomes difficult to distinguish them from the skeletals. The extremities of the skeletals often extend above the surface and the terminal, somewhat wider cell contains abundant protoplasm and in many cases has not yet developed a thick wall. At the edge of the structure entangled hyphae are found again; these extend outwards and are more or less parallel, but they do not form an

obvious meristemoid. As in *Hyphodontia*, the teeth are formed at regular intervals by hyphal bundles in which the hyphae do not adhere closely until a later stage (Pl. 37E). The skeletals and the intermediate forms can be distinguished immediately in the teeth.

CORIOLUS VERSICOLOR (L. ex Fr.) Quél.—The youngest stages form a cushion about 672 μm wide and 570 μm high. Beneath this cushion there may be a stipe or mat (about 400 μm long and 200 μm broad) made up of the same hyphae as the cushion; they are entangled or somewhat longitudinally orientated. At the very base of the cushion-shaped structure the hyphae are still entwined over an area of about 100 μm, after which they extend evenly towards the periphery, there being no differentiated margin. There are two kinds of hyphae; somewhat irregular hyphae with clamp connections and dark granular contents (diameter 1.5–2 μm), and straighter, paler and usually wider hyphae (up to 3 μm). The irregular kind are clearly generative hyphae while the latter are mostly skeletals, especially towards the periphery, where they are thick-walled and their lumen is reduced to a thin line. It is also probable that a great many of the paler hyphae are generatives which have lost their protoplasmic contents, as we also find a lot of pale hyphae in the stipe where they are intertwined so that the arrangement closely resembles that in *Irpex*. An older stage is about 2.2 mm wide. At that stage the pores form and a transverse section shows teeth about 240 μm long in which the trama consists of almost parallel generative hyphae. Palisade cells (about 13 μm long) are already present in the hymenium. At the margin the hyphae are almost parallel but lie free from one another and do not form a real meristemoid.

HIRSCHIOPORUS ABIETINUS (Dicks. ex Fr.) Donk.—For this species the young stages investigated did not differ much in structure. When the diameter is about 1750 μm and the height about 380 μm the hyphae are entwined over a small distance at the base, where this is centrally attached to the substrate (e.g. 64 μm high). The hyphae radiate further, producing a slightly arched cushion. At the margin there are nearly parallel hyphae that are partly separate from one another. The tubes have already been formed at this phase and the walls (dissepiments) are distinguishable in longitudinal section as nearly parallel teeth. The generative hyphae, recognizable by their dark colour and granular protoplasm, are about 1.5 μm wide and especially numerous at the base The skeletal hyphae, found mostly at the periphery, have a thick wall that does not stain with haematoxylin, and often coloured cell contents (diameter *c.* 2.5 μm). Here some colourless hyphae must also be regarded as generative hyphae that have lost their protoplasmic contents. The palisade cells of the hymenium soon form and are initially 15–20 μm long.

GLOEOPHYLLUM ABIETINUM (Bull. ex Fr.) P. Karst.—In this species the young fruitbodies are dorsally attached right from their early formation. Our specimen extended 5.5 mm forward; a median section was taken through the base. Here the hyphae are intertwined over a short distance (*c.* 220 μm), after which they grow

forward and then both upwards and downwards to produce an almost fan-shaped body (Pl. 37F). Three types of hyphae can be distinguished: (i) pale, septated, thin-walled hyphae with a granular protoplasm (diameter 1.5–2.5 μm). These generative hyphae are common in the entangled part at the base, but they may also be found elsewhere; (ii) strongly pigmented hyphae with dark, rather thin walls (diameter 1–2 μm) and few or no septa; the hyphae are abundant and are probably intermediate forms giving rise to iii; (iii) skeletal hyphae with a thick wall and no septa (diameter 1.8–3.8 μm). Rings, to be found in the trama, originate by the bending of some of the hyphae (especially type ii); the hyphae then lie more or less obliquely in the trama. The extremities of some of these hyphae widen and are brightly coloured (diameter 6.5 μm). Five rings were visible at the 5.5 mm stage. Club- or bottle-shaped ends develop on the lower surface (the hymenium). On the upper surface the hyphae sometimes become erect and form bundles; they are also partly intertwined, giving a floccose-hairy (pilose) surface texture.

GLOEOPHYLLUM ODORATUM (Wulf. ex Fr.) Imazeki.—The young stages of *Gloeophyllum odoratum* consist of a small cushion, arched on the upper surface and flat below. These cushions often rest on one another because it would seem that at a certain point new fruitbodies may be formed on the upper surface. We investigated such bodies, which were, for example, 9 mm wide and 4.3 mm high, or 13.3 mm wide and 5.5 mm high.

The median section shows that the frequently dark coloured hyphae (diameter 1.3–2 μm) are entangled at the point of attachment to the substrate. In many cases these parts (250–670 μm) are not sharply defined because the basal part of the young fungus incorporates much of the substrate. Many skeletal hyphae are found in this zone and even more where the hyphae radiate towards the periphery. They have a thick, often encrusted wall and no septa (diameter 1.5–4 μm). Between the skeletals are paler, thin-walled generative hyphae (diameter 1.3–3 μm). There are also paler hyphae where the wall is distinguishable as a dark line (i.e. intermediates?).

Even at this young stage rings in the trame are found that are approximately parallel to the arched upper surface (Pl. 37G). The direction of growth of the hyphae is different in the rings and the hyphae lie closer together. Many widened hyphal extremities are seen in the rings (diameter 3–4 μm). Occasionally the hyphae deviate so far from their original direction of growth that the part of them in the rings is perpendicular to it. Above the rings the hyphae are much looser (i.e. farther apart). At the edge of the cushion the structure is the same as elsewhere at the periphery: there is no meristemoid.

CONCLUSIONS.—Comparison of the initial developments of these seven species of Aphyllophorales reveals a remarkable uniformity. *Hyphodontia* is excluded; this really forms a cover of two layers, the lower of which consists of entangled hyphae in the young stages, which are usually attached by the centre of the base to the substrate. All the others have a basal zone with intertwined primordial hyphae and a zone

where the hyphae radiate towards the periphery. The basal zone is usually somewhat limited. There is no obvious growing-limb, at least not in these young stages; a real meristemoid has not (yet) developed. Where a diffuse developmental type in the Agaricales is discerned the fruitbodies of this type are still formed initially by a bundle of adhering, coordinated hyphae (Reijnders, *1963*: 221) which later widens at its extremity. This may be only a gradational difference. There is another difference in the development of Aphyllophorales in comparison with the Agaricales: the quite different nature of part of the hyphae. Skeletal hyphae cannot be distinguished in the Agaricales but cell inflation is very marked and especially important during the growth of the fruitbody.

Referring to the origin of the skeletals Lentz (*1971*: 100) wrote: 'In orthodox instances, development is not by transformation of a generative to a skeletal unit, but by apical outgrowth of the skeletal element from the generative.' Although we cannot provide any actual proof these assumptions seem rather dogmatic. The numerous intermediates between the two types of hyphae which are seemingly present in some species (*Irpex*, *Gloeophyllum*, *Osmoporus*) and which have also been found in other species indicate that there may exist at least one other type of hypha which because of its thickened wall is sometimes difficult to distinguish from a skeletal hypha (see also Corner, *1950*: fig. 13, *Pterula*).

CONCLUSIONS AND PHYLOGENY

The basal plectenchyma in the Agaricales, just like the bulb which in effect is an expansion of this tissue, is characterized by a special structure which can also be found in the trama of a primordial cap and not seldom in mature specimens. This cap trama is initially part of the bulb tissue formed by the primary protenchyma.

The characteristics of this structure are:

(1) Undulating, interlocking hyphae and loops.
(2) Spirals and sometimes rings closed around other hyphae.
(3) Inflated, intercalary elements.
(4) Many free extremities of ramifications, often with clavate or widened terminal cells (P. 36H, *Agaricus*), so that they may resemble acrophysalides.
(5) Hyphal knots consisting of at least one bundle of adhering hyphae or usually coiled hyphae, which are often locally divided into short cells, occasionally forming short branches.

In many instances around these groups of short or round cells there are other hyphae; the tissue then appears like groups of coiled hyphae with a centre of apparent spherocysts. These groupings may occasionally be found between straight hyphae of a different nature, but this need not necessarily be so. We find such a structure in the most diverse species (Reijnders, *1963*: pl. 8 figs. 4–6, *Russula emetica*; Reijnders, *1976*: pl. 13E, *Lactarius mammosus*; pl. 15D, *Russula ochroleuca*; pl. 16C, *Russula fragilis*; pl. 17E, *Arcangeliella*). In our investigations for this study we also came across many instances of it (Pl. 34E, *Chamonixia caespitosa* Rolland; Pl. 33D, *Gyroporus*

cyanescens (Bull. ex Fr.) Quél.; Pl. 34A, *Hygrophorus hypothejus* (Fr.) Fr.; Pl. 32E, *Agaricus bisporus* (Lange) Imbach, strain 59b; Pl. 34B, *Limacella guttata* (Fr). Konr. & Maubl.; Pl. 34C, *Amanita solitaria* (Bull. ex Fr.) Mérat, etc.). Thus it appears that this structure is a common one. We must also assume that in matrix layers with a marked formation of closely grouped cells the coiled hyphae are present but less clear. They probably play a part in the formation of cells and perhaps in their nutrition.

In contrast to the above, the hyphal knots sometimes lie in looser tissue (Pl. 33C, *Suillus aeruginascens* (Secr.) Snell; Pl. 34F, young bulb of *Scleroderma aurantium* L. ex Pers. In this last case it is probably a question of remnants of hyphal knots that were originally closer together (compare also Pl. 35B, *Cortinarius limonius* (Fr. ex Fr.) Fr., veil; Pl. 33F, *Chroogomphus rutilus* (Schaeff. ex Fr.) Lundell & Nannf., inflation of the hyphae and separation of the knots). When in due course no more new cells are being formed and the old cells are inflated, even fewer of the hyphal knots remain (Pl. 32F, *Agaricus bisporus* strain 59c).

The structures with coiled hyphae led to a comparison of the trama of the Agaricales in general with that of the Asterosporales. The spherocyst formation in *Arcangeliella* (Reijnders, *1976*: pl. 17E) and *Elasmomyces* appears to be identical to the occurrence of short cells in the hyphal knots of the Agaricales. It was only not possible to show the phenomenon of induction in the Agaricales but it has often been found that in the centre of a group of cells surrounded by a coiled hypha a free end of a wide hypha appears like in *Arcangeliella* (l.c.: pl. 17E). Instances of this have been photographed on Plate 33E *Gyroporus cyanescens*, Plate 34B *Limacella guttata*, Plate 32E *Agaricus bisporus* strain 59b. It may be assumed that in this kind of hyphal knot the hyphae have an effect on one another and possibly also on cell formation just like that in a meristemoid in which the cell division is coordinated but this has not been proved and it is possible that no central hypha is present in most hyphal knots (not even when they are very young?).

The structures during development in real Aphyllophorales with those in Agaricales were compared earlier. It is striking that there is no clear growth margin in very young stages. There is no bundle of interlocking hyphae which produce new hyphae by means of regular branching, nor is there a meristemoid. Hyphae grow much more separate; apart from secondary septation the new cells are formed at their tips, but growth is directed by the shape of the whole structure. Young stages (here it is difficult to speak of primordia) show that there is coordination in the growth and regularity in the increase in volume of the whole.

That there is no growth margin of interlocking hyphae is also demonstrated by the phenomenon of haptomorphosis, that is that the edge of the fruitbody can grow around all sorts of obstructions, or that different individual fruitbodies grow together at their edges to produce a single distinct specimen. This is not seen in the Agaricales.

Is there in the Aphyllophorales no meristemoid zone of adjacent hyphae in which the cell division is coordinated? This ought to be investigated in greater detail. Though tissue formation in these groups, or at least in the greater part thereof,

deviates from that in the Agaricales (and Gasteromycetes), this does not apply to the clavarioid and cantharelloid fungi. As far as the trama tissue is concerned these last two groups, which are regarded as related to each other, show striking resemblances to the Agaricales. Investigation of the stalk of certain *Ramaria* species showed that all the structures characteristic of the bulb of the Agaricales were also to be seen here (Pl. 36D, *Ramaria aurea* (Fr.) Quél.). The tissue of the branches in which the hyphae are parallel has, of course, been more closely investigated than that of the stalk. In young stages of *Cantharellus tubaeformis* the hyphae are loosely interwoven but their main direction or orientation is parallel. The tissue is not homogeneous, however; denser patches where the hyphae lie against one another alternate with thinner patches. The denser places often resemble hyphal knots and the cells are sometimes shorter. In *Cantharellus cibarius* such patches are more common in the interwoven cap trama than in the stipe, where the hyphae are approximately parallel. We (Reijnders, *1963*) were unable to study the basal plectenchyma because it had probably been cut off from the specimen.

The fact that the heteromerous trama of the Asterosporales may be regarded as a specialised instance of the trama of the Agaricales (and Gasteromycetes) in general also affects phylogenetic interpretations. Hyphal knots may be centres of intercalary cell formation. Frequently in young primordia of Agaricales groups of cells initiated in hyphal knots are formed. After inflation these knots become not spherocysts but ordinary hyphal cells. In the trama of the Agaricales, which do not belong in the Asterosporales, no spherocysts are found but there are many in the veils. In the veils they can be regarded as derived elements. The inflation that is so marked in the tissues of the Agaricales serves to increase the volume. The same occurs in the spherocysts of *Russula* and *Lactarius*, where the total volume of those elements is eventually much greater than that of the hyphae (Reijnders, *1963*: 272).

Although in the primordia of *Amanita* and *Limacella* structures of groups of small, round cells surrounded by coiled hyphae indeed occur, much of the increase in volume in these genera is also a result of numerous vesicular acrophysalides representing a special case of free-ending ramifications. Kühner, therefore, considered the Amanitaceae and the Russulaceae to be related. This relationship is based on the structure of the trama which in both families is derived from the original structure of the basal plectenchyma: in the one the cells formed by the hyphal knots are dominant, in the other the free hyphal extremities are dominant. In both families a large part of the carpophore is taken up by this tissue, while the part formed by the meristemoid of the cap margin is limited. Even so this resemblance between the Amanitaceae and the Russulaceae does not actually indicate a phylogenetic relationship; other Agaricales show the same structures, the proportions only being a little different. Singer (*1958*) and Smith (*1971*) proposed that the spherocysts originate from the cellular subhymenium of certain Gasteromycetes. Judging by the comparisons made in the present paper it is no longer necessary to find a special explanation for this origin of the so-called heteromerous trama; in the lamellae of

Russula both the spherocysts of the trama and the cells of the subhymenium are present (Reijnders, *1976*: pls. 14E, 15A) but apart from their different sizes they originate in different ways. According to Singer and Smith, spherocysts occur not only in the Asterosporales but also in the trama of several other hypogeal fungi, where they probably develop in the usual manner. This should be investigated more closely.

This study of the structure of the trama and underground parts also leads us to comment on the phylogeny of the Agaricales, Gasteromycetes, and Aphyllophorales. The dividing lines between these three groups—which are not natural taxa but only of practical value—are very vague. There exist Gasteromycetes which are much more closely related to Agaricales than to other Gasteromycetes. As it is known that Gasteromycetes also occasionally develop gymnocarpously, they can only be defined as Higher Basidiomycetes that do not eject their spores. That the demarcation between the Aphyllophorales and the Agaricales is also vague is demonstrated by Singer's (*1975*) inclusion of *Polyporus* in the Agaricales.

Moreover these groups are polyphyletic. For this reason it is pointless to attempt to show that the Agaricales are derived from the Gasteromycetes or vice versa. Much has been written about these interesting relationships, especially about the Asterosporales. We cannot cover the subject fully in this article. Our study of the ontogeny of both groups has led to certain general views which will be given below. Perhaps we shall have an opportunity to reconsider the whole problem in more detail at a later date.

(1) Basidia are complex organs which serve to produce the ballistospores. They would never have originated below ground level so that hypogeals with basidia must have derived from epigeals. If the first had undergone only development underground basidia would never have formed—only other sporulating structures. The question still remains whether fruitbodies with a peridium would have been formed. Though Singer & Smith (*1960*) reasoned that the spore-ejecting basidia of the Agaricales originated (by selection) from the spore forming cells of certain Gasteromycetes the fact that the Gasteromycetes show recognizable basidia, even in their underground forms, remains unexplained.

(2) In underground forms columellae are often present. These can be regarded (by comparison) as stipe rudiments, but a stipe cannot function underground. For what reason, therefore would they have developed?

(3) The underground Asterosporales often have bipolar, even gymnocarpous primordia (Reijnders, *1963*: 210–213). Those forms which developed underground would show a radial construction, bipolarity being of no use, and they would not be gymnocarpous.

(4) Like the stipe beneath the ground the spherocysts in the trama are also non functional. As previously stated, these should definitely be regarded as remnants of preceding development above ground level, their most important task being the enlargement of the carpophore (Reijnders, *1963*: 272, 360).

(5) Agaricales also often undergo a long period of underground development.

There they form bulbs inside of which a whole fruitbody develops, needing only to stretch to reach above ground and disperse the spores. It is less well known that the gymnocarpous primordia of *Russula* also remain hidden beneath ground level for some time. By the time the young growing specimens appear above the ground there are no longer any primordia in the vicinity (Reijnders, *1976*: 67).

At the time of Patouillard (1854–1906) it was thought that the Gasteromycetes were angiocarpous, the Agaricales hemiangiocarpous, and the Aphyllophorales gymnocarpous. It has since become apparent that this is not the case. One can say, however, that these three criteria are often applied to these groups. In the same way it can be said: Gasteromycetes: often completely subterranean; Agaricales: often partly subterranean; Aphyllophorales: usually not subterranean. In many cases it has been found that these subterranean parts are distinguished, initially at least, by a special structure. This structure also influences, to a greater or lesser extent, the trama of the parts above ground, which are not only formed by ramifying bundles of parallel hyphae. It is possible that a subterranean fruitbody might evolve to attain an above ground habit, that is a bulb could change into a stiped mushroom. It appears more probable, however, that an above ground mushroom would change into a subterranean form by growth retardation and reduction of the stipe; this has often been described.

Singer & Smith's (*1960*) most important objection to an evolution in the Asterosporales of agaricoid forms to gasteroid is that the different structures which could be explained by degradation are not correlated, i.e. that the typical *Russula* and *Lactarius* characteristics appear to a different extent and are scattered throughout the underground forms. Among these forms there is a distinction between different levels, new characteristics constantly being added; species of the genera of these levels may or may not have other characteristics. According to Singer & Smith this can be better explained by progressive evolution than by degradation.

We do not wish to exclude the possibility of progressive evolution. We do, however, object to the derivation of one recent form from another recent form. For the greater part the forms from which the recent Asterosporales are derived no longer exist. It is very probable that there was once a type of progressive evolution of agaricoid forms. Gasteroid forms could have appeared at any level of evolution. 'Gasteromycetation' does not seem to have taken up much time in the process of evolution. This is shown not only by the agaricoid forms, which start out with several subterranean characteristics, but also by the gasteroid anomalies of *Psilocybe* (See McKnight *in* Singer, *1975*.; Watling, *1971*). The structural difference is not so great because the main characteristics of the trama of the above and below ground parts can be the same. Only the external form changes, while some parts (meristemoid, formation of spherocysts) undergo reduction.

The fact that more primitive forms retained a gasteroid rather than an agaricoid form might be explained by the occupation of special niches by the gasteroid forms. This was previously discussed by Reijnders (*1971*). The appearance of new, further evolved types must have made the pressure of selection greater on the above ground

forms. More primitive forms may, therefore, still be present in a particular niche, giving the impression that the above ground forms actually developed from the gasteroid forms! The reverse may also occur; the subterranean form will have again adapted to an epigeous habit since the genes necessary for the development of the parts above ground will in many cases still be present. In general, however, 'gasteromycetation', with the degradation of certain characteristics only seems more probable.

Résumé

On trouve à la base du stipe dans les Agaricales le plectenchyme basal, qui peut s'élargir en formant un bulbe. Ce tissu, qui n'est pas homogène, est caractérisé par des structures particulières: des extrémités libres de ramifications, des hyphes sinueuses, des anses, des spirales et des anneaux qui peuvent renfermer une autre hyphe et des agglomérations d'hyphes dites: «nodules». Ces dernières sont en réalité des faisceaux d'hyphes, qui constituent souvent le centre de divisions cellulaires, ou bien elles se présentent sous la forme d'un groupe de cellules unies, entouré d'hyphes enroulées. Cette dernière structure qui se retrouve chez un grand nombre d'espèces d'Agaricales, se manifeste parfaitement dans la trame des Amanitaceae, qui rappelle celles des Russulaceae. La trame du jeune piléus de beaucoup d'espèces accuse souvent les mêmes particularités qui se présentent également dans le tronc des *Ramaria*, dans le jeune bulbe des Gastéromycètes et dans divers voiles.

Les différentes manières de la naissance des cellules dans les primordiums ont été étudiées en détail; la notion: «méristémoïde à hyphes» a été définie.

La trame hétéromère des Astérosporales et la trame des Amanitaceae dérivent de la jeune trame d'autres Agaricales.

Les tissus des bulbes des souches 59b et 59c de l'*Agaricus bisporus* ont été analysés. 59b est homologue au bulbe d'un carpophore normal d'*Agaricus bisporus*. En accord avec G. Fritsche, l'auteur est arrivé à la conclusion que 59c représente en outre «un type gigas». Les carpophoroïdes (formes aberrantes) de *Psilocybe merdaria* (décrites par Watling) ont été discutés.

Les différences fondamentales entre le développement des vrais Aphyllophorales, d'une part, et celui des Chanterelles des Agaricales et des Gastéromycètes, de l'autre, ont été considérées.

En ce qui concerne l'évolution au sein des Astérosporales, l'auteur raisonne qu'une dégradation de quelques caractères dans les formes gastéroïdes (Heim, Malençon) ne contrarie pas nécessairement les arguments qui ont été avancés par R. Singer et A. H. Smith. Une descendance de formes hypogées à partir de formes épigées est plus vraisemblable que l'inverse.

References

BAS, C. (1975). A comparison of *Torrendia* (Gasteromycetes) with *Amanita* (Agaricales). *In* Beih. Nova Hedwigia **51**: 53–60.

BERTHIER, J. (1973). Recherches sur les *Typhula, Pistillaria* et genres affines. Thèse. Lyon.

CORNER, E. J. H. (1929). The structure and development of the ascocarp. *In* Trans. Br. mycol. Soc. **14**: 275–291.

—— (1950). A monograph of *Clavaria* and allied genera. Oxford.

ESSER, K. & KUENEN, R. (1965). Genetik der Pilze. Berlin.

FRITSCHE G. (1968). Züchterische Arbeiten an „59c", einem Champignonstamm mit neuer Fruchtkörperform. I. Steigerung des Ertrages. *In* Theor. appl. Genetics **38**: 28–37.

—— (1972). Züchterische Arbeiten an „59c", einem Champignonstamm mit neuer Fruchtkörperform. II. Cytologische Untersuchungen. *In* Theor. appl. Genetics **42**: 44–50.

FRITSCHE, G. & SENGBUSCH, R. VON (1963). Beispiel der spontanen Entwicklung neuer Fruchtkörperformen beim Kulturchampignon. *In* Züchter **33**: 270–274.
KENNEDY, L. L. & LARCADE, R. J. (1971). Basidiocarp development in *Polyporus adustus*. *In* Mycologia **63**: 69–78.
KÜHNER, R. & ROMAGNESI, H. (1953). Flore analytique des Champignons supérieurs. Paris.
LENZ, P. L. (1971). Analysis of modified hyphae as a tool in taxonomic research in the higher Basidiomycetes. *In* R. H. Petersen (ed.): Evol. high. Basidiomycetes: 99–127.
REIJNDERS, A. F. M. (1963). Les problèmes du développement des carpophores des Agaricales et de quelques groupes voisins. Den Haag.
—— (1971). Over de ontwikkeling en morphogenese der paddestoelen. *In* Sterbeeckia **8**: 1–39.
—— (1974). Le développement de deux espèces de Cortinariaceae. *In* Trav. mycol. déd. R. Kühner, Bull. Soc. linn. Lyon **43**: 355–364.
—— (1976). Recherches sur le développement et l'histogénèse dans les Astérosporales. *In* Persoonia **9**: 65–83.
SINGER, R. (1949). The Agaricales in modern taxonomy. 1st Ed. Tucuman.
—— (1958). The meaning of the affinity of the Secotiaceae with the Agaricales. *In* Sydowia **12**: 1–43.
—— (1975). The Agaricales in modern taxonomy. 3d Ed. Vaduz.
SINGER, R. & SMITH, A. H. (1960). Studies on secotiaceous Fungi IX. The astrogastraceous series. *In* Mem. Torrey bot. Club **21–3**: 112.
SINNOTT, E. W. (1960). Plant morphogenesis. New York.
SMITH, A. H. (1971). The origin and evolution of the Agaricales. *In* R. H. Petersen (ed.): Evol. high. Basidiomycetes: 481–504.
TOWNSEND, B. B. & WILLETTS, H. J. (1954). The development of sclerotia of certain fungi. *In* Trans. Br. mycol. Soc. **37**: 213–221.
WATLING, R. (1971). Polymorphism in *Psilocybe merdaria*. *In* New Phytol. **70**: 307–336.
WERESUB, L. K. & LECLAIR, P. M. (1971). On *Papulaspora* and bulbilliferous Basidiomycetes *Burgoa* and *Minimedusa*. *In* Can. J. Bot. **49**: 2203–2213.

EXPLANATION OF PLATES 32–37

ABBREVIATIONS USED IN PLATES. — m. s., microtome section; f. s., freehand section of mature material.

PLATE 32

Figs. A–H. *Agaricus bisporus*. Fig. A. strain 59b, m s.: young bulb, initiation of hyphal knots, spiral hyphae (s), rings, ×320; Fig. B. strain 59b, m. s.: more advanced stage, coiled hyphae, ×128; Fig. C. strain 59b, m. s.: cortex layer, ×128; Fig. D. strain 59c, m. s.: inflated tips (t), ×80; Fig. E. strain 59b, m. s.: inflated tip in the centre of a cell group surrounded by coiled hyphae (t), ×200; Fig. F. strain 59c, m. s.: rather advanced stage, hyphal knot (hk), cell division (c), dolipores, ×80; Fig. G. m. s.: rather advanced stage, sinuous hyphae (sh), loops, ×200; Fig. H. f. s.: tips of short branches (t), ×200.

PLATE 33

Figs. A, B. *Agaricus bisporus*. Fig. A. strain 59c, f. s.: spiral growth of hypha, enclosing another hypha (s), ×200; Fig. B. strain 59c, f. s.: ring (r) enclosing a hypha, ×200.

Fig. C. *Suillus aeruginascens*, m. s.: pileus trama of young stage with hyphal knots, ×200.

Figs. D, E. *Gyroporus cyanescens*. Fig. D., m. s.: young bulb, hyphal tip (t), coiled hyphae, straight hyphae (sh), ×200; Fig. E., m. s.: pileus trama of a young stage, hyphal knots, a knot surrounding an inflated tip (t), ×200.

Fig. F. *Chroogomphus rutilus*, m. s.: stipe of a young stage, hyphal knots with cells which are due to inflation (i), ×200.

PLATE 34

Fig. A. *Hygrophorus hypothejus*, m. s.: stipe of a young stage, basal plectenchyma with coiled hyphae (ch), hyphal knots (hk) and layer of inflating hyphae (i), ×200.

Fig. B. *Limacella guttata*, m. s.: bulbus of a rather young stage, spiral growth around a hypha (s), coiled hyphae, ×200.

Fig. C. *Amanita solitaria*, m. s.: upper part of the stipe of a rather advanced stage, large acrophysalides, coiled hyphae around hyphal knots, ×200.

Fig. D. *Amanita rubescens*, m. s.: somewhat advanced stage, upper part of the bulb (stem), hyphal knots, coiled hyphae (ch) and straight hyphae (sh), ×200.

Fig. E. *Chamonixia caespitosa*, m. s.: young bulb with hyphal knots (hk), ×200.

Fig. F. *Scleroderma aurantium*, m. s.: young bulb, initiation of hyphal knots (hk), ×200.

PLATE 35

Fig. A. *Pleurotus dryinus*, m. s.: veil of a young stage with hyphal knots, ×200.

Fig. B. *Cortinarius limonius*, m. s.: veil with hyphal knots (hk) of a rather young stage and matrix layer, ×200.

Fig. C. *Psathyrella candolleana*, m. s.: veil with matrix layer (ml), ×200.

Fig. D. *Coprinus macrocephalus*, m. s.: veil with matrix layer (ml), ×200.

Fig. E. *Volvariella bombycina*, m. s.: hyphal knots (hk) in the volva of a young stage, ×200.

Fig. F. *Scleroderma aurantium*, m. s.: hyphal knots (hk) in the exoperidium, ×200.

PLATE 36

Figs. A, B. *Coprinus macrorhizus*. Fig. A., m. s.: very young stage with differentiation into three zones: basal plectenchyma (bp), young cells of the stipe, and meristemoid (m), ×80; Fig. B., m. s.: older primordium with intertwined hyphae of pileus trama (tr), surrounded by veil meristemoid (m) and stipe tissue (st), ×80.

Fig. C. *Boletus edulis*, f. s.: mature bulb, twisting hypha (s) enclosing other hypha (h), ×200.

Fig. D. *Ramaria aurea*, f. s.: mature trunk, hyphal knot (hk), ×200.

Fig. E. *Boletus satanas*, f. s.: club shaped extremity of hypha, ×200.

Figs. F, G. *Lycoperdon pyriforme*. Fig. F., f. s.: sinuous hypha (sh), tips (t), ×200; Fig. G., f. s.: spiral growth of hypha (s) enclosing another hypha, ×200.

Fig. H. *Agaricus osecanus* f. s.: short-celled tips (t), ×200.

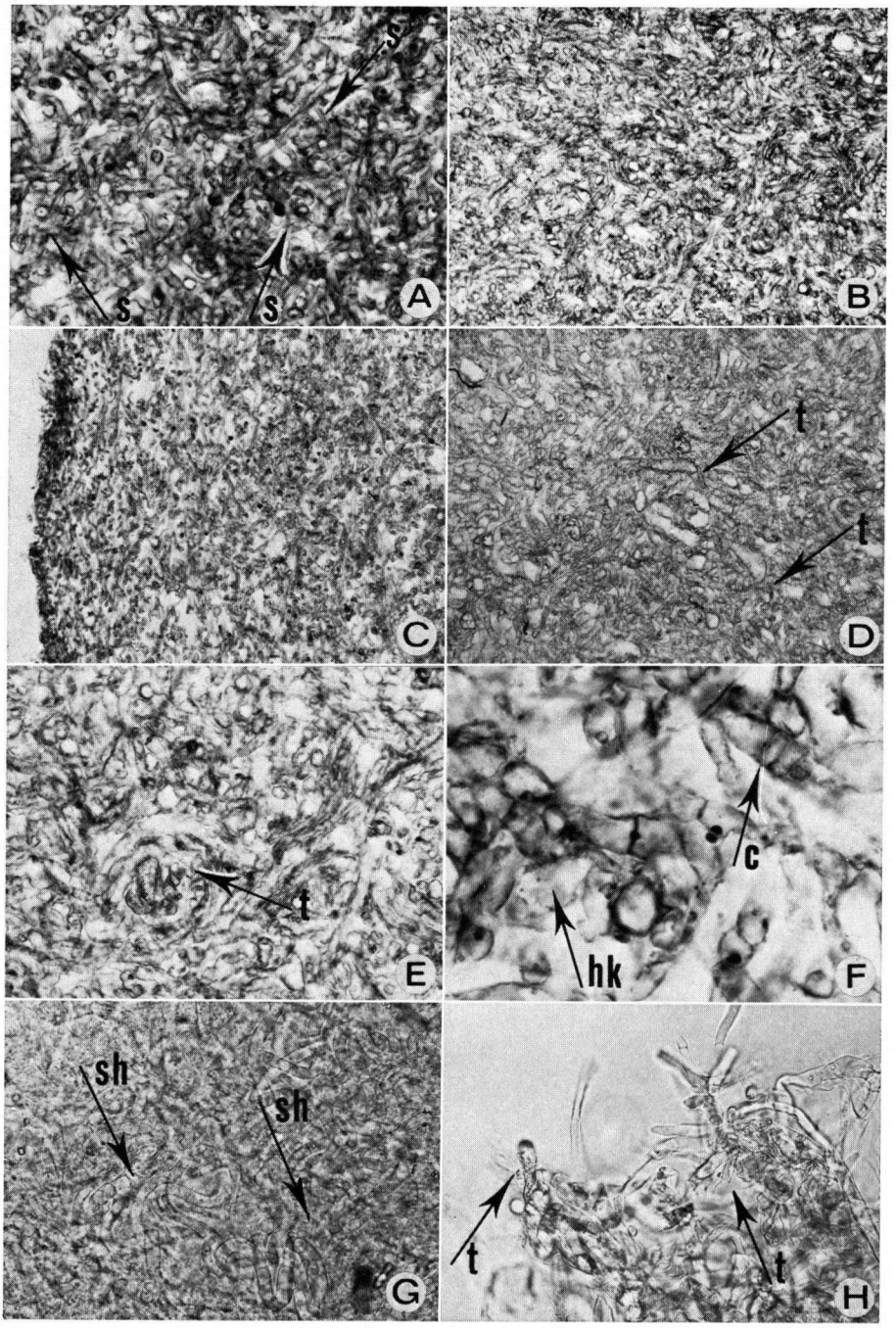
PLATE 37

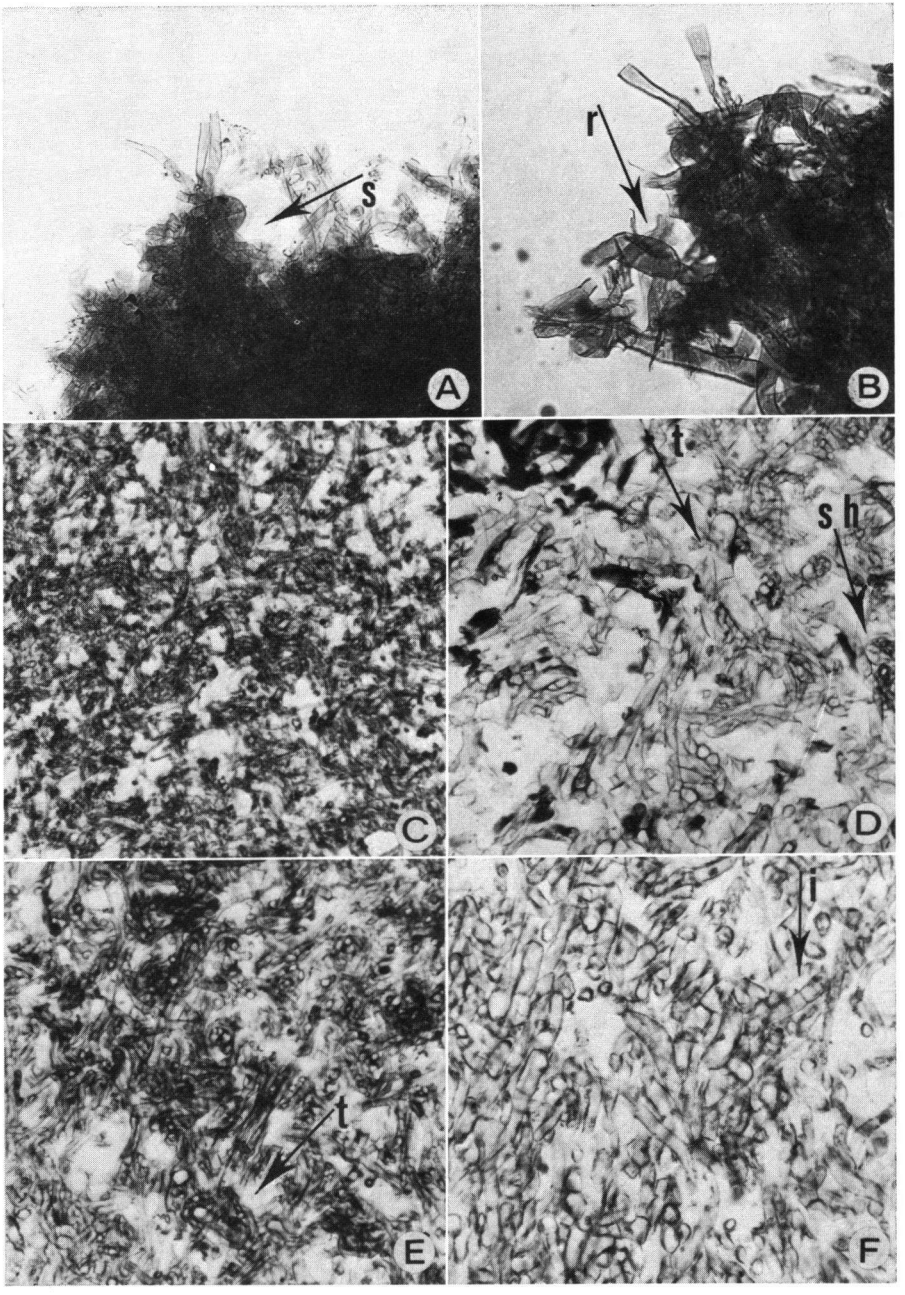
Figs. A, B. *Stereum sanguinolentum*. Fig. A., m. s.: young stage, intertwined generative hyphae (gh), ×32; Fig. B., m. s.: the same stage, margin, ×80.

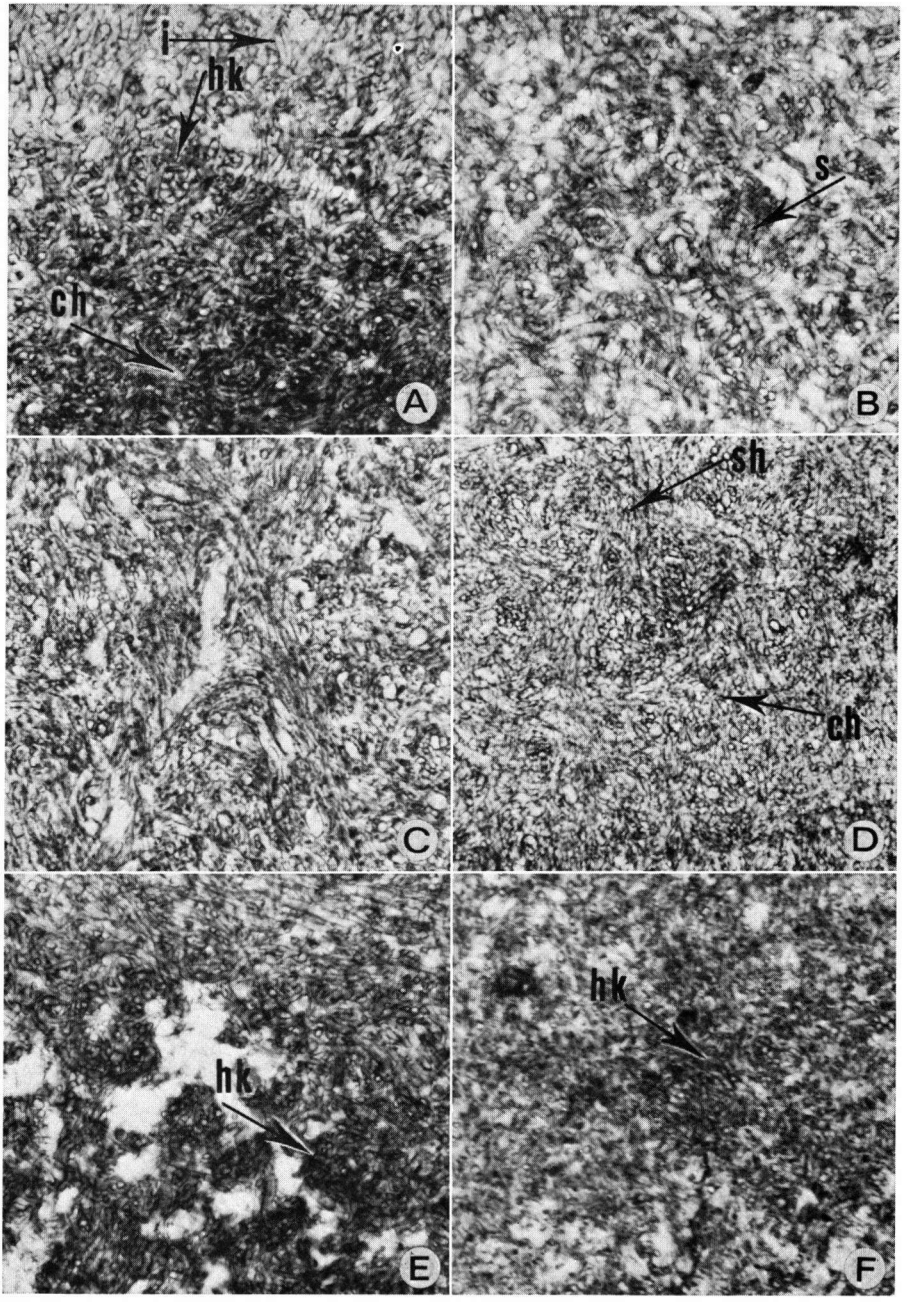
Figs. C–E. *Irpex lacteus*. Fig. C., m. s.: young stage, width 2150 μm, ×32; Fig. D., m. s.: basis of the same young button with intertwined generative hyphae (gh), ×80; Fig. E., m. s.: development of teeth in the same button, ×200.

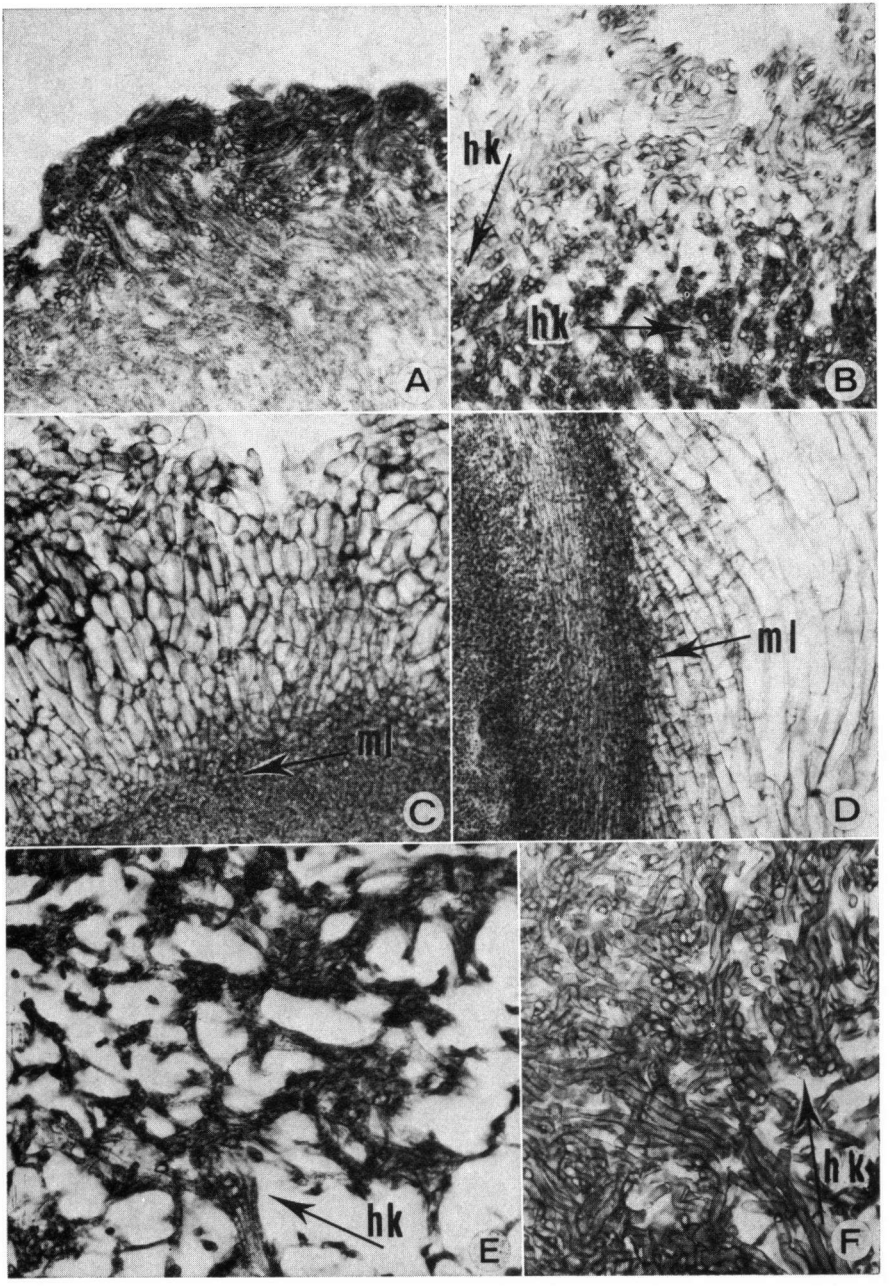
Fig. F. *Gloeophyllum abietinum*, m. s.: base of a young stage, intertwined generative hyphae (gh), ×20.

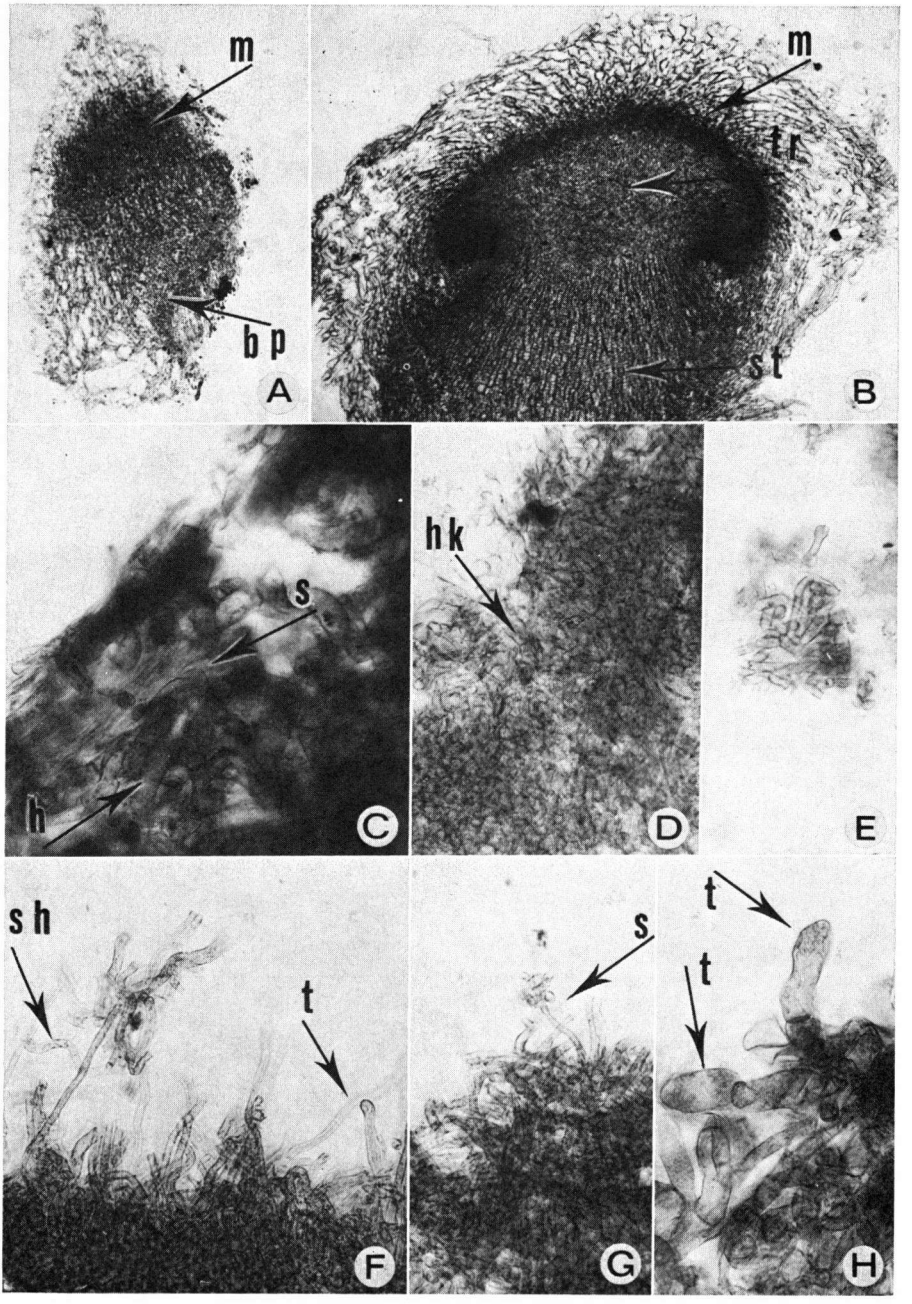
Fig. G. *Gloeophyllum odoratum*, m. s.: zonation of the trama, ×80.

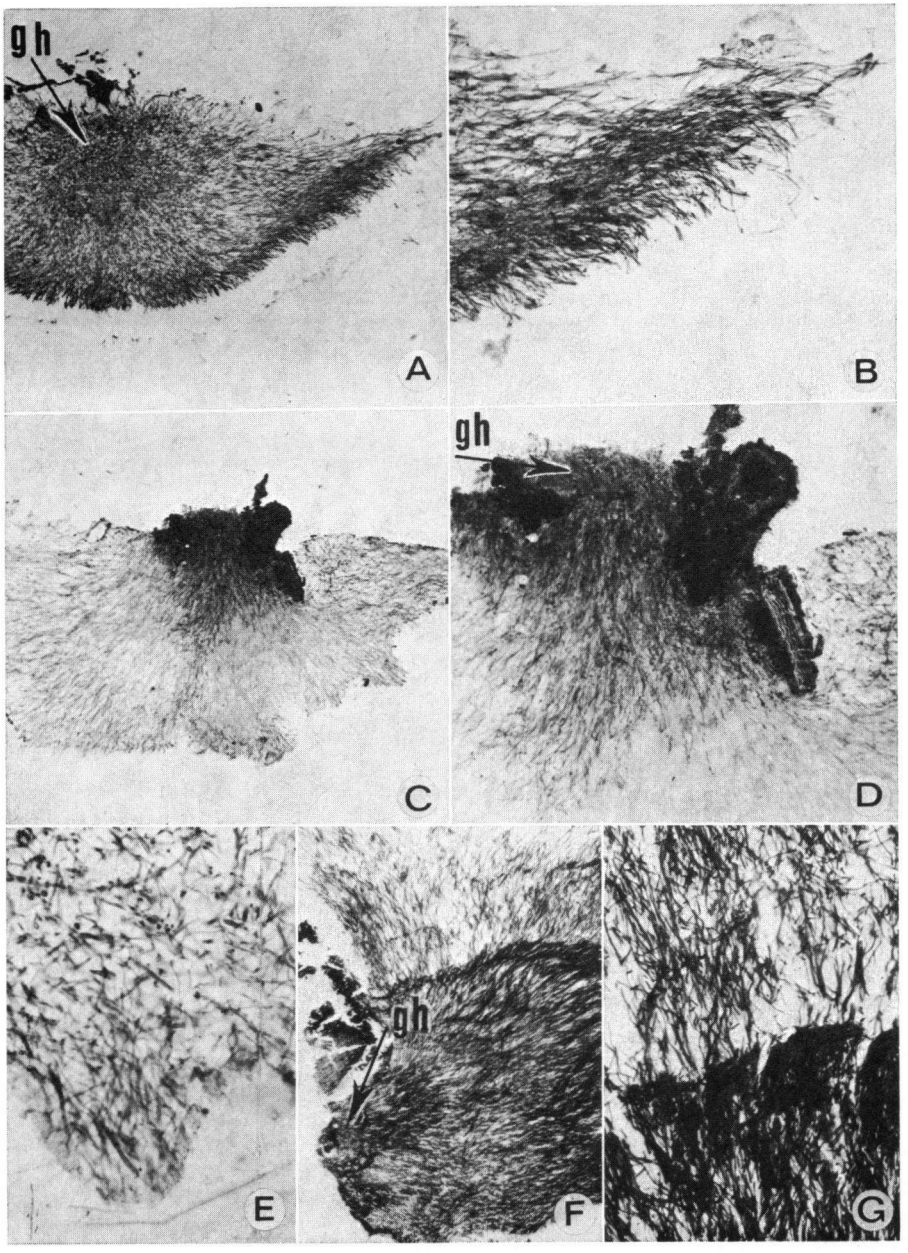

s
s
s
A
B
C
t
t
D
t
E
c
hk
F
sh
sh
G
t
t
H


s
A
r
B
C
t
sh
D
t
E
i
F


i
hk
ch
A
s
B
C
sh
ch
D
hk
E
hk
F


A
hk
hk
B
ml
C
ml
D
hk
E
hk
F


m
bp
A
m
tr
st
B
s
h
C
hk
D
E
sh
t
F
s
G
t
t
H


gh
A
B
C
gh
D
E
gh
F
G