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Developmental biology of agarics - an overview

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Introduction

We are not attempting a comprehensive survey in this chapter, and the references we will quote are offered for illustration, not as part of an extensive review. Rather, we will present some personal views and observations about the subject.

The following aspects will be dealt with:

- primordium initiation;
- cell formation by cross wall formation, and nuclear numbers;
- differentiation of cells corresponding with their location;
- cell inflation;
- the basal plectenchyma and bulb-tissue.

We will not deal with wall formation, nor with the influence of environmental factors on primordium initiation, both of which have been considered in recent reviews (Burnett & Trinci, 1979; Manachère, 1978, 1980; Robert & Durand, 1979).

It is obvious that morphogenetic research is only at the start of its development: the possibilities to tackle problems of this kind have greatly increased in the last decade. Fruit bodies of hymenomycetes are particularly interesting in this respect because histogenesis is accomplished here by the cooperation of individual hyphal elements and, though this applies also to many ascomycetes and Rhodophyceae, the size and complexity of the structures formed by hymenomycetes are in general much greater. The development of any organised fungal structure requires that hyphae grow toward one another and cooperate in formation of the differentiating organ; this is the diametrically reversed character of the invasive, 'undifferentiated' mycelium. We are almost totally ignorant of the factors which control this peculiar reversal in behaviour. Autotropic agents and surface-active molecules must be involved. Such molecules are known from classic researches with yeasts (the glycoproteins which determine mating type-specific agglutination), water moulds (sex hormones) and *Mucor* (trisporic acid synthesis) (for review see Moore, 1984), but apart from some ultrastructural indications of a surface architecture on basidiomycete cells (McLaughlin, 1982) we lack conclusive information about surface chemistry of basidiomycete hyphae and this will be necessary to explain how they can cooperate in the formation of an organ like the fruit body, sclerotium or rhizomorph. These fungi provide extremely good systems for the fundamental study of phenomena involved in cell homing and specific cell-to-cell adhesion, since they change from one state to the other as a normal part of their developmental pathway. In most other systems in which the biology of the cell surface is being studied, individual cells can only be investigated by culturing them in unnatural conditions.

Primordium initiation

Light microscopy does not reveal many differences between the generative hyphae (which in mass

have been called **protenchyma**) and mycelial hyphae. They have mostly a minimum number of nuclei (i.e. increase in the number of nuclei is an aspect of cell differentiation in fruit bodies of Agaricales) and may or may not bear clamp connections. The protenchyma of the primordial fruit body displays from the very first two types of organisation: a bundle of nearly parallel hyphae, and interwoven hyphae which form a **plectenchyma**. But also in primordia, which are in the beginning plectenchymatous, bundles of strictly parallel hyphae (called meristemoids) show up later in the stipe and in the lateral parts of the pileus. This gives rise to the question whether the factors which control such a directed growth in primordia are comparable with those which cause the same behaviour in strands, coremia, and ramified fruit bodies (Clavariaceae, etc., see Watkinson (1979)). The hyphae of these aggregates are generally embedded in a slimy coating (see Rayner *et al*.: Chapter 10) and it may be supposed that this sheathing has an important morphogenetic function with regard to binding the hyphae together and the transmission of stimuli. We should note that this may be relevant both to the earliest stages of primordium formation (van der Valk & Marchant, 1978) and to the more mature structure. Newer methods of preparation for the scanning electron microscope show the fruit body to be covered, and the subhymenium to be filled, with material which could serve as an adhesive and through which soluble control factors could be transmitted (Williams, Beckett & Read: Chapter 18).

Little attention has been directly devoted to the factors responsible for organising the shift from a ramifying to an aggregating mode of hyphal growth, though the more indirect agents which promote the formation of primordia (such as nutritional requirements and light) have attracted much interest. Nutrient depletion of the medium has long been known to be involved (see Leatham: Chapter 17), but this does not equate with starvation of the mycelium because nutrients are stored in the mycelium and then redistributed to the developing fruit bodies. There are good data for this with regard to nitrogen metabolism (especially for the polypore *Favolus* (Kitamoto *et al*., 1980)) and carbohydrate metabolism (particularly in *Coprinus* (Madelin, 1960)) but we are not aware of any serious attempt to look at lipids. This is worth remarking upon in view of the useful storage function which lipids can serve and the argument developed below for the importance of membrane-associated processes in primordium initiation. An extreme difficulty here is the problem of identifying causal events. For example, the data available on cyclic AMP metabolism (Uno & Ishikawa, 1982) and glycogen metabolism (Moore, Elhiti & Butler, 1979) in *Coprinus* are very promising, yet there is no necessary connection between these metabolites and fruiting, and no ready way of distinguishing causal from consequential events. Indeed, from knowledge of the nutritional control of fruit body initiation, coupled with the other environmental stimuli which are commonly involved, particularly the frequent requirement for light stimuli (Ross: Chapter 14) and the apparently universal need for a temperature shift-down, attention is focused on conformational shifts in important molecules and especially membrane-associated processes. Both temperature and light can be viewed as influencing metabolism via membrane architecture; the former through effects on membrane fluidity (which may affect the rate at which transmembrane phenomena occur) and the latter through direct interaction with membrane-localised receptors. Nutritional effects too, however, can also be seen as having a membrane relationship. We think it significant that many plasma membrane transport mechanisms are biphasic, having one phase which characterises the 'high external metabolite concentration' and another which characterises the 'low concentration' state (Scarborough, 1970a, b; Neville, Suskind & Roseman, 1971; Schneider & Wiley, 1971; Beever & Burns, 1977; Moore & Devadatham, 1979). The shift from one to the other, which in some cases involves derepression of previously unexpressed genes and in other cases involves conformational changes in existing proteins, and which is frequently associated with altered energisation states of the transport process, could well be integrated with differentiation processes. The corollary, of course, is that we need to know more about transport mechanisms and the way they change during the different phases of the life cycle of the organism.

Primordium initiation evokes many morphogenetic problems which have only been partially studied

despite the large quantity of work which has already been done. An equally serious deficiency is in the study of development with particular regard to the comparison of different systematic groups (Watling: Chapter 11). The number of species which have been subjected to morphogenetic research is still small: *Schizophyllum commune*, *Agaricus bisporus*, a few species of *Coprinus*, and *Flammulina velutipes*. Even study of aspects of somatic growth detectable with light microscopy is far from being adequate, let alone complete, and there is tremendous scope for biochemical and molecular investigation.

Cell formation

We distinguished above between meristemoids, with rows of cells in parallel hyphae where cell division is coordinated, and plectenchymatous tissue, where ramification and cross wall formation often occur in adjacent hyphal knots where short branches and cells are surrounded by coiled or straight hyphae with larger cells (Reijnders, 1977). A fact of fundamental importance is that in primordia of Agaricales cell division takes place exclusively by transverse cross wall formation. Corner (for example, in his monograph on *Clavaria*, 1950) called all cross walls which are not formed by the tip cell 'secondary walls', and this designation has been generally adopted. The formation of longitudinal walls seems to be almost impossible in agarics. This might correspond with the polarity of the tip cell and probably with the occurrence of dolipores in the cross walls. We have never seen longitudinal walls or walls in orientations other than transverse in primordia: neither in the stipe, nor in the pseudoparenchymatous subhymenium. When the stipe (or any other basidiomycete structure) increases in girth and inflation is insufficient to provide for this, more generative hyphae which in a young stage are always present in the axial portion of the stipe are utilised. Even the pseudoparenchymatous tissues of many sclerotia may arise only by ramification, as demonstrated for three different sclerotial types by Townsend & Willetts (1954). Although some exceptions seem to occur, it is nevertheless significant that cell division by longitudinal wall formation occurs only in very specialised cells such as the basidia of Tremellales or the multicellular spores of certain ascomycetes (Pleosporales), though longitudinal septa have also been reported in walls of pycnidia and perhaps some perithecia (Lohwag, 1941). Otherwise, longitudinal walls are not found.

There is only one apparently reliable description of a real meristem which is manifest in an organ of an agaric; Motta (1969) claimed that cell divisions in a narrow zone about 25 μm behind the extremity of a rhizomorph of *Armillaria* were effected by walls being formed in diverse directions. His comparisons with shoot- and root-tips of phanerogams led him to suggest the existence of histogens analogous to those proposed for higher plants. As we have seen (Rayner *et al*.: Chapter 10), there is reason to doubt the existence of a true meristem in *Armillaria* rhizomorphs, but Motta also described secondary meristems situated underneath the postulated apical meristem at the sides of the rhizomorph and, in these parts, cell formation proceeded by transverse cross wall formation.

Whatever may be realistic in these conceptions about the histology of the *Armillaria* rhizomorph there is certainly one striking conformity between this organ and cell division in the upper part of the *Coprinus* stipe. Motta states that one or two nuclei occur in 'meristem' cells, but the number of nuclei in cells which originate from these increases rapidly. This is a common characteristic of the cells of *Coprinus* stipes (Reijnders, 1979), but is observed also in many other agarics, though not in all as Kühner (1958) has pointed out. The number of nuclei in such 'coenocytes' can run up to 40-60 or even 100 or more (see also Wong & Gruen, 1977). The term nuclear bodies may be preferred to the description of these organelles as nuclei, in view of the disparity between their increase in number and the increase in the amount of DNA in the stipe (Gooday: Chapter 12). When first formed, at the onset of stipe formation in *Coprinus*, the cells have only one or two nuclei, and a narrow zone where this reduced number is retained is still evident in the very upper portion of the stipe for some time. Kühner (1977) supposes that the large number of nuclei is to a certain extent correlated with the volume of the cell, but Wong & Gruen (1977) found no correlation between the

number of nuclei and cell size in *Flammulina*. It should be noted that such a multiplication of nuclei appears to be absent in other cells of the primordium, even those which enlarge considerably, e.g. cells of the veil. The universal veil in *Coprinus* often consists of rows of cells which arise at the circumference of the cap; we could never observe in this tissue a similar nuclear behaviour, the mother cells usually contained two nuclei which gradually disappeared in the huge cells of the veil (there is an exception in *Armillaria*: when hyphae of the surface of the stipe pass into the veil, cells of the latter have more nuclei in some cases). For the sake of comparison it will be important to consider the **heteromerous trama** of the Russulaceae, where the multinuclear elements arise in a very specific way; is this multinuclear condition caused by the same morphogenetic factors? The descriptions of Motta are accompanied by a series of illustrative electron micrographs but we doubt whether extensive documentation of this sort exists for stipe cells of Agaricales. It is certainly lacking for trama tissues of *Russula* and *Lactarius* and in these cases would be extremely welcome to enable comparison of the ultrastructural data of the **induction-hyphae** and the **spherocytes** with those of ordinary stipe cells. The ultrastructure of elements of the hymenium has often been studied, but the available details of somatic cells are in this respect far from being sufficient. Understanding of the way cells and tissues differentiate is dependent upon knowledge in precise detail of the structure and histological relationships between cells; in too many cases this knowledge is lacking.

Differentiation of cells corresponding with their location

The cells of phanerogams and fungi, however different may be their origins, differentiate in relation to their location in the plant. This is one of the most important principles of morphogenesis. We often see that the cells of one recognisable hypha become abruptly different because they are influenced by another morphogenetic factor (the nature of which is obscure). Thus, in *Leucocoprinus cepaestipes* the lower cells of hyphae at the surface of the cap form the pileodermium and the narrower upper part of the same hyphae merge into the universal veil (Reijnders, 1948); and in *Coprinus poliomallus* the narrower hyphae of the gill trama suddenly widen and form isodiametric cells when they pass into the lipsanenchyma (Reijnders, 1979). Such differences in adjacent cells of continuous hyphae can be detected everywhere in primordia, in mature tissues (notably the differentiation of hymenial elements from the tramal hyphae (Moore *et al*., 1979)) and in vegetative structures (such as the distinction between thick-walled and thin-walled cells in sclerotia of *Coprinus cinereus* (Waters, Butler & Moore, 1975)). What signals are involved in directing such differentiation and how, in a basically hyphal structure, are they localised? Adjacent hyphal cells are separated by the dolipore septum (Moore: Chapter 7) which is obviously capable of extremely rapid response to experimental stress (Todd & Aylmore: Chapter 9) and must be involved in partitioning regulatory signals between cell compartments in the same hyphal strand. The structure of the dolipore/parenthesome septum is sufficiently complex to anticipate quite sophisticated involvement in localising differentiation signals in a longitudinal direction (relative to the long axis of the parent hypha). But even though the hypha is the very basis of the sorts of structures considered here, control of the longitudinal communication of organisational signals is probably insufficient to account for the regulation of the levels of differentiation which can be observed.

The scope of the differentiation seen in fruiting and vegetative fungal structures alike is every bit as complex as that of higher plant and animal systems. A consequence of the fungal dependence on hyphal organisation is that lateral communication between cells contributing to the same tissue must involve export and import of control signals. As discussed above, longitudinal secondary walls are not found; so lateral communication between adjacent cells must take place across two hyphal membranes and two mature hyphal walls. There can be no denying the probability (indeed, one is tempted to say the fact) that lateral communication plays an important role in defining the positional information on which tissue differentiation in fruiting and vegetative structures depends. Yet despite numerous ultrastructural studies of various fungal structures, there is no evidence for anything akin to plasmodesmata or gap junctions in the lateral walls of fungi (although channels

through thickened cell walls in peridioles of *Nidularia* (Reijnders, 1976) and pit-like structures in sclerotia of *Penicillium* (Lohwag, 1941) have been reported). In general, a cytoplasmic route for signals capable of conveying positional information is excluded (see Rosin, Horner & Moore: Chapter 13).

Another very interesting aspect is the apparent fact that most of the changes in shape which characterise the later stages of fruit body maturation depend on cell expansion. It follows from this that the distinction between cell division and cell expansion (in terms of their contribution to development) is an important one; yet we have very little information about it. The *Coprinus* species are probably the best served in this respect but even these data are fragmentary. More modern techniques may help in this type of analysis; even embedding specimens in resin allowing thinner, and ideally serial, sections to be examined with the light microscope would be rewarding. A considerable research effort has been devoted to the metabolism which underlies the cell expansions important in maturation (whether or not cell division is still occurring). The account is particularly well developed for *Coprinus cinereus* but we have only recently recognised how paraphyses insert into the basidial layer of the young hymenium and that a proportion of the paraphyseal population insert later in development (see Chapter 13). Nevertheless, the available biochemical evidence quite clearly associates amplification of the tricarboxylic acid cycle in the maturing fruit body cap of *C. cinereus* with specific derepression of an ammonium-scavenging system and amplification of the urea cycle, the whole metabolic shift leading to accumulation of urea as an osmotic metabolite which serves to drive water into the expanding cells of the hymenium (Ewaze, Moore & Stewart, 1978; Moore *et al*., 1979). It is interesting that urea has often been associated with basidiomycete fruits. So one wonders how general might be the specific metabolism identified so far in *Coprinus* (especially the potentially novel means of assimilating ammonium, the use of glutamate decarboxylation as part of the tricarboxylic acid cycle, and accumulation of urea). However, it must be recognised that cell inflation in different tissues (cap *versus* stipe in *Coprinus*) and in different organisms (*Coprinus versus Agaricus*) depends on different metabolic pathways for the provision of osmotic metabolites. These differences illustrate the versatility of intermediary metabolism; but, and we say this in the belief that the fundamental events underlying cell expansion are essentially similar wherever the process is encountered, such metabolic differences can direct attention away from the fundamental control processes. Recognising that those differences exist and that nevertheless there are similarities in the events observed can help in our search for those fundamental control mechanisms.

In these biochemical processes and in a few other cases (for example, involvement of laccase in fruiting of *Agaricus*, *Lentinus* and *Coprinus congregatus*, and of mannitol dehydrogenase and glucose 6-phosphate dehydrogenase in fruiting of *Agaricus* (Ross: Chapter 14; Wood: Chapter 15; Hammond: Chapter 16; Leatham: Chapter 17)) there are some excellent candidates for the application of recombinant DNA methods to study of the genes and gene transcripts involved in development-related processes and, indeed, it is encouraging to see that work is developing in this sort of direction (Ullrich & Novotny: Chapter 20; Wessels *et al*.: Chapter 21; Pukkila *et al*.: Chapter 22). However, this work can only fulfil its promise if it is firmly associated with particular metabolic steps which have particular morphogenetic consequences. We need a better and broader picture of the metabolism and biochemistry of developing structures and comparative details are essential. This means not only comparison between different species (so that, hopefully, causal events can be recognised among the complex of metabolic reactions) but also comparisons between tissues of the same structure. Far too often fruit bodies and other structures are dealt with as though they are homogeneous; they are not homogeneous and the value of data obtained is often considerably reduced if this fact is ignored.

There is another aspect of molecular analysis which deserves to be stressed. This is the use of restriction fragment length polymorphisms (which are naturally occurring polymorphisms in the

DNA) as genetic markers. Their use as such was first suggested as an aid in construction of the human linkage map (Botstein *et al*., 1980) and very recently some successful associations have been made between such molecular markers and particular human genetic disorders. The arguments which make this approach attractive as a means of studying human genetics also apply to the study of those basidiomycetes in which classic genetic approaches cannot be used very easily. This group includes the most important cultivated species, *Agaricus bisporus*. Casselton & Economou (Chapter 8) illustrate the use of mitochondrial DNA polymorphisms to monitor recombination between mitochondrial genomes, and Pukkila *et al*. (Chapter 22) demonstrate the segregation in spore tetrads of nuclear polymorphisms in ribosomal DNA sequences. Both of these studies used *Coprinus cinereus* which is an ideal organism for all types of experimental genetics. As pointed out by Raper (Chapter 23), *A. bisporus* has biological characteristics which make it an unsuitable candidate for even the simplest genetic exercise. However, DNA polymorphisms seem to be sufficiently common for one to expect to be able to recognise them fairly readily among the numerous strains of *A. bisporus* which are available. Such polymorphisms are attractive because they are natural deviations in genome structure that characterise specific genetic loci. Once the appropriate target sequence has been cloned, these molecular polymorphisms can be easily identified. They could be of immediate use in establishing the nuclear constitution of putative 'hybrid' heterokaryons, and in monitoring gene segregations in this two-spored, secondarily homothallic species. In the longer term, DNA molecular markers could also be associated with specific characters of importance to the value of this commercial crop; and since they can be scored in genomic DNA prepared from small samples of the mycelium they could offer a distinct advantage over larger scale fruiting trials which are otherwise necessary to score crop characters (Chapter 23). Thus as well as the intrinsic interest of this sort of study there could be genuine commercial advantage in moving in this direction.

Cell inflation

There are two types of cell inflation: a slow process which is often encountered in primordia, and a more rapid one involved especially in stipe and cap maturation. Strong inflation must represent a kind of differentiation of the cell and a mark of specialisation. The narrow generative hyphae, i.e. the basic tissue of the primordium, never have inflated cells. Large cells occur principally in fleshy fungi and are characteristic for Agaricales, Clavariaceae and some gasteromycetes; primordia of the most specialised genera of the Agaricales, e.g. *Mycena*, *Coprinus*, *Conocybe*, *Bolbitius* and *Pluteus*, have remarkably inflated cells even at very young stages. The elongation of the cells in primordia of Agaricales starts in general immediately after their formation. Motta (1969) makes the same observation for the rhizomorphs of *Armillaria*. Reijnders (1963) relates this early inflation to the general shape of the primordium; the different zones of the primordium enlarge proportionally; they do not impede the growth of other parts, and compressed tissues are seldom observed. Besides this continuous and slow inflation, whose morphogenetic control must be a complicated mechanism, the period of rapid expansion has attracted much more attention from as early as 1842 (Schmitz), through the work of Bonner, Kane & Levey (1956) and on to work such as that of Gooday (Chapter 12). This phenomenon has its parallels in higher plants. Modern research has examined the role of inflation in some selected species (Gooday, 1974, 1982, and Moore *et al*., 1979, on *Coprinus cinereus*; Bret, 1977, on *C. congregatus*; Wong & Gruen, 1977, on *Flammulina*; Craig, Gull & Wood, 1977, on *Agaricus bisporus*). We now know a lot more about these processes in the fruit bodies of these particular species. Wong & Gruen (1977) produced data accounting for the distribution of inflation over the whole stipe and for the correlation between length of stipe cells and that of the whole stipe. Other studies have focused on cell wall changes (especially chitin deposition) and osmotic agents. Although the subject is complicated the analyses done so far are promising and should be continued and expanded. We stress the need for further comparative studies and we draw attention once more to the heteromerous trama of the Russulaceae, to the specific trama (lateral branches, etc.) of the Amanitaceae; and to the fact that comparative studies of inflation would probably be of taxonomic interest.

The basal plectenchyma

The lowest part of the youngest agaric fruit body primordium is already made up of an entangled mass of cells; in older specimens this tissue often has an almost **pseudoparenchymatous** character. It represents an autonomous organ as it does not, in fact, belong to the stipe proper. It is not present at the inception of the primordium, when the lattice of ramifying hyphae is formed by mycelial threads (Matthews & Niederpruem, 1972), but it is one of the first parts which is subjected to differentiation. It is characterised by adjacent coils which are almost always present; these have in the centre short elements: cells whose ramifications deliver the elements for an extending **plectenchyma**. Corner (1950) depicted this interwoven tissue several times at the foot of clavarioid fungi, so that it appears that this phenomenon is widespread. Interwoven tissue has been found several times in the basal portion of poroid Aphyllophorales, but here no inflation occurred. The large deposits of polysaccharide which have been demonstrated in the lower part of the fruit body of *Coprinus cinereus* by Matthews & Niederpruem (1972) and Moore *et al*. (1979) are probably stored in this basal plectenchyma and not in the stipe itself (which is generally composed of parallel hyphae). Closer examination of these deposits reveals the fact that differentiation in this region is quite extensive, the polysaccharide accumulations being localised in a cup-shaped structure at the stipe base.

During development of the *Coprinus* fruit body, glycogen is first accumulated in this structure in the stipe base. Subsequently, glycogen levels decline in the stipe and glycogen is accumulated in the hymenium or subhymenium (Moore *et al*., 1979). The implication is that translocation occurs and the basal organ in which the glycogen is initially accumulated is involved. Metabolism to glucose or trehalose just for translocation appears pointless though it is not demanding energetically, but better experimental approaches remain to be examined. Nutrient translocation in general, both towards and within the fruit body (and discrimination of which initials will be allowed to develop), are further aspects of this same problem. One can ask how translocation is organised on a number of levels, but a fundamental question is the organisation at the metabolic level. Unless we do know the metabolism involved we have no hope of getting to grips with the molecular mechanisms.

When this basal plectenchyma acquires a larger extension we call it a bulb. Reijnders (1977) could show that the general features of the tissue in such bulbs are the same as in the basal plectenchyma. Still more conspicuous are protocarpic tubers which sometimes resemble sclerotia or pseudosclerotia and are sometimes described as such. They can rest for a long time but are able to produce normal fruit bodies (the stone fungus, *Pietra fungaja*). Besides these normal bulbous formations there exist what Singer (1975) has called ‘carpophoroids’, bodies arising from ‘a primordium which, when maturing, fails to ever achieve the last agaricoid stage of its individual development after it has reached the endocarpous stage or before it forms an exposed hymenium’. They consist of sterile hyphal tissue similar to that of the normal fruit body but are either entirely sterile or with noticeably reduced fertility, and without visible function. Singer discusses at length these various modifications of probably homologous structures. Reijnders (1977) had the opportunity to examine similar formations of a mutant of *Agaricus bisporus* isolated by Fritsche & von Sengbusch (1963): their histological composition was equal to that of the primordial bulb, except for the specific cortex. The supposed homology of all these formations can probably be better established by physiological and genetic data than by histological observations. Vegetative and fertile structures have much in common in cellular terms, but we need to investigate their relationships at a much deeper level than this. In *Coprinus cinereus* there is genetic evidence to show that sclerotia and fruit bodies share the same initiation pathway (Moore, 1981). Information like this is of both phylogenetic and ontogenetic value.

Conclusions

There is a finite number of ways of modifying the structure of a hyphal cell during differentiation, but there may be an infinite number of ways in which those differentiated cells can be assembled

into different structures. We are led to the conclusion that in the normal fruit body of an agaric, some genes are operative which account for a gasteromycetous bulb-like body and others regulate the formation and expansion of the normal 'mushroom' type of fruit body. It may be supposed that these genes are present in all species of Agaricales (they all have a basal plectenchyma) and that a normal development depends on the sequence of gene activity, which in some cases may be blocked by internal (mutational or regulatory) or external (environmental) factors. As every agaric can produce gasteromycete-like forms by the presence of the relevant genes (referring here only to the gross morphology) it cannot be reasonable to use these relations on behalf of phylogenetic speculations (derivation of Agaricales from gasteromycetes or *vice versa*), though we do not wish to pretend that every speculation on this problem is pointless. This conclusion that caution is required is corroborated by certain anomalies in Agaricales (Watling, 1971) which must be caused by disorder of genome activity. These anomalies are quite interesting, for the mycelium of a mutant of *Psilocybe* produces gasteromycete-like bulbs as well as specimens with a cyphelloid habit, where growth and elongation of the hyphae is not inhibited and development is of the diffuse type (Reijnders, 1983).

We have to acknowledge that mushrooms are commercially very important, and we must accept that scientists must often do research for which they can get funding. The message is that there is much interesting research still to be done on the crop species and their relatives. Another message is that the mushroom industry invests far too little of its profits in scientific improvements of the crop. Mushroom producers are interested in controlling fruit body initiation (so that they can determine the synchrony of the crop production process) and in fruit body maturation (again to enable control of cropping, but also to control shelf life of the crop). In both of these processes much fundamental research remains to be done.

We do not want to imply that the work that needs to be done is all 'molecular', exciting and timely though this research may be. Knowledge of the details of histology and biochemistry in many species is essential before we can even make guesses about the ways tissue patterns are established and controlled. Such knowledge will reveal the potential routes for control signals and the identities of regulatory compounds, and can also suggest appropriate regulatory strategies. There is plenty of scope for research of this sort and we look forward to seeing its results.

Neither would we want to imply that only the fruit body is of interest. There are a number of vegetative structures which contribute to the biology of basidiomycetes and have intrinsic interest in themselves, and which are suited to particular research interests. Naturally, we would claim that a part of their description is an account of their relationship to the fruit body. But really, all structures, whether sexual or vegetative, impose similar developmental requirements on the hyphae of which they are composed; so knowledge of one is bound to improve knowledge of the others.

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