CHAPTER

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Moulding moulds into mushrooms: shape and form in the higher fungi

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CONTENTS

Abstract

The classification of, and the understanding of relationships between, the larger fungi has been strangled by the rigid adoption in the early part of the 19th century of a system of identification based totally on the appearance of the mature fruit body – viz. the end-product of a multitude of changes of shape and form. It was almost 100 years later before microscopic characters were seriously employed for identification. Out of this sprang the appreciation that all was not well and that these microscopic structures could act as stronger markers of relatedness. Examples of these natural constructions will be given with emphasis on caution not to abandon completely all gross morphology. The classification of most organisms has a degree of developmental study in-built and although studies took place as early as the last decade of the 19th century, the importance of the understanding of the development of the fruit body is only now really percolating into our thoughts. Indeed, revealing studies are still under way. Not surprisingly, these are beginning to suggest that development of

fungal structures depends upon the exercise of relatively simple sets of 'rules' which seem to be organized into 'programming routines' governing the distribution and pattern of cell differentiation in space and time. What distinguishes developmental pathways which lead to grossly different end-product morphologies may be the temporal order of the routines and the spatial position of tissues in which particular routines are invoked. Some of the rules and some of the routines can be identified experimentally.

INTRODUCTION

It is often necessary to remind people that fungi are not plants. There are still a great many people whose education was completed before the revolution in systematics in the mid-1960s and who are firmly convinced that fungi are plants – peculiar plants, perhaps, but plants nevertheless. This notion, of course, is completely wrong. Plants, animals and fungi are now seen to be three quite distinct kingdoms of eukaryotic organisms (Cavalier-Smith, 1981; Margulis, 1974; Whittaker, 1969). This is a systematic arrangement but it is reflected in current ideas about the early evolution of eukaryotes in all of which the major kingdoms are thought to have separated at some protistan level. If this was really the case then plants, animals and fungi became distinct long before the multicellular grade of organization was established in any of them.

The three kingdoms differ from one another in ways that are crucial to determining shape and form. A major aspect of the original definition of the kingdoms (Whittaker, 1969) was nutrition (plants use radiant energy, animals engulf, fungi absorb), and this apparently simple base for separation embraces numerous other correlated differences in structure and life-style strategy that can be catalogued. Once the separation into three distinct eukaryotic kingdoms has been made, though, other non-correlated differences emerge and among these is the way in which multicellular architectures can be organized. A key feature during the embryology of even lower animals is the movement of cells and cell populations, so cell migration (and everything that controls it) plays a central role in animal morphogenesis. Being encased in walls, plant cells have little scope for movement and their changes in shape and form are accommodated by control of the orientation and position of the mitotic division spindle and, consequently, the orientation and position of the daughter cell wall which forms at the spindle equator. Fungi are also encased in walls; but their basic structural unit, the hypha, has two peculiarities which mean that fungal morphogenesis must be totally different from plant morphogenesis. These are that hyphae grow only at their tip and that cross-walls form only at right angles to the long axis of the hypha. The consequence is that fungal morphogenesis depends on the placement of hyphal branches. To proliferate, a hypha must branch; and to form a structure, the position at which the branch emerges and its direction of growth must be controlled.

If it is right that the evolutionary separation between the major kingdoms occurred at a stage before the multicellular grade of organization, then these kingdoms evolved, independently, the mechanisms to organize populations of cells. The fungal hypha differs in so many important respects from animal and plant cells that significant differences in the way cells interact in the construction of organized tissues must be expected. However, comparison can reveal common strategies and conserved pathways as well as alternative approaches, providing insight into the response of very different living organisms to the need to solve the same sorts of morphogenetic con-

trol problems. For the mycologist, parallels between fungi and other eukaryotes are worth seeking out so that the conceptual framework that has already been established, in embryology for example, as well as in cell and evolutionary biology, may be used. Rather than repeating past mistakes, lessons should be learned from them.

FUNGAL NAMES

In the study of fungi it has often been claimed that there are not enough characters to attempt a meaningful classification. It is true that the vast array of features offered to the flowering plant specialist are lacking, but careful attention to detail does allow the identification of meaningful traits. It is also true that the microscopic study of larger fungi has lagged behind that of the moulds and similar growths, under the misconception that macroscopic characters were sufficient. Amateur naturalists, and many professionals too, have tended to leave the larger fungi to one side as though everything was settled and even when they have taken them up, workers wax lyrical over such features as the pileus surface, the smell and the taste, so that identification and everything that flows from it becomes almost mystical. These characters, however, are only the final expressions of the truly basic features – the developmental patterns and biochemical pathways that characterize the species.

Perhaps matters were not helped by the 'Father of Mycology', Elias Fries, and his contemporaries all of whom had excellent observational powers and feel for the organism, but in the absence of a concept of evolutionary convergence, shape took an overemphasized part in the understanding of mushrooms and toadstools and their relatives. This fundamental mistake is still apparent.

Fayod (1889) used the microscope to study agaric structures and from his results suggested relationships, but it was not until Patouillard (1900) and his contemporaries that the microscope became a regular tool in identification and classification. Perhaps the necessity of the microscope in identification today has driven the sytem the other way and critical field observations are now less frequently made. It is relevant, however, that the use of scanning and transmission electron microscopes have assisted in the unravelling of many problems.

In very few plants or animals has shape been such a dominant factor in driving 20th century classification. Botanists and zoologists are used to dealing with notions of homology, analogy, neoteny and the like, resolving their differences by application of detailed developmental, structural and anatomical studies. This is not so in many areas of mycology where there is little critical study of anatomy and little consideration of development.

Fries (1821) developed a classification based on the earlier work of Persoon (1801) which was primarily an arrangement founded on the shape and form of the spore-producing tissue, the hymenium, and on the hymenophore, the structure on which the hymenium was borne. Thus, agarics with plates (i.e. gills) beneath an umbrella-shaped pileus, as in the ordinary cultivated mushroom, were brought together in a single group irrespective of spore colour, tissue texture and general aspect (facies). They were contrasted with those fungi that had tubes in a spongy layer beneath the pileus (boletes and bracket fungi) and those with teeth or spines hanging down below (hydnoids). Both of the last groups included taxa which lacked a pileus and were formed as a sheet of fertile tissue on the substrate (resupinate forms). Other major

groups included those that bore spores externally on a club-shaped (clavarioid) or coral-like (coralloid) structure and those in which they were borne internally (gasteroid) – a group which was to be expanded many-fold as specimens were sent back for identification from the colonies newly conquered by the European nations.

Although groups such as the boletes with fleshy, putrescent, tube-bearing fruit bodies (basidiomes), but otherwise quite like the mushroom, were separated on morphology alone, it was Fayod's (1889) studies on development and anatomy that forced the realization that the Friesian groupings were artificial. Unfortunately, his observations made no impact on the mycological community until over 40 years later when Roger Heim reintroduced the modern audience to these studies (Heim, 1931), quickly followed and expanded subsequently by Rolf Singer (1936, 1951 *et subseq.*). At the end of the 19th century Fayod's studies were almost heretical and the Friesian classification held sway; indeed it was quite a shock when the conservative British mycologist was exposed by Carleton Rea (1922) not to the traditional approach but the new ideas. This work followed, in part, that of Patouillard (1900) where relationships and groupings not considered before were expressed. The close relationship between some small cup-shaped basidiomycetes and agarics was proposed, the joining together in a single grouping of large woody bracket fungi with those of resupinate structure, etc. In fact this was a preview to the separation of white wood rotters and brown wood rotters, and other similar ecological groupings. At last, after 100 years of stagnation, during which superficial characters were the basis of a classification, the marrying of anatomical and developmental information came about, and when later correlated with chemical data produced suites of characters which led to radical rearrangements. It was not that the early mycologists had not recognized these natural groupings, but rather that they did not have the resources available to them (technical and conceptual) which made the rearrangements possible.

THE SIGNIFICANCE OF THE STRUCTURE OF TISSUES

Taking the structure of the flesh of the basidiome first: it can be shown quite easily that, although the naive view might be that this is fundamentally homogeneous, it differs in detail from one group of larger fungi to another. Fayod (1889) clearly demonstrated this for different groups of agarics; the approach was followed for the bracket fungi (Corner, 1932a,b, 1953; Cunningham, 1965), clavarioid fungi (Corner, 1950) and hydnaceous fungi (Maas Geesteranus, 1971, 1975).

The function of the basidiome is to produce as many basidiospores as the structure will allow, and the structure can be expanded in many ways to give optimum spore production. Thus, in the Russulales this is achieved by columns and rosettes of hyphae expanding in an orchestrated way (Reijnders, 1976), whereas other agarics have simple, gradually elongating and inflating hyphae, accompanied in *Coprinus* by narrow elements (Hammad *et al.*, 1993) which resemble the inducer hyphae in *Russula* and *Lactarius* (Reijnders, 1976; Watling & Nicoll, 1980). In Amanitaceae the formation of the gills is schizohymenial and so differs from other families in the character, but it is correlated with what is called an acrophysalidic tissue (Bas, 1969) by which flesh hyphae through massive inflation of individual cells allow the fruit body to expand. In some members of the Tricholomataceae a further modification is found leading to a two-component flesh termed sarcodimitic (Corner, 1966, 1991); Redhead (1987)

believes this is such a fundamental method of basidiome expansion that he has adopted the family Xerulaceae for agarics exhibiting the character.

Bracket fungi achieve massive spore production by increasing the longevity of the basidiome either over several months, as in *Polyporus*, or as a perennial fruit body with resurgence of growth at regular intervals (e.g. *Fomes*). Examination of such flesh reveals an intricate pattern of hyphae which may branch profusely to bind adjacent hyphae together or elongate, thicken and lose their living contents to form strong tubes which then act as structural members in much the same manner as the units in tubular furniture. These hyphae increase in number as the basidiome grows. The major group exhibiting this type of hyphal construction possess woody fruitbodies and a poroid hymenium (polypores), but it can be found in a rudimentary form in some fungi with gills, e.g. *Lentinus*. It is now considered that *Lentinus* is more closely related to the polypores than to the other agarics. In some taxa it may be a complex of two or three hyphal types, viz. dimitic or trimitic. The presence or absence of such mixtures of hyphae agrees with other characters used in the classification of the polyporaceous taxa (Ryvarden, 1992). In general, this approach can be applied to the clavarioid fungi and to the resupinates, both groups of which can then be shown to be heterogeneous groups with some members now considered more advanced than others.

Fayod (1889) also showed that in the homoiomerous agarics (trama composed only of hyphal tissue) the flesh between the hymenial surfaces might be one of four kinds, and although this has had to be modified as more agarics have been examined, the basic idea holds true, viz. that in mature specimens, bilateral (divergent), convergent, regular and irregular patterns of hyphal arrangement can be demonstrated. In each case they correlate with other characters and together are used to define families, a taxonomic rank that appeared late in agaricology. Just as the structure of the flesh is reflected by demonstrable field characters, so can the gill tramal types be recognized.

By careful observation of developing basidiomes, it hs been found, particularly by the critical work of Reijnders (1948; 1963), that there are at least ten different ways by which the familiar mushroom shape can be formed, a shape which is excellently designed to give protection to the developing hymenia in exposed environments (Fig. 1). These vary from those with naked development (Fig. 1A), which includes the majority of the bracket fungi developing from a concentration of tightly bound hyphae forming a rounded structure known to foresters as a 'conk', to those with a complete enclosing tissue (Fig. 1J), or enclosing membrane or membranes which only break before maturity (Fig. 1B–1I). The exciting thing is that the type of development complies with the proposed classification based on other features. Thus, the boletes, with their hymenium exposed at all times during development (gymnocarpic, Fig. 1A) are considered to be close to the Paxillaceae where the pileus gives protection by being pressed against the stipe surface and enclosing the hymenium (pilangiocarpic, Fig. 1G), and Gomphidiaceae, where hyphae from an initially naked primordium envelop the developing hymenium (metavelangiocarpic, Fig. 1E). In addition to this developmental connection there are similarities in morphology of the basidiome, basidiospore structure and chemistry.

The veils which form in the agarics (Fig. 1B–1E) are considered to be protective, allowing the hymenia to develop in a rather well-defined environment. The shape of the gills is strongly tied to the constraints of this environment within the developing basidiome, and has led to the use in identification of a traditional feature, gill attach-
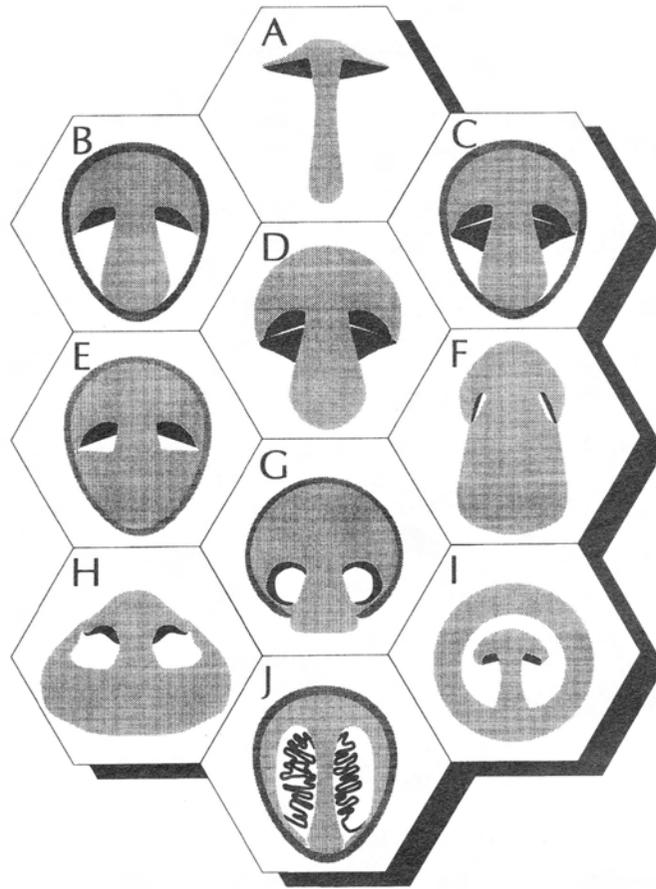
Figure 1 Ten ways to make a mushroom. A montage of diagrammatic sections illustrating the various primordial tissue patterns that eventually mature to form mushroom-like basidiomata; hymenial tissues are shown in black. **A** gymnocarpic, where the hymenium is naked at first appearance and develops to maturity on the fruitbody surface; **B** monovelangiocarpic, with a single (universal) veil enveloping the whole primordium; **C** bivelangiocarpic, in which an inner (partial) veil provides additional protection to the hymenium; **D** paravelangiocarpic, where the veil is reduced and often lost at maturity; **E** metavelangiocarpic, where a union of secondary tissues emerging from the pileus and/or stipe forms an analogue of the universal veil; **F** gymnovelangiocarpic, in which the hymenium is protected by a very reduced veil, seen only at adolescence, formed between the stipe and the closely applied pileus; **G** pilangiocarpic, the hymenium is protected by tissue extending downwards from the margin of the pileus; **H** stipitoangiocarpic, the hymenium is protected by tissue extending upwards from the stipe base, but this does not enclose the primordium; **I** bulbangiocarpic, where the tissue protecting the hymenium is largely derived from the basal bulb of the stipe and initially completely encloses the primordium; **J** endocarpic, where the mature hymenium is enclosed or covered over, just one (the pileate type) of a number of patterns of this gasteromycetous form of fruit body is shown.

ment to the stipe apex. At least eight different types of attachment have been used and they are now being analysed (Pöder, 1990).

There is a large group of fungi which have their basidiospores enclosed in the basidiome, even to maturity (Fig. 1J). They are called the 'gastromycetes', although

many of their members do not really follow the original definition. They include puffballs, earth-stars, earth-balls, all 'reduced' to an epigeous or hypogeous sack of spores. In addition, the stink horns are included and these parallel the agarics in gross morphology. It is true that their basidia are stigmatosporic, but the hymenium is designed for insect dispersal as opposed to wind dispersal. Shape and form in this group is highly specialized, and is similar to what may be seen in the colours, bizarre shapes and penetrating smells of insect-attracting flowering plants.

The basidiomycetous hypogeous fungi, as with their ascomycete cousins the truffles, are attractive to animals, often having a distinctive odour which in some taxa resembles the male pheromone of pigs. Many quite unrelated groups have developed hypogeous taxa, which retain the internal form of the ancestor although looking alike from outside, something that the mycological pioneers did not appreciate. This same range of ancestral types is seen in the secotioid fruitbody which resembles a large drumstick. In addition, however, forceful or passive spore dispersal may be found in the species, linking them to their equivalent agaric relative. Thus, instead of a single family (Secotiaceae) there are now up to 20 groupings. These are clearly derived groups and should simply be placed in classification with their undoubted mushroom relatives, although some authorities would argue otherwise (see Singer, 1958, 1986) (Table 1).

Although this paper concentrates on basidiomycetes, it should be emphasized that a similar approach is being applied to the classification of the ascomycetes. The old groups, pyrenomycetes and discomycetes, originally based on the shape of the fruiting body, are now being split in more natural ways; the lichens are being included in their respective groups within the system; the cleistothecium is now dispersed in many families, e.g. Erysiphaceae, Eurotiaceae, Sordariaceae even Ascobolaceae (as *Seliniella* which is really *Ascobolus immersus* (von Arx & Müller, 1955; van Brummelen, 1967)). The yeasts pose rather different questions although they too are no longer classified together simply because they are single-celled. It is clear that yeasts have evolved in several groups, especially amongst the jelly fungi where they may play a part in the life-cycle or may replace the filamentous stage completely.

Amongst the basidiomycetes, there has been some tinkering with the classification and some major alterations have been made, but in the main Fries' classification has stood up well to scrutiny, especially as he did not have the benefit of information on the thousands of taxa throughout the world which is now available. What would Fries have thought of a *Russula* with a ring, as some species have in Africa and South and Central America? Although the facies is dissimilar, at least the heteromerous trama, amyloid basidiospores and presence of macrocystidia show their true relationships. Suites of characters are the key to natural classification and the fungi are no exception. The production of purplish brown or dull pigments, flesh greening in aqueous solutions of ferrous sulphate, with basidiospores which exhibit blunt spines, warts or angled facets are considered fundamental to the delimitation of the Thelephorales, thus bringing together species with teeth (*Hydnellum*), with pores (*Boletopsis*), clavarioid (*Thelephora*), and resupinates (*Tomentella*); i.e. irrespective of the final shape of the basidiome (Table 2). Parallels can be seen in other groups (e.g. Hymenochaetales). Cultural studies have helped to support this, bringing together fungi that were formerly thought dissimilar. The suite of characters including prominent latex channels (lactiferous hyphae ending in macrocystidia on the pileus and stipe surfaces and in the hymenium) has demonstrated a relationship between

Table 1 The Boletales and Russulales illustrate the broad range of hymenophore configurations which members of an order can span; they also have gasteroid relatives – a feature found throughout the agarics

| | Hymenogastrales | | |
	Secotiaceae	Hymenogastraceae and Rhizopogonaceae	Additional hymenophore configurations
Traditional taxa			
Boletales, predominantly form poroid hymenophore			
Hygrophoropsidaceae			Agaricoid
Gyrodontaceae			Agaricoid (?)
Meiorganaceae			Agaricoid
Gomphidiaceae			
Chroogomphus	*Brauniellula*		
Gomphidius	*Gomphogaster*		
Paxillaceae			
Paxillus	*Austrogaster*		Agaricoid
Boletaceae			
Boletus			
Suillus	*Gastroboletus*		
Leccinum			
Phylloporus	*Paxillogaster* *Gymnopaxillus*		
Chamonixiaceae			
Gyroporus?		*Chamonixia*	
Boletellaceae			Agaricoid
Strobilomycetaceae			
Coniophoraceae			Cantharelloid/hydnoid/merulioid, resupinate
Rhizopogonaceae		*Rhizopogon*	
Corneromycetaceae			Cantharelloid/hydnoid/merulioid, resupinate
Russulales, called the Astrogastraceous series, predominantly with gilled hymenophore			
Russulaceae			
Lactarius	*Arcangeliella*		Agaricoid and poroid
Russula	*Macowanites*		Agaricoid
Elasmomycetaceae	*Elasmomyces*	*Zelleromyces* *Gymnomyces* *Martellia*	

Taxa according to Julich (1981).

Lentinellus and *Clavicorona* made even closer by *Clavicorona* fruiting bodies being formed in cultures of *Lentinellus* (Miller & Stewart, 1971) and species of *Clavicorona* being described as new taxa but in reality being immature *Lentinellus* (Maas Geesteranus, 1971) – parallels to *Seliniella*.

Much still has to be done in the study of the development of the basidiome, and the relationship between pileus, stipe and hymenium. This requires cellular and bio-

Table 2 Comparison of the Ganodermatales, an order with only poroid basidiomes, and the Thelephorales and Hymenochaetales, which each show a wide spectrum of hymenophore configurations (indicated by the extent of the horizontal bars)

Modern orders and families	**Traditional families**							
	Clavariaceae	Thelephoraceae	Cantharellaceae	Hydnaceae	Polyporaceae			Agaricaceae
Hymenophore configuration	Club- to coral-shaped	Smooth to wrinkled	Ridged and veined	Toothed	Tubes resupinate	Tubes Annual Non-resupinate	Tubes Perennial Non-resupinate	Gilled
					Annual or perennial (*Poria*) Poroid	(*Polyporus*) Poroid	(*Fomes*) Poroid	
	Clavarioid	Thelephoroid	Cantharelloid	Hydnoid	Poroid	Poroid	Poroid	Agaricoid
Thelephorales	■	■	■	■		■		■
Thelephoraceae		■						
Lenzitopsidaceae						■		
Bankeraceae				■				
Boletopsidaceae						■		
Verrucosporaceae*								■
Hymenochaetales		■			■		■	
Clavariachaetaceae	■							
Hymenochaetaceae		■						
Coltriciaceae					■			
Phellinaceae					■		■	
Ganodermatales							■	
Ganodermataceae							■	
Haddowiaceae							■	

*There is some doubt that *Verrucospora*, the sole representative, belongs to this order. Taxa according to Julich (1981).

chemical analysis, although Reijnders (1963) has provided a terminology on which such studies can be based. Further studies on the structure of selected components of the hymenia are required. The development and role of brachycystidia (paraphyses) and the cystesium–cystidium combinations have been studied in *Coprinus* (see later); Price (1973) has examined cystidial development in agarics from a purely morphological point of view, as have Eriksson *et al.* (1978) in *Peniophora sect. Peniophora.*

With the plasticity in form of the basidiomycete fruitbody, variation in response to environmental change might be expected, and is indeed found; Bondartsev (1963) was the first to offer a cautionary note to taxonomists for placing too much emphasis on a single character. The taxonomist should not be carried away with the narrow focus of single approaches. Neither microscopic nor macroscopic characters are sufficient alone, each must be measured by its merits. The recent synthesis of fruitbody structures by Reijnders & Stalpers (1992) is a baseline from which to work.

The same range of hymenophoral configurations have now been accepted amongst the distantly related hymenomycetous Heterobasidiae, viz. *Tremella* and *Auricularia* and their allies, with little consternation. Thus the poroid hymenium is found in *Aporium*, hydnoid in *Pseudohydnum*, coralloid in *Tremellodendron*, cupuloid in *Auricularia* and resupinate in *Sebacina*. Even gasteroid heterobasidiae are now known.

VARIATION IN SHAPE AND FORM

Clearly, fungal systematists are now appreciating that fruitbody shape and form should not hold the central position it once did. This is a conceptual point – it is a matter of interpretation of the value of particular features in establishing relationships between a group of fungi, and the belief is growing that fruitbody form is less useful because it is a more flexible feature than has previously been considered. Surprisingly, in biological terms, fruitbody shape and form seems to be equally flexible. From this point this chapter will focus on this variation in fruitbody shape and form. An interpretation of shape and form will be promoted which could have an impact on the understanding of development, evolution and systematics.

The first issue to be addressed is that variation in shape and form occurs at different levels and for different reasons. There is variation (more properly called plasticity) in the shape and form of fruitbodies produced by a particular strain which can be demonstrated by *in vitro* culture; there is variation between collections of what might, on other grounds, be judged the same species; and there is variation at the supraspecific level. It is with the last two categories that taxonomists must be most concerned, but the first category can yield the most valuable information.

Many morphological mutants or variants have been induced or isolated from nature, especially in *Coprinus cinereus* (Schaeff.: Fr.) S.F. Gray and *Schizophyllum commune* Fr. (Kanda & Ishikawa, 1986; Raper & Krongelb, 1958; Takemaru & Kamada, 1972). Such mutants can be instructive in establishing development pathways (Esser *et al.*, 1977; Moore, 1981) and allowing detailed study of particular phenotypes (Kamada & Takemaru, 1977a,b; Kanada *et al.*, 1990; Kanda *et al.*, 1989). Here, more stress will be placed on epigenetic plasticity: instances where, for some reason, the development of a normal genotype is disturbed, but without change to that genotype.

Plasticity in fruiting morphogenesis may be a strategy for adaptation to environmen-

tal stress. The 'rose-comb' disease of the cultivated mushroom, *Agaricus bisporus* (Lange) Imbach (syn. *A. brunnescens* Peck.), in which convoluted growths of hymenium develop over the outer surface of the pileus, seems to be caused by mineral oil fumes in mushroom farms (Flegg, 1983; Flegg & Wood, 1985; Lambert, 1930). Viral infections have been involved in some instances, e.g. in *Laccaria*, *Armillaria* and *Inocybe* (Blattny *et al.*, 1971, 1973), and fungal attack in others. For example, Buller (1922) showed that gill-less fruitbodies of *Lactarius piperatus* (L.:Fr.) S.F. Gray were caused by parasitism by *Hypomyces lactifluorum* (Schw.) Tul. and Watling (1974) showed that primordia of *Entoloma abortivum* (Sprague: Donk) can be converted to a puff-ball structure by interaction with *Armillaria mellea* (Vahl.: Fr.) Kummer.

This sort of fruitbody polymorphism, or developmental plasticity, has been reported in various fungal species (Buller, 1922, 1924; Keyworth, 1942; Singer, 1975), but thorough studies have only been made on *Psilocybe merdaria* (Fr.) Ricken (Reijnders, 1977; Watling, 1971), *Agaricus bisporus* (Atkins, 1950; Flegg & Wood, 1985; Reijnders, 1977; Worsdell, 1915) and *Volvariella bombycina* (Schaeff.: Fr.) Singer (Chiu *et al.*, 1989). In *Agaricus bisporus* the developmental variants reported include: carpophoroids (sterile fruitbodies; Singer, 1975), forking (where a single stipe bears two or more pilei; Atkins, 1950; also called bichotomy by Worsdell, 1915), proliferation (additional secondary pilei arise from pileus tissues; Worsdell, 1915), fasciation (a bundle of conjoined basidiomes; Worsdell, 1915), and supernumerary hymenia (the basidiome has additional hymenia on the upper surface of the pileus; Langeron & Vanbreuseghem, 1965). All of these forms have also been observed in *Volvariella bombycina* (Chiu *et al.*, 1989) and in *Psilocybe merdaria* (Watling, 1971).

In addition, in both *V. bombycina* and *P. merdaria* other fruitbody forms, including morchelloid and gasteromycetoid fruitbodies, arose spontaneously alongside the normal agaric fruitbodies. Thus, an agaric fungus is able to produce both morchelloid (n.b., *Morchella* is an ascomycete) and gasteromycete-like fruitbodies alongside its normal fruitbodies. To put this into the context of an approximate animal counterpart, the parallel would be for cats to be able, quite normally, to give birth to litters containing the odd kitten looking like an aardvark, dolphin or even iguana. Obviously, this assumes that the taxonomic ranks are equivalent; not surprisingly, there is a great debate about taxonomic rankings in fungal systematics!

In *V. bombycina* these teratological forms arose spontaneously, in two different strains, and were found in cultures bearing normal fruitbodies, regardless of the composition of the substrate. Importantly, all hymenia in these forms were functional in the sense that they produced apparently normal basidiospores. The function of the plasticity in fruiting morphogenesis seems to be to maximize spore production and favour dispersal of spores even under environmental stress.

Fruiting is a complex polygenic process in these fungi (Leslie, 1983; Leslie & Leonard, 1984; Meinhardt & Esser, 1983; Prillinger & Six, 1983) further modulated by environmental factors (Leatham & Stahmann, 1987; Manachère, 1985; Manachère *et al.*, 1983; Raudaskoski & Salonen, 1984). There is some genetic evidence that different structures (specifically sclerotia and basidiomes) share a joint initiation pathway (Moore, 1981), and the common growth of basidiomes directly from sclerotia may also suggest morphogenetic similarities. Fruiting in haploid, primary homothallic species, such as *V. bombycina* and *V. volvacea* (Bull.: Fr.) Singer (Chang & Yau, 1971; Chiu & Chang, 1987; Royse *et al.*, 1987), and in homokaryons in heterothallic species

(Dickhardt, 1985; Elliott, 1985; Graham, 1985; Stahl & Esser, 1976; Uno & Ishikawa, 1971) shows that fruiting is independent of the sexual cycle regulated by the incompatibility system in heterothallic species (Kües & Casselton, 1992). It is against this sort of background that basidiome variants must be interpreted.

Transition of the agaric hymenial pattern to the morchelloid one, particularly the position of the hymenium on the upper surface of the pileus, have been suggested to be due to reversion or atavism to a fruitbody organization seen in ascomycetes (Worsdell, 1915). Similarly, the gasteromycetoid forms of *Volvariella bombycina* might, by the same logic, be taken to reflect some phylogenetic relationship with the so-called gasteromycete genus *Brauniella* which Singer (1955, 1963, 1975) has, on other grounds, suggested to be ancestral to some species of *Volvariella*. However, making phylogenetic points on the basis of morphological variants is inherently dangerous. In stressing the value of developmental features in taxonomic and evolutionary interpretations, there is the risk that history will be made to repeat itself and the old notion of ontogeny recapitulating phylogeny might be resurrected in some minds. The zoologists have battled through this stage in the development of evolutionary ideas; mycologists should strive to avoid it. In the first quarter of this century animal evolution was thought of as resulting mainly from modification of adult form and development was seen as a recapitulation of previous mature stages. This was encapsulated in 'the individual in its development recapitulates the development of the race' in MacBride's *Textbook of Embryology* (1914). Walter Garstang's views were diametrically opposed. He coined the term paedomorphosis which he summed up as 'Ontogeny does not recapitulate Phylogeny: it creates it.' He published his views in the usual way (e.g. Garstang, 1922) but most memorably, in verse (Garstang, 1962):

> MacBride was in his garden settling pedigrees,
> There came a baby Woodlouse and climbed upon his knees,
> And said: 'Sir, if our six legs have such an ancient air,
> Shall we be less ancestral when we've grown our mother's pair?'

A MATTER OF ROUTINE

Basidiome developmental variants can be used to comment on the ontogenetic programme. Because they are actually or potentially functional as basidiospore production and dispersal structures, they have been interpreted (Chiu *et al.*, 1989; Moore, 1988) as indicating that normal fruitbody development is comprised of a sequence of independent but coordinated morphogenetic subroutines, each of which can be activated or repressed as a complete entity. For example, there is a 'hymenium subroutine' which, in an agaric, is normally invoked to form the 'epidermal' layer of the hymenophore (gill lamella); but if it is invoked aberrantly and additionally to form the upper epidermis of the pileus, it forms, not a chaotic travesty of a hymenium, but a functional supernumerary hymenium. Similarly, the 'hymenophore subroutine' produces the classic agaric form when invoked on the lower surface of the pileus, but if wrongly invoked on the upper surface, it produces, not a tumorous growth, but a recognizable inverted cap. Thus, development of fungal structures in general is thought to depend upon organized execution of such subroutines; the sequence and location in which they are invoked determining the ontogeny and form of the

fruiting structure (Fig. 2). Invocation of these developmental subroutines may be logically equivalent to the 'mode switches' between different mycelial states discussed by Gregory (1984) and Rayner & Coates (1987). Some of the subroutines can be identified with specific structures, such as basal bulb, stipe, pileus, hymenophore, hymenium and veil, but others are rather subtle, affecting positional or mechanical morphogenetic features. One such might be a 'grow to enclose' capability, possibly associated primarily with the veil subroutine but perhaps expressed in the stipe base to generate pilangiocarpic basidiomes.

Essentially the same subroutines could give rise to morphologically very different forms, depending on other circumstances. For example, the agaric gill hymenophore subroutine seems to be expressed with the rule 'where there is space, make gill' (Chiu & Moore, 1990a,b). When this is combined with mechanical anchorages the contortions initially produced by this rule are removed as the gills are stretched along the lines of mechanical stress. Where such anchorages are absent the expansion forces are not communicated through the gills and the labyrinthine structure remains – as in morchelloid forms.

CELL FORM, FUNCTION AND LINEAGE

A cell described as a basidium is quite clearly characterized by karyogamy meiosis and the formation of basidiospores. In other words, application of the nomenclature involves consideration of the past and future behaviour of the cell. Usually, other descriptive terms, like basidiole, paraphysis, sterile element or cystidium, are applied on the basis of the immediate morphology and/or position of the cell without reference to its ontogeny or fate, yet these are important considerations. If the mechanisms of differentiation and morphogenesis are to be understood, the descriptions of developmental pathways must be precise. A tramal hyphal branch which becomes a
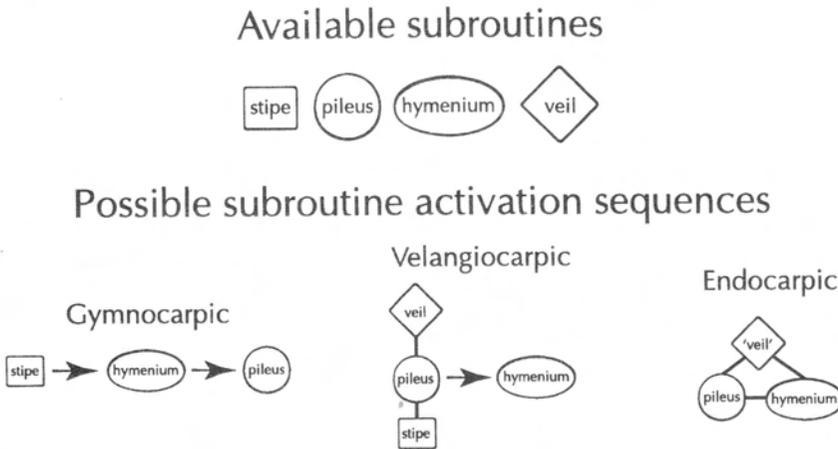

Figure 2 The notion of developmental subroutines illustrated in the form of abbreviated flow diagrams. It is envisaged that development is effectively segmentalized into specific subroutines (four are illustrated here, there are undoubtedly many more) and that different outcomes result from these subroutines being invoked in different sequences.

hymenial cell may be pluripotent initially, but it must follow one developmental pathway and the varied pathways of differentiation open to it involve commitment to expression of particular (probably different) sets of characters at different stages in morphogenesis so that the hymenium is furnished with cells that have appropriate functional characteristics.

Some cell lineages are unable to express morphologies developed by others. In the hymenium of *Agaricus* the 'epidermal pavement' which provides the structural support for basidia is made up of basidioles in an arrested meiotic state. Even after many days of existence, when the fruitbody was close to senescence, 30–70% of the basidioles were in meiotic prophase (Allen *et al.*, 1992). This is not wastage of reproductive potential but use of one differentiation pathway to serve two distinct but essential functions. *Coprinus* illustrates the other extreme in having a highly differentiated cell type, the paraphysis, with which to construct the epidermal pavement. These cells arise after the numerically static basidiole population commits to meiosis, branching from beneath the basidia and forcing their way into the hymenium (Rosin & Moore, 1985). At maturity, individual basidia are surrounded by about five paraphyses; thus, more than 80% of the hymenial cells in *Coprinus* serve a structural function. *Agaricus* and *Coprinus* hymenophore tissues reach essentially the same structural composition by radically different routes.

Some cell lineages reach the same final morphology through different routes. Both *C. cinereus* and *V. bombycina* have facial (pleuro-) and marginal (cheilo-) cystidia. Both types of cystidium in *V. bombycina* are established when the hymenium is first laid down on the folded gills and, apart from location, their differentiation states and ontogeny appear to be identical. Facial cystidia in *C. cinereus* are also established as components of the very first population of dikaryotic hyphal tips which form hymenial tissue (Horner & Moore, 1987; Rosin & Moore, 1985) and are mostly binucleate as a result. Marginal cystidia in *C. cinereus* are the apical cells of branches from the multinucleate gill trama, which become swollen to repair the injury caused when primary gills pull away from the stipe; marginal cystidia retain the multinucleate character of their parental hyphae (Chiu & Moore, 1993).

REGIONAL PATTERNS OF COMMITMENT

The distributions of cystidia and gills in *Coprinus cinereus* have been interpreted as being dependent on interplay between activating and inhibiting factors (Horner & Moore, 1987; Moore, 1988) in a pattern-forming process similar to the model developed by Meinhardt & Gierer (1974, and see Meinhardt, 1984). Successful application of this model to fungi as well as to plants and animals concentrates attention on the fact that the distribution of stomata on a leaf, bristles on an insect and cystidia on a fungal hymenium have a great deal in common at a fundamental mechanistic level. Other similarities emerge when a search for commitment is made.

The classic demonstration of commitment involves transplanting the cell into a new environment; if the transplanted cell continues the developmental pathway characteristic of its origin then it is said to have been committed before transplantation. On the other hand, if the transplanted cell embarks upon the pathway appropriate to its new environment then it was clearly not committed at the time of transplant. Most fungal tissues produce vegetative hyphae very rapidly when disturbed and 'trans-

planted' to a new 'environment' or medium. This is a regenerative phenomenon which creates the impression that fungal cells express little commitment to their state of differentiation. Very little formal transplantation experimentation has been reported with fungal multicellular structures. The clearest examples of commitment to a developmental pathway has been provided by Bastouill-Descollonges & Manachère (1984) and Chiu & Moore (1988) who demonstrated that basidia of isolated gills of *Coprinus congregatus* Bull.: Fr. and *C. cinereus*, respectively, continued development to spore production if removed to agar medium at early meiotic stages. Other hymenial cells, cystidia, paraphyses and tramal cells, immediately reverted to hyphal growth but this did not often happen to immature basidia. Evidently, basidia are specified irreversibly as meiocytes and they become determined to complete the sporulation programme during meiotic prophase I. Once initiated, the maturation of basidia is an autonomous, endotrophic process that is able to proceed *in vitro*. Clearly, then, even if only to a limited extent, commitment to a pathway of differentiation some time before realization of the differentiated phenotype can occur in these fungi. Although these experiments have been discussed mainly for their value in understanding commitment to the basidium differentiation pathway, it is equally important to stress that other cells of the hymenium showed no commitment; immediately reverting to hyphal growth on explantation as though they have an extremely tenuous grasp on their state of differentiation. That these cells do not default to hyphal growth *in situ* implies that their state of differentiation is somehow continually reinforced by some aspect of the environment of the tissue which they comprise.

FUZZY LOGIC

Discussion of differentiation in fungi often involves use of words like 'switch' in phrases that imply wholesale diversion at some stage between alternative developmental pathways. There are now many examples which suggest that fungal cells behave as though they assume a differentiation state even when all conditions for that state have not been met. Rather than rigidly following a prescribed sequence of steps, differentiation pathways for the sorts of fruitbodies discussed here appear to be based on application of rules that allow considerable latitude in expression; 'decisions' between developmental pathways seem to be made with a degree of uncertainty, as though they are based on probabilities rather than absolutes. For example, facial cystidia of *C. cinereus* are generally binucleate, reflecting their origin and the fact that they are sterile cells, yet occasional examples can be found of cystidia in which karyogamy has occurred (Chiu & Moore, 1993) or of cystidia bearing sterigmata. This suggests that entry to the cystidial pathway of differentiation does not totally preclude expression of at least part of the differentiation pathway characteristic of the basidium (Fig. 3). Equally, the fact that a large fraction of the basidiole population of *A. bisporus* remains in arrested meiosis (Allen *et al.*, 1992) indicates that entry to the meiotic division pathway does not guarantee sporulation. There are many other examples in the literature.

Potential contributions to differentiation
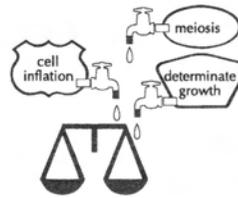
Potential pathways for differentiation

Basidium differentiation

Cystidium differentiation

Cystidium with basidial characters
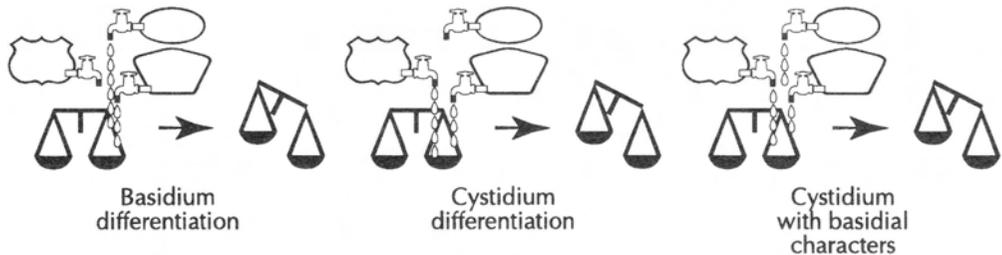
Figure 3 Cartoons illustrating the idea that fungal differentiation involves the cell reaching a state which can be sustained as being different from the vegetative hyphal compartment. The different characters which an undifferentiated cell might express are viewed as making contributions to a balance of differentiation. In most instances the normal state of differentiation results from a specific combination of these contributions. Occasionally, unexpected contributions leads to cells that are unmistakably of one sort, but are expressing characters of another sort. In the example illustrated in the bottom panel, cystidia with basidial characters would result, for example having sterigmata (observed by Watling, 1971) or undergoing karyogamy (Chiu & Moore, 1993).

CONCLUSIONS

The last 25 years have seen the final break away from the vice-like grip of the Friesian system of classification for larger fungi. By the use of developmental and anatomical characters correlated with chemical and microscopic features, natural groupings have been demonstrated. These, however, cut across the old guidelines which were based on the gross morphology of the end-product – be it mushroom, bracket fungus or puff-ball. Throughout, unifying ideas are now becoming evident, allowing worthwhile comparison with related phenomena in the plant and animal kingdoms. The careful examination of teratological forms provides insight into gross developmental patterns, allowing interpretation of developmental strategies. A marriage of information is required and overemphasis of the monstrosities themselves at the expense of using them to understand normal developmental pathways cannot be supported. At the cellular level, too, careful analysis reveals analogies with animal and plant development, giving evidence for varied levels of commitment, for regulation of distinct pathways of differentiation which differ in both time and space, and for pattern-forming processes which might be dependent upon morphogens. On the other hand, differ-

ences emerge from these analyses which suggest that analogy with animal and plant development should be limited. Fungal differentiation seems to be far less 'final' than is usually expected of animal and plant cells. Few fungal cells show complete commitment to a pathway of differentiation; except for the meiocytes, even the most highly adapted cells revert readily to the filamentous mode of growth. Also, fungal cells appear to be capable of expressing a state of differentiation even when all of the attributes of that state have not been attained. It seems that steps in fungal developmental pathways depend on balancing probabilities rather than all-or-none switches. These interpretations are important in suggesting the design of experiments but it is important that laboratory data and field observations are given equal weight.

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