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Fungi: a Place in Time and Space

The basic shape, form and structure of an organism (whether fungal, plant or animal) does not arise all at once. Rather, the shape and form emerge as a result of a sequence of developmental adjustments. Each of these is usually irreversible within its morphogenetic sequence although often reversible by some gross disturbance; for example, differentiated cells being put into tissue culture, nuclear and cell transplants, regeneration after injury, etc. The whole process in which the final organisation and pattern of the organism is established is termed 'morphogenesis'.

The most extensive research on the topic has been done with animals and from this a vocabulary has been established which describes morphogenetic events without pre-judging the mechanisms which may be involved (Slack, 1991). It is evident that as the embryonic organism develops towards adulthood, each intermediate state represents a reduction in developmental potential compared with the previous state. Each adjustment (or developmental 'decision') is made by cells already specified by earlier adjustments to belong to a particular developmental pathway. Consequently, developmental decisions are made from among progressively smaller numbers of alternatives until the particular structure to which the cell will contribute is finally determined. Classic embryological transplantation experiments revealed these states. Where the explant differentiated to a state representative of its old position then it was said to have been determined prior to transplantation. If it developed in accord with its new position, then it had not been determined, but may have been specified.

Within the developing tissues, cells embark on particular routes of differentiation in response to the playing out of their intrinsic genetic programme, in response to external physical signals (light, temperature, gravity, humidity), or in response to chemical signals from other regions of the developing structure. These chemicals may be termed organisers, inducers or morphogens, and seem to inhibit or stimulate entry to particular states of determination. Chemical signals may contribute to a *morphogenetic field* around a structure (cell or organ) which permits continued development of that structure but inhibits formation of another structure of the same type within the field.

All of these phenomena contribute to the *pattern formation* which characterises the ‘body plan’ which is created by the particular distribution of differentiated tissues in the structure (organ or individual). Pattern formation depends on *positional information*, which prompts or allows the cell to differentiate in a way appropriate to its position in the structure. Positional information is usually thought to be conveyed by concentration gradients of one or more morphogens emitted from one or more spatially distinct organisers. The responding cell senses the concentration of the morphogen and initiates a differentiation programme appropriate to the physical position at which that morphogen concentration is normally found. In essence, the cell ‘triangulates’ on the incoming signals and adjusts its morphogenetic response in accord with its position relative to the controlling organisers. Populations of cells which respond like this are said to show *regional specification*. The operation can be divided into (i) an *instructive* process which provides positional information, and (ii) an *interpretive* process in which the receiving cell or tissue responds.

The basic rules of pattern formation seem to be that regional specification (directed by organisers producing morphogens) occurs first, regulating gene activity in ways specifically geared to morphogenesis so that particular cells are first specified (a state which is still flexible) and then determined (a state which is inflexible) to their differentiated fates. Cell differentiation is a consequence of these events – cells which are either specified or determined are not necessarily morphologically different from their neighbours or predecessors (the morphological change may occur much later, or the differentiation may involve change only in molecular or metabolic attributes).

The vocabulary outlined above highlights the major events contributing to animal development and is useful, too, in descriptions of plant morphogenesis. One might ask why it is featured so early in a book about the development of fungal structures. Unfortunately, fungal development has been rather ignored as a topic in its own right. The great majority of the published research on fungal morphogenesis has been done with taxonomic intentions. It has great value for its descriptive and comparative content, but precise developmental accounts are extremely rare and experimental approaches rarer still. The dearth of research on experimental fungal developmental biology forces us to seek parallels between fungi and other eukaryotes so that we can make use of the conceptual framework which has been established, in embryology, cell and evolutionary biology. It is not a negative comparison because it 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 structural and morphological problems.

But just as an organism develops and evolves, so the science of studying organisms develops and evolves, but along a tortuous route which includes the turns and roadblocks of misinterpretation and misconception. By making bold comparisons across the boundaries between the major eukaryotic kingdoms we can learn from past mistakes rather than repeat them.

This urge to compare must be tempered with full appreciation that fungi have attributes which are unique to them which must affect their developmental mechanisms. Fungi are ‘modular organisms’, like clonal corals and vegetatively-propagated plants, among others (Harper *et al.*, 1986; Carlile, 1995). In modular organisms growth is repetitive and a single individual (though the definition of ‘individual’ is open to debate) will have localised regions at very different stages of development (Andrews, 1995). The constituent cells are generally considered to be totipotent (able to follow any pathway of differentiation), because a mycologist would expect to be able to produce a tissue (mycelial) culture in a culture dish from a fragment removed from a mature, fully differentiated structure, like a mushroom fruit body, collected from the field. This cannot be done routinely with animals, and most plants demand far more stringent *in vitro* growth media and conditions than do most fungi. This behaviour reflects the nutrient-absorptive fungal lifestyle, but it also says something about the control of fungal development because even highly differentiated fungal cells will revert readily to vegetative growth if they are explanted to a (relatively simple) nutrient medium (see section 6.5).

This is not to say that fungal cell differentiation is any less sophisticated or complex than is found in animals and plants, but fungi can vary the timing, extent, and mode of differentiation in response to external signals, interconverting growth forms and reproductive phases of their life cycle in ways which make them supremely adaptable to challenging conditions. This results in a morphological plasticity which surpasses that of other organisms and provides an intellectual challenge in terms of developmental biology, taxonomy and genetics (Watling and Moore, 1994).

It is still often necessary to remind people that fungi are not plants. Even mycologists are not immune to an occasional lapse, maybe referring to ‘saprophytic’ (rather than saprotrophic) fungi in the heat of an argument, but though this does great disservice to the study of fungi as a unique kingdom (Hawksworth, 1995) it is usually just a slip of the tongue.

More dangerous is the fact that there are still a great many people whose education was completed before the revolution in systematics in the mid-1960s, or who were taught by teachers whose education was completed before then, and who are consequently firmly convinced that fungi are plants – peculiar plants, perhaps, but plants nevertheless. Any such idea is completely wrong because plants, animals and fungi are now considered to be three quite distinct kingdoms of eukaryotic organisms (Whittaker, 1969; Margulis, 1974; Cavalier-Smith, 1981, 1987).

Arranging organisms into kingdoms is a matter of systematics – an agreed scheme of categorisation – but this arrangement is mirrored in current ideas about the early evolution of eukaryotes (Fig. 1.1).

Whilst there is debate over the most likely sequence of early evolutionary events, all of the schemes argue that the major kingdoms separated from one another at some unicellular level. If it really is the case that the last common ancestor of plants, animals and fungi was a unicell, then these kingdoms have independently evolved all of the mechanisms which they currently use to organise populations of cells into multicellular organisms.

1.1 Fungal lifestyle

It is worth dwelling on evolutionary aspects, because the three main eukaryote kingdoms are very different from one another in ways that

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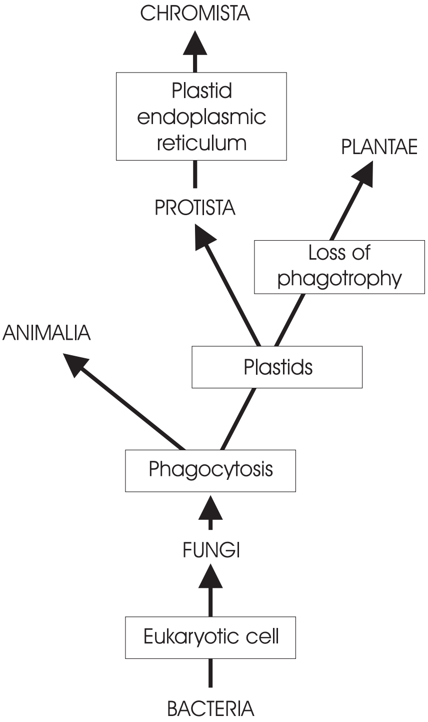

Figure 1.1 Simplified, elementary phylogeny and six-kingdom classification of living organisms. The major evolutionary events are shown in the boxes. The kingdom Protista as shown here is a heterogeneous group which would include myxomycetes and most organisms normally understood to be protozoa. Kingdom Chromista includes a range of golden and brown algae and diatoms (but green and red algae are included in kingdom Plantae) as well as fungus-like phyla interpreted as having lost plastids secondarily, including the Oomycota, Hyphochytriomycota and Labyrinthulomycota. Redrawn from Cavalier-Smith (1981).

are crucial to determining shape and form. A key part of the original definition of the kingdoms (Whittaker, 1969) was their mode of nutrition (plants use radiant energy, animals engulf food, fungi absorb nutrients), and this apparently simple basis for systematic separation then reveals other differences in structure and lifestyle which are correlated with nutrition (presence of chloroplasts, internalised digestion, export of digestive enzymes, etc.).

Approaching consideration of metabolic processes from an evolutionary viewpoint is appropriate since the mode of nutrition has always been a major characteristic in schemes of classification. The photosynthetic plants have always been clearly distinguishable from ingesting animals;

but only recently have the fungi been properly placed in the scheme of living things in a way which clearly recognises the fundamentally different mode of nutrition they employ. In placing the fungi in an entirely separate kingdom, Fungi, Whittaker (1969) emphasises that the "... nutritive mode and way of life of the fungi differ from those of the plants. Fungi characteristically live embedded in a food source or medium, in many cases excreting enzymes for external digestion, but in all cases feeding by absorption of organic food from the medium. Their organisation, whether mycelial, chytrid, or the unicellular of yeasts, is adapted to this mode of nutrition."

This, then, is how fungi have evolved to grow: effectively embedded in a substratum which they digest by the excretion of appropriate enzymes. The smaller molecules produced by the activity of those enzymes are the nutrients which can be absorbed across the plasmalemma. In this the fungi are distinct from both plants and animals for, as Whittaker (1969) also points out, these latter groups have internalised the absorption process; animals by the process of ingestion, but plants too, by the elaboration of membranes around their photosynthetic organelles. Among eukaryotes only the fungi (though this is a character they share with bacteria) must digest their substrates externally prior to absorption of the smaller molecules of which the substrates are composed. There are ecological and structural, as well as biochemical, consequences of this. A protozoan or metazoan can immediately capture a morsel of food by ingesting it into a food vacuole or digestive tract where it can be converted to its components without fear of loss to competing organisms. A fungus may be capable of digesting the same food source, but must perform most of that digestion externally with the valuable products of the digestion being open to absorption by competitors until they can be internalised by the fungus. This may have influenced the evolution of extracellular mucilages, cell walls, membrane components and digestive enzymes so that the fungus can improve its competitive effort by exerting effective control over the environment in the immediate vicinity of its cell surface.

The kingdom Fungi encompasses a tremendously diverse and enormously versatile range of organisms. It is unlikely that there is a compound, organic or inorganic, on the planet that some fungus cannot utilise, transform, modify or otherwise deal with. It could reasonably be argued that lignin is the most exotic and biologically demanding potential nutrient. Lignocellulose constitutes about 95% of terrestrial biomass (Janshekar and Feichter, 1983), and except for the activities of the very few organisms which are able to degrade the lignin component,

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the rest of us would be overwhelmed! But there are examples of some extreme fungal abilities. *Phanerochaete chrysosporium*, one of the key organisms in studies of lignin breakdown, has also been shown to degrade PCBs the polychlorinated biphenyls used as electrical insulators which are such persistent pollutants (Bumpus *et al.*, 1985; Eaton, 1985). This, and other fungi, can also degrade pesticides (Kumar *et al.*, 1996), packaging materials (Pagga *et al.*, 1995) and other xenobiotics (Shah *et al.*, 1992; Singleton, 1994), abilities which make them ideal candidates as contributors to the microbial degradation of industrial wastes as a cost-effective method of removing such pollutants from the environment by a process now known as bioremediation (Alexander, 1994).

Some species of the yeast *Candida* can use n-alkanes as sole carbon source, and specifically modify the structure of their walls to enable them to do so (Kappeli *et al.*, 1978). Hydrocarbons, and other organic vapours, in the atmosphere can also be scavenged and used for growth (Mirocha and DeVay, 1971; Tribe and Mabadeje, 1972). At the other end of the molecular spectrum, fungi can fix CO_2 from the atmosphere (Tabak and Bridge-Cooke, 1968), some being able to use CO_2 as sole carbon source indefinitely (Mirocha and DeVay, 1971), and others are claimed to fix more CO_2 when illuminated (Hilgenberg and Sandmann, 1977; and see Wainwright, 1988). Although these are some of the most unusual (and debatable) metabolic situations, it is becoming increasingly evident that some soil fungi can grow under oligotrophic conditions; i.e. in a purely mineral medium (Wainwright *et al.*, 1994).

The genetic apparatus of the cell encapsulates its form and nature in an informational archive, which is expressed through the metabolic activities of the cell. Through its metabolism the cell interacts with its environment and neighbouring organisms; metabolism provides for the energy requirements of the cell and satisfies the demands of its biosynthetic machinery for the precursors of those polymers whose assembly creates, maintains and modifies the physical form of the cell itself.

The metabolic apparatus is both powerhouse and workshop, and is the working, responsive interface with whatever may be ‘outside’ the cell. The key word here is ‘responsive’, for metabolism is continually changing to accommodate changing circumstances both within and outside the cell. It must be appreciated that the biochemical transformations occurring in a cell at any one time are only a small subset of those that are possible. The adjustments and changes between those subsets emphasise different aspects of metabolism suiting the prevailing conditions and often occurring for reasons of economy. Indeed, politico-economic phrases like cost-effective, return on the investment made, and profit-and-loss relation can

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all be applied effectively in discussion of metabolic regulation. The ‘choice’ (not a conscious choice, of course) between alternative metabolic processes is always made on the basis of economy of effort, because in competitive evolutionary terms greater economy of effort is a selective advantage. Of course, this does not mean that the most energetically economic path is always taken, though it often is. It does mean that the advantage which accrues to the organism must be worth the costs incurred. In some cases the advantage is in successful completion of a developmental pathway and intermediary metabolism is adapted to some morphogenetic purpose, rather than to a purely nutritional one (examples in Chapters 3 and 4).

1.2 The essential nature of fungi

Other differences between the eukaryotic kingdoms, not obviously correlated with mode of nutrition, include the way in which multicellular structures can be organised. In animals, even lower animals, the movement of cells and cell populations plays a crucial role in development, so cell migration (and everything that controls it) is a key feature of all aspects of animal morphogenesis. Plant cells, on the other hand, are encased in walls and have little scope for movement relative to each other. Changes in shape and form in plants are dependent upon control of the orientation and position of the mitotic division spindle because the new cell wall which will separate the parental cell into two daughter cells arises from the phragmosome at the equator of the mitotic division spindle. Consequently, the orientation and position of the dividing parental nucleus will determine the orientation and position of the daughter cell wall.

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 tips 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 (see Chapter 2).

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1.3 Evolutionary origins

Most aspects relating to the origins and subsequent evolution of fungi are impossible to establish from any fossil record, so ideas and concepts must be gleaned from other sources (Rayner *et al*., 1987). Key events in fungal evolution probably took place in the early Palaeozoic or late Precambrian (see Table 1.1), and the likelihood of finding definitive fossil evidence for them is small (Sherwoodpike, 1991). Fungal spores are often well-preserved, but in addition, fungi characteristically interact with other organisms, particularly plants, and the fossil record can provide some information about these (Taylor and Osborn, 1996; and see below). However, the general lack of convincing fossil records of fungal origin means that comparative analyses of molecular sequences (protein and nucleic acid) provide the strongest evidence about the nature of evolutionary relationships between existing groups of organisms. Hendriks *et al*. (1991) examined the small ribosomal subunit RNA sequence of 58 eukaryotes. Evolutionary trees constructed from the data showed a nearly simultaneous radiation of metazoa, the red alga *Porphyra umbilicalis*, the sporozoa, the higher fungi, the ciliates, the green plants, plus some other groups. Higher fungi formed a monophyletic cluster when all alignment positions were used to construct the evolutionary tree. Although the red alga and fungi seem to diverge at nearly the same evolutionary time, no evidence could be detected to support the idea that higher fungi and red algae might have shared a common origin.

There are probably at least 1.5 million species of fungi in the world today (Hawksworth, 1991) and if Whittaker's paper made 1969 a memorable year by establishing their true importance in terms of their rank in the scheme of things, 1993 seems to have been another golden year, this time for publications establishing fungal relationships.

Margulis (1992) had already pointed out that the field of systematic biology had been reorganised with logical, technical definitions for each of the three major kingdoms of eukaryotes (Mycota, 'true' fungi; Plantae, bryophytes and tracheophytes; and Animalia) "This classification scheme requires changes in social organisation of biologists, many of whom as botanists and zoologists, still behave as if there were only two important kingdoms (plants and animals)." So 1993 seems rather special as a year in which papers appeared with the titles 'Monophyletic origins of the Metazoa – an evolutionary link with fungi' (Wainright *et al*., 1993) and 'Animals and fungi are each others closest relatives – congruent evidence from multiple proteins' (Baldauf and Palmer, 1993). Wainright *et al.* (1993) analysed small subunit ribosomal RNA sequences and deduced

Table 1.1. *A version of the geological time-table. Inspired by a figure in J. A. Moore (1993).*

Million years ago	Eon	Era	Period	Description
13,000				Universe forms and expands.
4,600	Hadean			Earth forms by accretion and was probably under repeated bombardment by meteorites, each cataclysmic event destroying any prior chemical evolution.
3,800	Archean			Oldest known rocks, meteorite bombardment declines sufficiently for evolution to progress. Autotrophic carbon fixation dated to 3800 million years ago (on the basis of carbon isotope ratios in sedimentary organic carbon). Oldest prokaryotic fossils about 3500 million years old.
2,500	Proterozoic			Prokaryotes abundant. Atmospheric oxygen about 0.2%. Eukaryotes appear during this Eon, about 2000 million years ago. Last common ancestor of fungi, animals and plants about 1000 million years ago. Plants diverge first. Fossil algae known about 1000 million years old. Fungi and animals shared a common ancestor more recently than either did with plants. Metazoans emerge about 800 to 1000 million years ago.
670	Phanerozoic	Palaeozoic	Ediacaran	Some fossils interpreted to be of lichen origin. Oldest known metazoans (coelenterates, annelids, arthropods).
570			Cambrian	Atmospheric oxygen reaches 2%. Trilobites and brachiopods abundant. All metazoan phyla present.
510			Ordovician	Terrestrial fungi diverge from chytrids about 550 million years ago. Earliest vertebrates appear.
435			Silurian	Possible fungal fossils. First fishes with jaws. Animals and plants invade land. Atmospheric oxygen reaches 20%.

405		Devonian	Mycorrhizas evident in plant fossils 400 million years old. Ascomycetes separate from basidiomycetes. Land plants and land arthropods abundant. First insects. First amphibians. Continents move towards one another.
355		Carboniferous	Widespread forests of primitive plants eventually form coal deposits. Reptiles appear at the end of the period.
290		Permian	Land masses form a single continent. Mammal-like reptiles. Frigid conditions and massive extinctions at the end of the period.
250	Mesozoic	Triassic	First dinosaurs. Cycads and conifers abundant. Continents move apart.
205		Jurassic	Fungal spores in amber about 225 million years old. Basidiomycete radiation begins, poroid and agaricoid forms evident. The genera *Penicillium* and *Aspergillus* may have appeared about 200 million years ago. Dinosaurs abundant. First birds and mammals.
135		Cretaceous	Fossilized fungal remains known from this period. Major radiation of flowering plants. Amber 90 to 94 million years old contains gilled mushrooms strongly resembling current species. Dinosaurs become extinct; this and many other extinctions possibly associated with meteor impact at the end of the period.

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Table 1.1. (*cont.*)

Million years ago	Eon	Era	Period	Description
65		Cenozoic	Tertiary	Continued diversification of birds, mammals and flowering plants. Grasses and grazing mammals abundant. The genus *Homo* appears at the end of the period.
1.6			Quaternary	Humans widespread. Large mammals become extinct. Glaciation in northern hemisphere.
0				Present day. Mycorrhizas essential to all terrestrial plants. Wood decay fungi essential to lignin degradation. Fungi essential to many daily human activities, social and commercial. Fungi rule!