Published in Dutch in a special issue of the Journal *Coolia* produced to honour the 100th birthday (on October 28, 1999) of A.F.M. Reijnders.

Moore, D. (1999). De aap, de walvis en de paddestoel: Bert Reijnders' lichtend voorbeeld. Coolia 42, 210-216.

Monkeys, whales and mushrooms - Bert Reijnders' guiding light

David Moore

School of Biological Sciences, The University of Manchester, Manchester M13 9PT, U.K.

We live in enlightened times. Today, much of that enlightenment comes from the media - magazines like this one, but especially television. Thanks to many years of TV programmes about all sorts of aspects of natural history the ordinary viewer has a quite sophisticated understanding of the lives of animals and plants from around the world. It's likely that this is centred on relationships to, and evolution of, the human animal but that is understandable and the general knowledge of the "man-in-the-street" is impressive. Chances are that we've seen or read about Jane Goodall and her chimpanzees, about the plight of mountain gorillas in the interminable civil wars in Africa, and about the sad predicament of orangutans in the dwindling forests of Sumatra and Borneo. We know about Lucy - that 3 million year old fossil from Ethiopia - and, indeed, most people probably have a good understanding of relationships and evolution in the primates. And the understanding goes further than that.

In the same TV schedules and the same magazines we have watched whales migrating from Arctic to Antarctic; been amazed by the aquabatic feats and communication skills of dolphins, and appreciated the family structure of killer whales (and we can happily chat about Orca families called pods). Hell, we even freed Willy! So when Herman Melville has the Mate Starbuck ask of Captain Ahab '...what more wouldst thou have? Shall we keep chasing this murderous fish till he swamps the last man?' when talking about *Moby Dick, The White Whale*, I think most people today would stop and say that there's something wrong with that '...murderous fish...' part of the quotation.

Of course, *Moby Dick* is not a zoological text book. It's a novel and the 'mistake' is excusable in the context of a nineteenth century writer putting words into the mouths of nineteenth century fictional whalers. But to think that the 'whale = fish' equation in *Moby Dick* is an ignorant mistake would be doing Melville an injustice. Melville, through his narrator Ishmael, explains it like this: '... There are some preliminaries to settle. First: the uncertain, unsettled condition of this science of Cetology ... that in some quarters it still remains a moot point whether a whale be a fish. In his *System of Nature*, A. D. 1758, Linnaeus declares, "I hereby separate the whales from the fish." ... The grounds upon which Linnaeus would fain have banished the whales from the waters, he states as follows: "On account of their warm bilocular heart, their lungs, their movable eyelids, their hollow ears, penem intrantem feminam mammis lactantem, and finally, ex lege naturae jure meritoque." I submitted all this to my friends Simeon Macey and Charley Coffin, of Nantucket, both messmates of mine in a certain voyage, and they united in the opinion that the reasons set forth were altogether insufficient. Charley profanely hinted they were humbug. Be it known that, waiving all argument, I take the good old fashioned ground that the whale is a fish, and call upon holy Jonah to back me.'

That good, decisive argument was published by the American novelist in 1851. Nearly 150 years later, we've all seen so much on TV and film, and in books and magazines that most people now would think it uneducated to hear someone describe a whale as a fish.

There's enough available in books and on film to convince even Charley Coffin, of Nantucket. In these enlightened times, then, why do so few people understand fungi?

We still encounter many people, even professional biologists, who are convinced that fungi are plants. They're not plants, of course. They never have been and they never will be plants. Unfortunately, some of those whose education was completed before the mid-1960s (when the revolution occurred in our understanding of relationships between organisms) remain firmly convinced that fungi are plants - peculiar plants, maybe, but plants nevertheless. This idea is now accepted as completely wrong, and plants, animals and fungi are assigned to three quite distinct Kingdoms of higher organisms. Arranging organisms into Kingdoms is a matter of what is called systematics - an agreed scheme of naming things. It really is only a matter of looking, comparing and making categories - but the arrangement we have reached now does seem to square with current ideas about the early evolution of these organisms. So it seems to be a natural, meaningful systematics in which the fungi have been allocated a kingdom, the so-called Third Kingdom, all of their own.

A major aspect of the original 1960s definition of the Kingdoms was their nutrition: plants use radiant energy to make their food. Animals, from amoeba to killer whales, engulf their food, and fungi degrade food externally and absorb the nutrients which are released. Once this apparently simple basis for making the grand separation between Kingdoms has been used, numerous other differences in structure and life style become evident. One thing worth emphasising is that the three Kingdoms are very different from one another in ways that are crucial to determining shape and form. 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 development. Being encased in walls, plant cells have little scope for movement and their changes in shape and form are achieved by regulating the orientation and position of the wall which forms when a plant cell divides. Fungi are also encased in walls; but their basic structural unit is a tubular, thread-like cell, called a hypha. It has two peculiarities which result in fungal development being totally different from that in plants. These are that the hypha grows only at its tip and that new walls form only at right angles to the growth axis of the hypha.

This sounds like a nice piece of academic detail, but it has a significance beyond that because it raises an important consequence for arguments about the evolution of all organisms. The evolutionary separation between the major Kingdoms must have occurred at a stage when the most highly evolved things were single cells. The consequence is that each Kingdom must have 'learned' independently how to organise populations of cells in order to make the multicellular organisms we now know as mushrooms, mice or marigolds. So studying *how* a mushroom *makes* a mushroom is an investigation every bit as deep and meaningful (and difficult!) as studying how a human embryo develops or how a tree is shaped and sculptured in the forest. Sadly, in the popular imagination mushrooms don't have the same status as human animals or forest trees.

The 'Father of Mycology', Elias Fries, and his contemporaries in the early nineteenth century put far too much emphasis on shape in their attempt to understand mushrooms, toadstools and their relatives. This fundamental mistake is still with us. Academic mycologists may have moved well away from this position now, but they have taken a long time to do so and external shape is still the guiding light in the minds of many non-academic mycologists. With plants and animals, shape was important in ancient herbals and beastiaries but it has not been a dominant factor in 20th century science. Indeed, as my quotation from *Moby Dick* shows, the 'Father of Classification', Linneaus, distinguished the shape of whales from the shape of fish (sufficiently strongly for a novelist on a different continent to pick up on it) on the basis of comparisons of their structure, anatomy and development. Not so for fungi. Most of the early workers were content to rely solely on current shape and form - the most simplistic sort of study. Detailed studies of development, structure and anatomy did not start until the middle of the twentieth century and even today their practitioners have to fight to be heard and deep ignorance abounds.

Remember that classification of organisms is an exercise in arranging them into groups to make it easy to study them and, more importantly, to make it easy to interpret the results of the studies. It's a clerical exercise, like arranging all the papers in an office in files and then into filing cabinets. The arrangement that Fries produced used the shape and form of the fruit body and especially the nature of the tissue on which the spores were made. So he had a group called *agarics* which have plates (or gills) beneath an umbrella-shaped cap, just like the ordinary cultivated mushroom. And 'mushrooms with gills' were 'filed' into that group whatever their other characters were like. This agaric group was contrasted with fruit bodies which had tubes (or pores) in a spongy layer beneath the cap (called *polypores*). Toadstools in this group were called *boletes* but *bracket fungi* whose fruit bodies grow directly on the trunks of trees were also included. Then there were those with teeth or spines hanging down below their cap or bracket, and these were called *hydnoids*. Other major groups included some with spores formed over the outside of a club-shaped (called *clavarioid*) or coral-like (called *coralloid*) fruit body, and then there were the completely enclosed fruit bodies (called *gasteroid*) which had their spores inside the fruit body like puff-balls.

On the face of it, this is a nice simple scheme. Just the sort of thing you could apply as you trek through a forest. Sadly it was applied too rigidly. It was as if the 'experts' insisted that everything that flew should be called 'bird' whether they were actually fruit bats, bumble bees or buzzards. Look closer and you can see the limitations of the scheme; but very few mycologists looked closely enough. Even though some studies done soon after Fries published his views indicated that his groupings were artificial, his views were so fervently believed that at the end of the 19th century any contrary suggestions were considered heresies.

In fact it's taken over a hundred years to break the grip of the Friesian system of classification of larger fungi, and most change is the result of work in the last 50 years of the twentieth century. Work which has used developmental features and detailed comparisons of anatomy, chemistry and microscopic characters to reveal natural groupings and evolutionary relationships. Work which was largely pioneered - and mostly done - by A. F. M. Reijnders. This is supposed to be an essay in honour of Bert Reijnders' birthday, yet mention of the man himself has been much delayed. There's a good reason. You need to see the whole picture: Reijnders is more than just a great mycologist, he is one of the great ***biologists*** of this century. Stand up close to a painting and you can admire the skill of the brush strokes. Take a few steps back and you can appreciate the artist's perceptive genius. We all know of Bert's numerous contributions to a variety of specific areas of fungal biology and an easy way of honouring the man is to make an annotated list of his publications over the past 70 years or so. But that would miss the majesty of the contribution he has made. Bert Reijnders' hard-working industry is obvious - it seems as though he must spend every waking hour studying his beloved fungi! But his *approach* is even more important than this. He recognised what others had ignored. He innovated by studying *development*. And by so doing he provided the 'platform technology' to revolutionise our understanding of an entire Kingdom of organisms.

Ironically, the zoologists battled through this sort of thing as evolutionary ideas emerged in the first quarter of the twentieth century. Initially, 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* in 1914. Progressive views were diametrically opposed and by the mid-1920s it was widely agreed that animal embryology does not recapitulate evolution, but contributes to it. Reproduction - or rather *success* in reproduction - is the winning ticket in the evolutionary lottery. So all features which influence that success are subject to evolutionary selection. For an animal, that might mean efficiency in finding a mate; efficiency in egg-laying; efficiency in dispersal of larvae; efficiency in care of the young; or any of a host of other factors which contribute to one set of genes being distributed to the next generation in preference to some other, competing, set of genes. If the watchmaker is blind, then that set of evolutionary principles apply just as much to fungi as to animals and plants. Only the details change.

The function of the fungal fruit body is to distribute as many spores as the structure will allow. The familiar mushroom shape has evolved to give protection to the developing spores. It really is an umbrella protecting the spores from rain. The first step in improving the basic mushroom shape is to expand spore-production capacity. Making gills and pores are both strategies to increase the surface area available for spore production. If that has positive evolutionary advantage is it any wonder that careful observation of developing fruit bodies shows that there are at least ten different ways by which the mushroom shape can be constructed? It's relatively easy to show that geometrical constraints make pores a less efficient way of expanding spore production than gills. So, don't be surprised to find that there are some gilled-mushrooms which are closely related to polypores and only distantly related to 'real' agarics. Oyster mushrooms and the shiitake mushroom are like this. Presumably, at some stage in their evolution they found advantage in folding their spore-forming tissue into gills and they have now converged onto the agaric shape. It's *convergent evolution* just like swimming mammals evolving towards efficient swimming in water and finishing up fish-shaped, like dolphins, because fish *also but quite independently* evolved towards efficient swimming in water.

Look closely at the tissue structure for more wonders of evolutionary architecture. There are different ways of constructing gills. Not all dinner plates are the same, so why should all mushroom gill-plates be the same? Again, all mushrooms must increase in size as they develop. Some hold the *number* of cells unchanged but pump fluids into what they've got to increase their size by 10, 20 or 50 times. Others hold the *size* of cells unchanged and just make more of them to increase the volume of the tissue. Both strategies, though, seem to use the same simple management system whereby one cell organises and controls a rosette of cells immediately surrounding it. These little families of hyphae orchestrated by a central *inducer* hypha are now called Reijnders' knots after the man who first described them. Guess who!

Bert Reijnders' book (1963) *Les problèmes du développement des carpophores des agaricales et de quelques groupes voisins* is the mycological guiding light of the twentieth century. It showed the power of the approach and helped turn an observational science into an experimental one. It appeared about the time that Kingdom Fungi was first being written about with conviction and by illuminating the new Kingdom the Reijnders approach helped fungal systematics to come of age. Almost 100 years behind its sister sciences of botany and zoology, mycology is now appreciating that fruit body shape should not hold the central position it once did. This is a matter of interpretation of the value of particular features in establishing relationships between groups of organisms.

Taking the work further, it's becoming clear that one reason why fruit body shape is less useful in fungi is that it's a more flexible feature than previously thought. Variation in shape and form of mushrooms occurs at different levels and for different reasons. Many mutants or variants in shape have been induced in the laboratory or isolated from nature. These mutants have been very instructive in establishing developmental pathways and future molecular analysis will be even more revealing. But there are also many instances where, for some reason, the development of a normal fruit body becomes disturbed without change to its genes. This sort of variability seems to be a strategy to cope with environmental stress. If there is a prime rule in fungal fruit body development then it seems to be '*distribute spores*'. If the environmental conditions are so damaging that only a monstrous distorted fruit body can be produced then it is counted as a success if it disperses some spores. The fungi really take this tactic to extremes. An agaric fungus that normally produces a mushroom fruit body can, if the atmosphere gets too dry or the temperature too high, form coralloid or gasteroid fruit bodies alongside the normal agaric fruit bodies; and all functional as spore production and dispersal structures. To compare this with an approximate animal counterpart, the parallel would be for cats to be able, quite normally, to give birth to litters containing kittens looking like an aardvark, dog or even iguana.

Such mushroom variants indicate that normal fruit body development is made up of separate but co-ordinated subroutines, each of which controls the structure and shape of a different component of the fruit body. So development of fungal fruit bodies in general depends on organized expression of these subroutines; the sequence and location in which they are invoked determines the shape of the fruiting structure and the progress of its development. It's quite similar to the way different component production lines contribute to the manufacture of a product like a car. Change the way the components are assembled and you change the product. In fungi, essentially the same subroutines can give rise to very different fruit body shapes, depending on other circumstances. For example, the agaric gill subroutine is expressed with the rule 'where there is space, make gill'. When this is combined with a routine providing mechanical anchorages the gills are stretched along the lines of mechanical stress as the fruit body expands and end up straight and radial. If the anchorages are left out (because of some mutation, say), then the gills are formed but are never pulled straight and remain tangled and contorted.

A highly flexible developmental process like this allows the fungus to adapt to a wider range of conditions. The criterion for successful adaptation is successful production of spores and even the most monstrously abnormal mushroom can do that. This is not true for animals and plants, where even mild abnormalities can reduce their ability to reproduce quite drastically. So it appears that fungi differ from animals and plants by having much less selection pressure against developmental abnormality. Maybe that's why the fungi have ruled the Earth for 2 billion years!

Once the story is put together it looks obvious but to see the obvious you have to be a rare and gifted man. Reijnders is the man!