
Fungal behaviour and fungal evolution : the role of internal factors

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With reference to fungal evolution, the role of natural selection versus internal factors is discussed in general terms. The inadequacy of natural selection as an explanation is highlighted with special reference to Alister Hardy's concept of 'behavioural selection'. Fungal behaviour is the basis of fungal evolution: the prime factor is an internal one and resides in the genome itself. There are countless such genomes, co-existing and co-evolving with other biota and with each other in a system that is balanced and self-sustaining. Each genome has a life-style, a style unto itself, and has the potential to evolve on its own. Examples of speciation in the fungal kingdom are cited to show that fungal species are dynamic and are evolving as seen from allopatric speciation. Fungal behaviour rather than selection plays the prime role in their evolution. Evolution is not the product of a struggle for existence but a process of being and becoming. It is suggested that we de-link the question of survival of species (and their extinction) from the question of their origins.

Key-words—Fungal behaviour, Evolution, Natural selection, Internal factors, Behavioural selection.

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सारांश

कवकीय विकास एवं व्यवहार : आन्तरिक कारकों की भूमिका

सी० वी० सुब्रामनियन

कवकीय विकास के सन्दर्भ में प्राकृतिक वरण एवं आन्तरिक कारकों की पारस्परिक भूमिका की समीक्षा की गई है। एलिस्टर हार्डी की "व्यवहारिक वरण" नामक धारणा के विशेष सन्दर्भ में प्राकृतिक वरण की अननुकूलता की विवेचना भी की गई है। कवकीय व्यवहार ही कवकों के विकास के लिए आधार है। इनमें मुख्य कारक आन्तरिक है जो जीनोम (संजीन) में विद्यमान रहता है। एक तंत्र में साथ-साथ विद्यमान तथा अन्य जीविता के साथ सहविकसित इस प्रकार के अनेक जीनोम होते हैं और प्रत्येक जीनोम का अपना विशेष जीवन-प्रारूप होता है। कवकीय जगत में विभिन्न जातियों के बनने के उदाहरण भी इस शोध-पत्र में दिये गये हैं। इनके विकास में वरण की अपेक्षाकृत कवकीय व्यवहार की अधिक भूमिका है। विकास 'जीवन-संग्राम' का परिणाम नहीं है अपितु विद्यमानता एवं पुनर्विकास की प्रक्रिया है।

THE subject of fungal evolution is both fascinating and intriguing and can be viewed from different angles. One who has comprehension and appreciation of fungal diversity and fungal form may consider the range in structure, morphology, including developmental morphology and reproduction, and can speculate on how the fungi have evolved. Such speculation would include considerations of cell wall structure and chemistry, cell structure including ultrastructure, nuclear behaviour and life cycles, even metabolic pathways (see Rayner, Brasier & Moore, 1987, for a recent and comprehensive appraisal; also the chapters by

Cavalier-Smith and by Bartnicki-Garcia in the same volume). Such an exercise doubtless gives insight into the course of fungal evolution, but clearly reinforces the point that we still know very little. For example, data on cell wall chemistry and metabolic pathways are limited to very few taxa. When more taxa are studied, we may have to change our current ideas about these.

Fungal behaviour, fungal nutrition, fungal metabolism—indeed, fungal biology—provide

another facet. We are immediately concerned with fungal nutrition, with the uniqueness of the fungi in this regard, with questions of heterotrophy versus autotrophy, the dependence of fungi on living plants, animals, other fungi, etc., the co-evolution of fungi with higher plants, with algae, cyanobacteria, insects, other animals; their extraordinary ability to break down substrates and, in the process, throw out secondary metabolites, and the armoury of countless enzymes that they produce to break down diverse substrates and to synthesize an amazing array of metabolites. Many are the interesting questions in fungal evolution, such as, the origin of parasitism, the origin of hyper-parasitism, the origins of symbiosis, the origins of the habit of vascular colonization, and so on. We can speculate on the origins of parasitism, saprophytism, symbiosis (Cooke & Whipps, 1987; Heath, 1987; Lewis, 1987). Whatever fossil record may be available may help us in understanding some aspects of co-evolution.

The evolution of fungi is tied up with the chemical origins of what they are composed of, and the origins of the host or substrates they colonize; the origin, for example, of cuticle and xylem, of wood and bark, and of cellulose, chitin, cutin, lignin, keratin, etc.

THE MECHANISM OF EVOLUTION : NATURAL SELECTION

Evolution is a grand idea. There is no question about it. And though we connect Charles Darwin's and Wallace's names with it, we all know Darwin inherited the idea from his predecessors. The idea had been with him since 1838, but he published it only in 1859. Why? Why did he, in the intervening years, devote himself largely to a study of barnacles? And what was Darwin's grand idea? All of us know the idea of evolution by *natural selection*, the *origin of species* by natural selection. As has been pointed out by students of Darwinism, Darwin developed his theory of natural selection as a conscious parallel to Adam Smith's Economics. Yes, the principle of individual struggles is the principle of *laissez-faire* which means, should one want an ordered society, one should let individuals struggle for profit. Likewise, should you want order in nature, you let individuals comprising the biota struggle for success, success in growth and reproduction. Darwin made natural selection the prime factor in evolution, its driving force. What does this mean? This means that there is competition, struggle between individuals, species, groups, and in this struggle the fittest survive as in a war, where there are only survivors. Those that do not survive disappear and

become extinct. Yes, this seems logical, and simple enough.

THE INADEQUACY OF SELECTION AS AN EXPLANATION

But one must ask: is this how plants and animals become extinct? or evolve? The rocks and the plant and animal fossils seem to tell a different story. Not individual species but a whole group of animals (e.g., dinosaurs) or plants becomes extinct all of a sudden, yielding their place to an entirely new and totally different group of animals or plants. This point was noted and stressed by Seward (1924), and Sahni, and especially by Sahni (1937) who wrote:

"These revolutions in the organic world are the landmarks of geological history. Each of them marks a large-scale extinction of plant and animal life as well as a more or less sudden appearance of forms of life previously unknown. So striking is this fact of the sudden appearance of new species, genera and families that it is in sharp conflict with the Darwinian doctrine of natural selection as the only or even the chief explanation for the origin of new forms of life. Evolution in the sense of a gradual, orderly process of change is an undisputed fact. But evolution in this gradual sense is not the whole of organic evolution as revealed by the geological record. Periodic revolutions are an integral and essential part of evolution, and it may well be that they form the more important part, so far as the creation of new forms is concerned. At all events the orthodox idea of natural selection through the gradual accumulation of continuous variations utterly fails to explain some of the glaring facts of palaeontology".

Of the palaeontological break between the Palaeozoic and the Mesozoic eras, Seward (1924, p. XC) wrote:

"The threads of life' seem to have almost snapped, and one wonders whence came the new arrivals which, to our restricted vision, appear as aliens rather than the direct descendants of Palaeozoic types.....We may be led astray by a too rigid faith in the doctrine of continuity".

In the light of these objections to taking for granted continuity in speciation, and the conventional view that discontinuities are only gaps in the fossil record, one might rather accept such discontinuities as real and postulate that the evolutionary process involves long periods of stasis punctuated by interludes of very rapid change. This is exactly what Eldredge and Gould (1972) did when they put forward the hypothesis of punctuated

equilibria and the theory of allopatric speciation. With this theory, the long periods of stasis that are punctuated by episodic events of (allopatric) speciation reflected in the fossil record are readily explained.

As far as animals are concerned, the theory of evolution by natural selection is largely based on data from competition, predation, etc. It is strange that no thought is given to animal behaviour and to animal learning in studying evolution in animals. Darwin himself wrote about animal behaviour in his "The expression of the Emotion in Man and Animals" in 1872 and yet the impact of this work on the development of biology came much later. And we now have interesting and exciting studies of animal behaviour such as those by Rensch (1967), by Koehler, Karl von Frisch, Lorenz, Tinbergen and others (see Thorpe, 1979).

Be that as it may, it is a terrible idea, this, the idea of a struggle for existence and the survival of the fittest which is the backbone of the theory of origin of species by natural selection. Most of the supportive examples for natural selection such as predation come from observations of animals, and form, only a partial view of animal behaviour. Time and again we are reminded of the fierce struggle, the terrible competition to survive-as if nothing can *co-exist*, or *co-evolve* or *evolve on its own* ! Supposing we have a situation where there is no competition: does that mean there will be no evolution?

And, in any case, what is it that natural selection selects from? Natural selection must select from extant genomes. With Darwin's theory, we must suppose that there is competition between genomes. Each genome, it would seem, is always on the defensive against some (other) genome. Each genome is perennially under threat and natural selection must have its course! What an appallingly pessimistic view of life! Yes, it is really pessimistic, depressing. No wonder, Bertrand Russell (1935, p. 81) wrote over fifty years ago:

"From evolution so far as our present knowledge shows, no ultimately optimistic philosophy can be validly inferred".

The trouble is: evolution by natural selection is wholly a *chance process*. It is chance that dictates the mix of genomes that might form a population or the biota. The genome is at the mercy of external factors. This is a totally negative view of the process and the mechanism involved. It rules out completely even a moiety of a role to a given genome in the process of evolution.

EVOLUTION : A PROCESS OF BEING AND BECOMING

According to the theory of allopatric speciation

(Eldredge & Gould, 1972) already referred to, the first step in speciation is the isolation of a local population of 'peripheral isolates' at the margin of the geographic range of its parent species. A new species develops in the peripheral isolate in a short time relative to the duration of the species; and, should it migrate to the region of the parent species, the two species would co-exist sympatrically, but would not interbreed. Carlson (1975) proposed a saltatory origin of species that is not adaptive, unlike that in origin in classical 'phyletic gradualism' in which selection is in key control of random point mutations. Reproductive isolation accompanies the fast and conspicuous saltatory genetic changes. The saltatory origin of species is discontinuous and non-adapting and, if at all, natural selection plays only a secondary, not primary, role in speciation (Gould, 1982). Indeed, it is also questionable to assume that evolution occurs by natural selection of adaptive genes that in the beginning are produced by random mutations. It is unlikely, moreover, that natural selection can account for the extraordinary diversity that has accompanied the evolution of life and of biota.

The fact is that there are extant countless genomes that are part of our biota and are in the process of evolving on their own. It is obvious that they have to co-exist and/or co-evolve. The genomic diversity that one sees in the biota has a functional meaning: autotrophy and heterotrophy form a package, inseparable in the context of evolution. The balance of nature is such that there is birth and death, there is decay, there is decomposition of substrates and re-cycling of nutrients and of the elements, all of which need to be viewed as a system of nature that is beautifully balanced and self-sustaining. "Dust thou art, to dust thou returnest", wrote the poet, lines which echo the beauty of the balance of nature.

Pause, and for a moment, consider the time when life first appeared—or rather, manifested itself. There was then no competition, no struggle. On the theory of evolution by natural selection, with no external pressures, how do you think life appeared and evolved? And, what do you think was the factor or factors involved in evolution? When one tries to answer these questions, one realizes that it is not as if one genome must defend itself against another genome, or that one genome must wipe out another genome, but simply, *each genome has a life-style, a style unto itself, and each genome has the potential to evolve* (And, how beautifully the integrity and identity of the fungal genome is protected and maintained by the fungus cell wall!). Evolution, then, is not the result (or product) of a struggle, but a process of being. The process of BEING and

BECOMING—that I call evolution, not the perennial struggle for existence and the chance of survival. Quite clearly, also, the process of becoming is in the genome, and there are countless genomes. This is a positive view of Evolution (and an optimistic one at that). The prime factor in evolution is clearly and simply the power—an internal one—to evolve. There is thus in every genome a built-in factor that operates in evolution.

This is not my idea. It may sound unorthodox, but it is certainly not new. Though steeped in British and Darwinian tradition, the late Alister Hardy, zoologist and thinker in the University of Oxford, believed that evolution is largely the result of what he called 'behavioural selection' (Hardy, 1965, 1966, 1975). According to Hardy, animals also have 'internal' behavioural selection—the effects of habits developed by active exploring, inquisitive, initiative creatures! As Ewer (1952) wrote: "Behaviour will tend to be always one jump ahead of structure, and so plays a decisive role in the evolutionary process". Somewhat in similar vein, Waddington (1959) suggested that "an animal by its behaviour contributes in a most important way to determining the nature and intensity of the selection pressures which will be exerted on it". Schroedinger (1958) also considered behaviour to be a key factor in evolution. For, he wrote: "Without changing anything in the basic assumptions of Darwinism we can see that the behaviour of the individual, the way it makes use of its innate faculties, plays a relevant part, nay, plays the most relevant part in evolution". Even Jacques Monod (1972) believed "that the initial choice of this or that kind of behaviour can often have very long range consequences, not only for the species in which it first appears in rudimentary form, but for all its descendants, even if they constitute an entire evolutionary sub-group".

One can find support for 'behavioural selection' in Erasmus (grandfather of Charles) Darwin's *Zoonomia or The Laws of Organic Life* (1794) and also in Lamarck's *Philosophie Zoologique* (1809). The many examples of 'behavioural selection' in animals, birds, insects, Alister Hardy has so admirably documented can be supplemented by examples in the fungi and these can also be fully documented. Indeed, this is true of all organisms in so far as each is able to 'improve its programs'. It is a pity that fungal behaviour has not generally been viewed in this light either by mycologists or biologists. Fungal behaviour, I believe, is the key to understanding fungal evolution.

FUNGAL BEHAVIOUR AND FUNGAL EVOLUTION

In a host-pathogen system or interaction like

black rust (*Puccinia graminis tritici*) on wheat there are two possibilities on the 'Survival of the fittest' theory: (i) the host may be wiped out, or (ii) the pathogen is unable to establish itself on the host. In the former case, the host must disappear; in the latter case a similar fate befalls the pathogen. That is putting it in simple terms, though that is not entirely true. And yet, the point to be noted is that both genomes in this interaction, the pathogen as well as the host, are active and act in their own way, the former in infecting the latter or trying to do so, and the latter in defending itself or, rather, resisting infection by the former. And, when there are several cultivars of wheat with a range of resistance-susceptibility and similarly several strains/races of the rust fungus varying in virulence, one comes to realize that both the host-genome and the pathogen-genome are just operating on their own. Each has an individuality marked and sustained by characteristic capabilities. In the final analysis, then, it is *not natural selection* that decides their fate, but *their own activity*. The biodiversity that is around us is thus a summation of the uniqueness of the genomes that constitute it and their evolution is primarily the product of their innate power and attributes rather than of natural selection.

There is a whole range of *formae speciales* of *Fusarium oxysporum* with specialisation and circumscribed host range. Specialisation calls for mechanisms of not only overcoming host resistance but acquiring features contributing to virulence. *F. oxysporum* is a dynamic species ever acquiring new abilities, e.g., the ability to infect, colonise and cause disease in a variety of specific crops or crop cultivars, ability to break down substrates, ability to produce metabolites. The *formae speciales* of powdery mildews (e.g., *Erysiphe graminis*) and of rusts (e.g. *Puccinia graminis*) on different cereal crops and on grass genera are other examples and represent the biotrophic path in evolution. Thus, within a single morphological species we may have subgroups with either very narrow, or sometimes quite broad host ranges as, for example, in *Gibberella fujikuroi*/*Fusarium moniliforme* (Hsieh, Smith & Snyder, 1979), *Nectria haematococca*/*Fusarium solani* (Matuo & Snyder, 1973; Kuhlman, 1982) and *Phytophthora megasperma* (Hansen, 1987). Examples of subgroups that occur within some fungal morphospecies are listed by Brasier (1987). Their continued presence suggests that they function in reproductive isolation and it can be argued that they are a product of allopatric speciation.

A major internal factor in evolution could be mutation, despite the fact that mutants for any one gene arise very rarely (see Caten, 1987). Neither

heterokaryosis nor parasexuality can account for the extraordinary diversity in the fungal Kingdom and obviously are of little significance in fungal evolution. Indeed, the fungal genome maintains its identity firstly by its own cell wall (so much so, we have to get rid of this barrier in our attempts at protoplasmic fusion!) and, additionally, by developing a vegetative incompatibility system that restricts or blocks heterokaryon formation or hybridisation between genetically dissimilar strains. The identity is reflected in the isogenic or near isogenic and even clonal relatedness of isolates of taxa obtained from locations hundreds and thousands of miles apart and is confirmation of the widespread occurrence of individual clones that show little variation. As Caten (1987) pertinently notes, "the very existence of an individual is testimony to the fitness of its genotype".

Saprophytic fungi also have their strategies and the saprotrophic fungal genome can acquire abilities on its own. Thus, Brasier (1987) notes that "opportunistic nutritional strategies may often lead to divergence among saprotrophs". In a study of strains of *Neurospora* collected from nature, Perkins, Turner and Barry (1976) recorded two sub-populations in *N. intermedia*, one occurring on food and food wastes in Southeast Asia, and the other on burnt substrates in the tropics in general. Though compatible and capable of hybridising, hybrids between individuals of these sub-populations apparently do not survive in nature.

From a study of numerous isolates of *Phytophthora megasperma* on diverse hosts Hansen (1987, p. 332) concluded that *P. megasperma* "is actively speciating with differences in host specificity and karyotype providing the requisite isolation between populations". These, and other similar examples which can be cited (see Brasier, 1987) testify to the fact that specialisation may not be visible at the level of traditionally acceptable taxonomic characters such as morphology, but is reflected in host specificity, or substrate or habitat preference, or other similar parameters.

Among the Hymenomycetes, the genus *Armillaria* (Watling, Kile & Gregory, 1982) appears to be unique in having a diploid mycelium in nature (Korhonen & Hintikka, 1974). *A. mellea* is probably one of the most 'successful' among the Hymenomycetes and so one might ask many questions concerning its evolution: has diploidy been advantageous, if so why? Is it essential for the development of highly differentiated structures such as rhizomorphs? How old or ancient is it a feature on the time scale of evolution? (*Armillaria* has cutinised rhizomorphs which might help

preservation as a fossil). And finally, does this evolutionary step, the diploid Hymenomycetes, represent a static, declining or expanding group? (Korhonen, 1987). Taking the genus as a whole, Korhonen (1987, p. 308) notes that "there are many closely related species with different nuclear cycles within the genus, suggesting a recently active period of evolution....genetical isolation between intersterility groups of *Armillaria* within continents seems to be complete, even between these groups which, externally, are still almost impossible to distinguish from each other".

A given fungal genome can on its own generate innumerable enzymes at the appropriate time and in the appropriate sequence enabling it to be itself—and evolve on its own. Consider, for example, the remarkable biosynthetic pathways and enzymes by which a *Penicillium* synthesises penicillin G and a *Cephalosporium* (*Acremonium*) synthesises cephalosporin C as part of their lifestyles! Each of these genomes has an identity of its own and a potential to evolve on its own. And there are thousands and thousands of fungal genomes, each unique in its way. The naturalist and the taxonomist know some of them, but they are but a fraction of the summation of fungal genomes still extant, but not yet extinct. How then do we expect to trace the course of evolution of these lowly, unpretentious but beautiful organisms? Why is it that we have as yet no answer to the question of specificity in fungi? Because we expect perfect correlations based on our concept of pathogen versus host, aggressor versus victim. Unfortunately, the more the number of systems we work on, the more remote our chance of getting at a correlation. It is as if when you have had a wonderful correlation, an ugly fact turns up and kills your hypothesis. And that is how it often is in biology. And we must note that species are dynamic; they are evolving; they must and they do.

Host-pathogen interactions are complex and when viewed from the angle of co-evolution (but not from the angle of aggression, parasitism, defence, selection), they assume evolutionary significance. *The validity of interdependence of genomes as a positive (not negative) force in evolution must needs to be reckoned with*, particularly in light of available evidence for and speculations about horizontal gene transfer (see Pirozynski, 1988 for a stimulating exposition of the problem), but this is not the equivalent of natural selection. Let me cite a few examples of co-evolution: the fungus-scale insect-tree association seen in *Septobasidium* (Couch, 1938), fungal-ambrosia beetle and fungus-leaf cutting ants association (see Subramanian, 1983) and the fungus-

insect association seen in fungal groups so widely separated and distinct as *Coelomomyces* (Couch & Bland, 1985) and the Laboulbeniales (Tavares, 1985).

EPILOGUE

Some years ago I wrote a paper on the subject of the mechanisms of evolution especially as reflected in the philosophy of the Vedanta which presents a most remarkable synthesis of science and religion (Subramanian, 1973). This paper attracted some attention, notably from scientists and molecular biologists. Later in 1982, I had the opportunity of discussing the problem with Sir Alister Hardy at Oxford on one of my visits to Britain. From then I have moved further and have been strengthened in reiterating what I wrote then with renewed vigour, but now with support from documented data on fungal behaviour and fungal evolution, not to mention impressive data on animal behaviour and evolution.

In simple terms what all this makes up to is that the prime factor in evolution of the fungi or, for that matter, of any group of organisms, is an internal one I said the prime factor: that means I do not rule out a secondary role for external factors, including natural selection. In any case, we should de-link the question of survival of species from that of their origin.

By now you must be convinced that I am not an evolutionist, and clearly not a scientist! Whatever I may or may not be, I confess I find it difficult to subscribe to reductionism, though I am quite convinced that new knowledge might still come by taking a reductionist posture. Someone asked Gunther Stent. "Are you then not a reductionist? Do you not believe that all human behaviour can be simply reduced to molecular biology in the long run?" Let me conclude by quoting Stent's reply:

"On the contrary, I believe that science is, by nature, reductionist, but I also believe that reductionism will not carry us all the way. One of the reasons why I think science will eventually peter out is because you must always explain some higher level in terms of some lower level—that's what scientists have to do. But I think that when finally we get to sufficiently complex things, this will not be possible. It is precisely because I think reductionism will have to fail, that I believe that science is coming to an end."

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