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Review article

Symbiosis Redefined: Symbiotic Features of Virus-Host-Interactions

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Abstract

A new definition of the term "symbiosis" is given by describing it as "the interaction of dissimilar genomes". This definition excludes any statement as to harm or benefit and includes interactions between viruses and hosts, genomes within cells, and between cells and multicellular organisms.

Keywords: genome, viruses, symbiosis

Since its introduction by de Bary (1879) the term "symbiosis" has gone through an interesting history of changes in definition and practical use. Different meanings range from a sort of counterpart of parasitism including such anthropogenic features as harm and benefit to the Gaia-hypothesis (Margulis, 1990) which postulates that our whole planet is a giant symbiotic system.

In recent time growing consensus (Reisser, 1992) is observed to go back to the "roots", i.e. to use the term symbiosis in its original sense according to the definition of de Bary as "living together of dissimilar organisms" and thus to abandon the fatal triad of "symbiosis – mutualism – parasitism" which because of its anthropogenic definition has caused much unfruitful discussion and wasted much effort in symbiosis research. However, unquestioned until now is the fact that the classical definition of "symbiosis" refers to "organisms", i.e. to organizational structures to which apply the traditional features of division,

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metabolism, reaction to outside stimuli and mutability. With the exception of the last one, viruses do not show those characteristics and therefore are traditionally not regarded as organisms. However, it is well established that organization and behaviour of organisms are directed by their genome. Thus the concept of the organism or the cell as the basic entity of life has changed since the times of de Bary. Instead, genes have been recognized as the essential organizational structures on which the phenomenon of life is based.

A genome may be defined as a set of genes which carries the information necessary to guarantee its own replication and proliferation. Accordingly, a cell or an organism may be regarded as the tool used by a genome to interact with its environment and thus to guarantee its replication and evolutionary success. Thus, as to the definition of "symbiosis" by de Bary, I propose to replace the term "organism" by "genome" and to define instead "symbiosis" as the "interaction of dissimilar genomes".

As to cells, this interaction can take place on different organizational levels, i.e. within and between individual cells as well as between multicellular organisms. Each cell contains at least one genome. This is the case in prokaryotes and few eukaryotes. Most eukaryotic cells contain several genomes which interact with each other: two genomes in fungal and animal cells, and three in plant cells.

The above definition of a genome applies also to viruses. Actually, viruses contain those types of genomes which are most abundant in our biosphere. For their replication they need to interact with genomes of cells by establishing with them a relationship which is symbiotic by definition.

The commonly held view found in most textbooks that viruses are generally detrimental to their hosts is biased by the fact that indeed traditionally most research on virus-host-interactions centers on viruses causing diseases and death in bacteria, animals, and plants. However, I will try to show that virus-host-systems, in principle, reflect the same plethora of different types of symbiotic interactions as is observed among cells. They range from interactions which are detrimental to the host by killing it to those where hosts continuously bear or release viruses without being harmed by them, and to systems where viruses are essentially needed for host development.

In prokaryotes, two types of host-virus-interactions have been studied best. They are well known from textbooks and do not need to be discussed in detail: the lytic and the lysogenic type of interaction. The lytic type ends up in a destruction of the host cell whereas in the lysogenic status, host and virus have established a stable relationship potentially enduring many cell generations. In a lysogenic relationship induction of the lytic cycle is possible either spontaneously or, at higher rates, after cells have undergone special treatment by

UV, heat, chemicals, etc., i.e. agents which are not necessarily and commonly present in their natural milieu. It is admissable to assume that the lytic type of host-virus-interaction although being spectacular *in vitro* under the auspices of high host cell titers might not be typical for the bulk of prokaryote-virus-interactions *in situ*. In the natural ecosystem population densities of hosts and thus the chance of a virus to meet an appropriate host are usually much lower. Thus the lysogenic type of host-virus-interaction could offer a better chance for survival of both partners.

As in prokaryote, also in eukaryote hosts the interaction with viruses has not to be detrimental per se. Well known examples are viruses which are transmitted by a special carrier organism (vector) such as arthropods, without causing any harm to them. In some cases viruses such as arboviruses and phytoarboviruses even can replicate in their vectors. A growing amount of data indicates that viruses might even be necessary for host development and survival; some parasitoid wasps can develop only in interaction with special viruses (Polydnaviridae) (Louis, 1989).

Non-lethal virus-host-interactions are also common in kormophytes. Most spectacular examples are: e.g. mosaic formation in *Abutilon* sp. due to the Abutilon Mosaic Virus or colour breaking in petals of *Tulipa* sp. by the Tulip Breaking Virus (Bos, 1983).

Recent studies on phycoviruses (viruses of eukaryotic algae, for an overview, see Reisser, 1991) indicate that also in thallophytes different types of host-virus-interactions exist. The lytic type has been studied best: *Chlorella*-viruses invade special strains of *Chlorella* sp. (Chlorophyceae) by a phage-like mechanism. After viruses have been replicated to about 200–400 particles per cell, the host bursts (Reisser et al., 1986). Although less well documented, there are however conclusive data indicating that also other types of host-virus-interactions exist in thallophytes. In multicellular specimens of chlorophycean algae, virus-infection is usually restricted to only few cells, leaving other parts of the host intact (Reisser, 1991). There is even some evidence for a lysogenic type of interaction in some phaeophyceae (Müller et al., 1990) and chlorophyceae (Dodds, 1979).

In conclusion, a growing amount of data shows that viruses are not generally detrimental to their host but may instead be necessary for its development or at least neutral to its well-being. This also makes sense under the aspects of the ecology of virus-host-interactions; for a virus it is of general advantage not to wipe out the complete host population, i.e. the vehicle of the propagation of its genome.

Considering all available information together makes plausible that virus-host-interactions show an amazing plethora of different kinds of relationships which are all truly symbiotic in the sense of an interaction of different kinds of genomes. As to the general concept of symbiosis formation, this again stresses its importance as an evolutionary factor. Viruses are well known as vehicles of a lateral gene transfer which thus may be involved, besides mutation, in the establishment of new characters and species.

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