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The Importance of Symbioses in Biological Systems

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Jan Sapp opined back in 1994 that "*Symbiosis is still not taught as a central principle of biological evolution on par with Darwinian theory and the neo-Mendelian synthesis of heredity*" [1]. A decade later she came to the same conclusion that things had not really changed much [2]. So why is the concept of symbiosis generally treated as a niche aspect of biological principles, rather than a fundamentally morphological and functional component of terrestrial and aquatic biological systems? The answer is likely three-fold: 1) The history and sequence of biological discovery has been relatively slow, excluding of course the last 100 years; 2) Scientific procedures and thought processes, by nature, basically dictate skepticism until a preponderance of empirical data support a paradigm shift; and 3) Those of us who study formally symbioses must articulate the need for biologists to re-examine biological systems at all levels to include these intimate inter-species interactions.

Before I go any further, I think it is necessary to ensure that a common definition of symbiosis is used. H. Anton De Bary (in the late 1800's) originally coined the term symbiosis to encompass interactions where different species live together. Because he worked with lichens, which most scientists today assume are mutualistic associations, some have limited the use of the term symbiosis to mutually beneficial encounters. However, modern symbiologist generally use the term symbiosis to include all intimate inter-species associations, including parasitism (where one symbiont is harmed) and commensalism (where one symbiont benefits, while the other is essentially unaffected in any significant way).

Prior to the advent of microscopy, symbiotic interactions between species were limited to macroscopic observations. Even then, numerous, clear examples of symbioses were known both terrestrially and aquatically, including ectoparasites like fleas and ticks on humans and other mammals, crustaceans attached to the scales of fishes, remoras associated with larger fishes and aquatic mammals, etc. With the expanding development and use of microscopy in the late 1800's, and subsequent development of electron microscopy, studies on the basic unit of life on Earth – the cell – expanded exponentially. With the additional tools of molecular biology added to the mix, we have subsequently discovered more about life in the last 50 years than all previously recorded human history combined.

Two salient discoveries have emerged, relative to the assertion that symbioses are integral parts of terrestrial and aquatic biological systems: 1) All organisms are involved in symbioses, especially when we look at bacterial presence on and in tissues and cells of biota; and 2) The basic differences between the two major cell types – prokaryotes and eukaryotes – are arguably directly the result of symbioses. On point one, no organisms are axenic (or aposymbiotic; i.e., without symbionts); thus, the evolution of all species is potentially influenced by symbioses [3]. On point two, although skepticism was extremely high when the Serial Endosymbiotic Theory (SET) was initially proposed indicating eukaryotic cells are the result of symbioses between various types of bacteria, few now doubt the veracity of this theory given the discovery of mitochondrial and plastid genomes [4,5]. The first organisms were likely anaerobic and lived in ancient seas. As cyanobacteria started using water for a metabolic hydrogen source, oxygen gas – toxic to many of the anaerobes - began to increase in the oceans and atmosphere. Aerobic bacteria, which were able to cope with these rising oxygen levels, were engulfed by soft-bodied anaerobic bacteria to form a mutualism. The aerobic bacteria eventually became mitochondria, but retained part of their genome. Subsequently, some lineages of these cells engulfed cyanobacteria, which eventually became chloroplasts with independent genomes as well. So the evidence shows the cradle of complex organisms started as symbioses in the primitive oceans!

Those of us who study symbioses, at all levels, spend considerable amounts of research time attempting to characterize the cost/benefit ratios of the symbionts involved in specific associations. My specific research area involves marine behavioral and physiological symbioses. Regardless of the organismal focus, cost/benefit data are required if we are to effectively evaluate the relationships to determine whether they are mutualistic, commensalistic or parasitic, as this can help us understand why the associations exist and persist. However, Speidel [6] suggests "*Perhaps it would be better to see them not so much in terms of what each partner is getting out of the relationship, but in terms of how the structure as a whole is functioning.*" How an organism functions in many symbioses cannot be defined without referring to both the host and its symbionts. For example, a termite without its symbiotic gut microbes providing the ability to process cellulose starves and dies, even though the termite still ingests wood [3]. Thus, genetically speaking, the phenotype of a termite (or many other herbivores) must include the genotypes of both the host and symbionts. This same principle could be applied to the marine environment where corals (and other cnidarians) house symbiotic algae called zooxanthellae in their tissues. In many cases, "bleaching" or loss of zooxanthellae can trigger rapid health decline and potential death of corals. So again, the coral animal and its photosynthesizing symbionts form a functional unit. Betsy Dyer [7] illustrates the point that the phenotype is a composite of all organisms in associations, and states specifically "*Organisms as separate, completely definable entities may not exist.*" To accentuate this point, a recent study has shown that symbiotic bacteria in the guts of mice are critical components in ensuring the normal development of neural pathways for motor and anxiety behaviors [8].

So clearly symbioses are critical components in the evolutionary process of nearly all organisms on the planet. This conclusion holds true for present-day bacteria, too, as "life-like" bacteria-phage viruses associate and spread genetic material among bacteria and potentially their hosts. So how do we move from the ancillary discussions of

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fascinating symbioses as side-notes to our mainstream biological tenets (such as evolution, genetics, etc.)? … And at what level (scholastically) do we start? The good news is the information movement has already begun with the integration and introduction of the endosymbiotic eukaryotic origins topic into textbooks for introductory biology majors. Thus, students early on are learning about the power of symbiotic interactions in biology. However, those same textbooks generally fall short on the topic of composite genotypes and phenotypes. To compensate, those of us who teach these introductory biology classes have an excellent opportunity to "supplement" the textbooks, and point out with lucid examples why the traditional definitions of genotype and phenotype - in reference to "an" organism - are often wrong. The concluding sentence in Betsy Dyer's provocative paper entitled "Symbiosis and Organismal Boundaries" [7] illustrates this final point when she states "*Is the organism necessary? The answer from the point of view of this paper is … Yes, all of them.*"

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