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Symbiont Acquisition as Neoseme: Origin of Species and Higher Taxa

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Abstract

We examine the hypothesis that, in the origin of species and higher taxa of eukaryotes, symbiont acquisition followed by partner integration has been equivalent to neoseme appearance leading to speciation.

The formation of stable symbiotic associations involves partner-surface recognition, behavioral and metabolic interaction, and, in some cases, gene product (RNA, protein) and genic (RNA, DNA) integration. This analysis is applied here to examples of neosemes that define specific taxa and to neosemes in plants, fungi and animals that involve the appearance of new types of tissue.

If this hypothesis is correct — if the origin of major genetic variation leading to speciation and even higher taxa may occur through symbiont acquisition and integration — then the analysis of "origins of species and higher taxa" becomes analogous to the study of microbial community ecology.

Keywords: cell evolution, higher taxa, macroevolution, microbial ecology, neosemes, origin of species, semes, serial endosymbiotic theory

A NEODARWINIST DILEMMA

"Striving to be man, the worm mounts through all the spires of form."

Ralph Waldo Emerson, "May-Day", 1867

Neodarwinists, in defining evolution as "changes in gene frequency in natural populations," have been severely criticized for never having adequately explained the appearance of new structural or functional parts of an organism formed of one or usually more genes (i.e., semes; Hanson, 1977; Margulis, 1981). If evolution proceeds by accumulation of chance mutations, what is the explanation of "sudden" appearance (Eldredge and Gould, 1972; Gould and Eldredge, 1977; Simpson, 1944) of new traits (i.e., neosemes, Hanson, 1977; Margulis, 1981). Statements such as "...the evidence is accumulating that chance is insufficient to explain the appearance of marvellously coordinated structures and perfectly adapted behavior which biologists are now uncovering" (Taylor, 1983, p. 15) are common in the secondary literature. In spite of external chiding the origin of semes has not been fully addressed in either the primary literature or the professional textbooks of evolution (e.g., Ayala and Valentine, 1979; Futuyma, 1986; Kimura, 1983; Stanley, 1979; White, 1978). Macroevolutionary theories postulating processes qualitatively different from those of microevolution to explain the origin of semes are considered unfounded (Hecht and Hoffman, 1986).

The inability to account properly for complex semes such as heat-resistant endospores, photosynthesis, cilia, eyes, and seeds from putative precursors by accumulation of mutations has led to criticism and even rejection of the entire neodarwinist point of view: "While it is not difficult to believe that some small structural change, such as a change in the shape of a bird's bill, occurs by chance, it is very difficult to believe that a complex structure like the eye, which involves many coordinated changes, came about by chance, and especially as it did so several times. Darwin himself was flummoxed by this. 'When I think of the eye, I shudder,' he said" (Taylor, 1983, p. 2–4). "The ascription of all changes in form to chance has long caused raised eyebrows" (Taylor, 1983, p. 4).

We agree with the many critics of neodarwinism: the accumulation of small mutations alone is grossly inadequate to explain all neoseme appearance and speciation associated with it. Alternatively, the importance of symbiosis in speciation was forcefully argued by Wallin (1927). A rationale for the importance of symbiosis in evolution has been described by Margulis and Bermudes (1985) and Taylor (1979; 1983). Here we further discuss the sudden appearance of certain new semes which are correlated with – and in many cases define — the appearance of new taxa. We conclude certain taxa are products of the acquisition and integration of symbionts.

PROKARYOTIC SEME ACQUISITION

> For biologists, eukaryotic evolution seemed to be unavoidably related to genetic isolation of different species.... In contrast, bacteria lacked genetic isolation and consequent differentiation into species. (Sonea and Panisset, 1983, p. 112).

Prokaryotes have single, homologous genomes, hence they are monogenomic monads (if "unicellular") or polymonads (if "multicellular") (Taylor, 1974). Having single genomes, unlike the eukaryotes, the bacteria are not products of symbiosis. Yet even in bacteria neoseme appearance is not merely attributable to accumulation of single mutations. Rather, some neoseme appearances in prokaryotes are apparently ascribable to DNA acquisition, viral and plasmid transfer, and other nucleic acid accumulation, transposition, and transfer phenomena. One of the clearest examples of neoseme accumulation in prokaryotes is heavy metal resistance in gram-negative bacteria (Silver, 1983). The resistance is plasmid-borne. This explanation defers the problem of the origin of heavy metal resistance but it does provide a mechanism for rapid genetic change (seme acquisition) in prokaryotes.

In bacteria the major evolutionary process requiring explanation is the origin of these prokaryotic semes: the plethora of metabolic pathways, genetic regulation phenomena, motility, spore-formation, and other kinds of physiological and morphological differentiation. There is general agreement that since the time these semes originated many sorts of nucleic acid transformations have been involved in their modification and acquisition, including, of course, single base-pair mutations. Much progress has already been made toward a molecular understanding of microbial evolution (Saier and Jacobson, 1984; Mortlock, ed., 1984; Schleifer and Stackebrandt, eds., 1985).

Because of the ease and ubiquity of seme flow (via transferable "small replicons") in prokaryotes, the existence of "bacterial species" is the subject of much contentiousness (Sonea and Panisset, 1983). In spite of the difficulty of unambiguous delineation of bacterial species, most biologists feel that bacteria are distinctive enough to be identified, named, and grouped into genera and species. It is likely that stabilizing selection is the primary agent of maintenance of bacterial species in nature. Horizontal genetic transfer, very common in prokaryotes, is far more limited in eukaryotes. Hence in eukaryotes species are far more stable entities than in prokaryotes.

EUKARYOTE NEOSEMES AND THE ORIGINS OF SPECIES

> The correlation of bacterial products and the products of specialized cells in plants and animals demonstrates the feasibility of the principle of Symbionticism* in the origin of species (Wallin, 1927, p. 145). . . .*Symbionticism is a fundamental causative factor in the origin of species* (Wallin, 1927, p. 214).

Species of eukaryotes, unlike those of bacteria, tend to be clearly recognizable. Naturalists as taxonomists, including paleontologists, concur more readily than microbiologists on the erection of new species names and descriptions. In both zoological and botanical literature, species are perceived as relatively stable and distinguishable: they are populations of individuals with measurable and observable traits in common. The traits used tend to be distinctive and both qualitative and quantitative (Blackwelder, 1967), i.e., they are semes. These semes are described sufficiently to yield a species definition satisfactory to professional systematists and taxonomists even in the protistological and mycological literature. In protoctista, fungi, plants, and nearly all animals, the assignment of an individual to a species can be determined solely on the basis of comparative morphology of individuals in populations. Descriptions of new species depend on consistency in populations that is judged, by the specialist, sufficiently different from others to warrant formation of a new specific group. Even in the case of angiosperms, insects, or mammals, groups in which investigators can often study matings and their fertility, species assignments are still nearly exclusively on distinctive morphology.

We examine the following hypothesis:

> Neoseme appearance in eukaryotes which, in certain cases, leads to speciation (and, in some cases, forms the bases of lineages that become higher taxa) sometimes occurs by symbiont acquisition followed by partner integration.

We have listed some examples of symbioses as emergent from presumed ancestors and the correlated change in taxa (Table 1). All organisms listed in column 3 (emergent partnerships) are found in nature as regularly associated symbionts.

In perhaps thirty-million species of eukaryotes (Lewin, 1986) speciation is likely to have occurred by many different processes. However, in many cases

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* Wallin (1927, p. 8) defines Symbionticism as "The establishment of intimate microsymbiotic complexes. . ."

Table 1. Symbioses correlated with taxonomic changes: some examples*

"Symbiont"	+	"Host"	Emergent partnerships	Level of taxon change of host
Bacteria (monogenomic)				
	+	bacteria	all eukaryotes[1,2]	kingdom or superkingdom
	+	protists	*Cyanophora paradoxa*[1,2]	genus
	+	legumes	nodulated legumes[1,2]	subfamily
	+	ferns	*Azolla*[1,2]	genus
	+	fish	luminous fish[1,2]	genera, families
	+	tunicates	*Pyrosoma*[2]	genera, families
	+	tunicates	green didemnids[1,2]	species, subspecies
	+	amoebae	xD-amoeba[1,2]	subspecies
Fungi (digenomic at least)	+	*Fucus*	*Ascophyllum*[1]	genus
	+	termites	gardening termites[1]	families
Protists (tri- or quadri-genomic at least)	+	cockroaches	wood-eating cockroaches, termites[1,2]	families, classes
	+	quadruped mammals	ruminants[1,2]	families
	+	protists	*Paramecium bursaria*[1,2]	species

*See Table 2 for list of phylum-level symbioses.

[1] See Ahmadjian and Paracer, 1986

[2] See Smith and Douglas, 1987

symbiont acquisition is the explanation of the origin of semes associated with the characterization of a given taxon, leading us to believe that symbioses have apparently played an important role in forming higher taxa. A survey of phyla reveals a strong correlation of symbiosis with evolutionary lineage. At least 28 of 75 phyla (bacteria excluded) in the five kingdom system either possess symbiotically-derived organelles unique or defining to the taxa, have their appearance in the fossil record correlated with symbiosis, or are comprised largely or entirely of symbiotic members (Table 2). The relative number of symbiotic phyla in each kingdom is presented in Table 3.

Through the assessment of higher taxa, an answer to the problem posed by Taylor (1979) on determining the impact of symbiosis is postulated: a symbiosis is important evolutionarily if it is ubiquitous or defining to a higher taxon such that all or most members are unified by possessing it (Margulis and Bermudes, 1985). This assumes that at least some populations which

Table 2. Phyla with members which are completely or largely symbiotic

Kingdom	Phyla	Characteristics of symbionts or hosts
Protoctista		
	Karyoblastea	methanogenic endosymbionts
	Chrysophyta	plastids*
	Haptophyta	plastids*
	Euglenophyta	plastids*
	Zoomastigina	symbiotic in termites and roaches
	Xanthophyta	plastids*
	Eustigmatophyta	plastids*
	Bacillariophyta	plastids*
	Phaeophyta	plastids*
	Rhodophyta	plastids*
	Gamophyta	plastids*
	Chlorophyta	plastids*
	Apicomplexa	symbiotic in animals
	Cnidosporidia	symbiotic in animals
	Plasmodiophoromycota	symbiotic in plants
Fungi		
	Basidiomycota	ectomycorrhizae
	Mycophycophyta (usually ascomycetes)	symbiotic with photoautotrophs (forming lichens)
Animalia		
	Cnidaria	symbiotic origin of nematocysts?**
	Acanthocephala	symbiotic in animals
	Pentastoma	symbiotic in vertebrates
	Vestimentifera	harbor symbiotic sulfide-oxidizing bacteria
Planta		
	Psilophyta	mycorrhizae
	Filicinophyta	mycorrhizae
	Cycadophyta	cyanobacterial root symbionts
	Coniferophyta	mycorrhizae
	Angiospermophyta	mycorrhizae
	Ginkophyta	mycorrhizae

* Plastids derived by symbiosis

** Prof. Pierre Tardent, Dept. of Zoology, University of Zürich, Zürich, Switzerland, personal communication, 1986.

Based on phyla as presented in *Five Kingdoms* (Margulis and Schwartz, 1987).
For protoctista details see Margulis et al., (eds.), in press.

Table 3. Relative numbers of symbiosis-correlated phyla in the four eukaryotic kingdoms

Kingdom	#Phyla	#Symbiotic	%Symbiotic
Protoctista	27	15	56
Fungi	5	2	40
Animalia	33	4	12
Planta	10	7	70
Total	75	28	37

Based on the phyla as presented in *Five Kingdoms* (Margulis and Schwartz, 1987).

belong to taxa correlated with symbionts would have lost their symbionts were they not essential to the taxon in question. A red alga is not a red alga without its symbiotically-derived rhodoplasts (red plastids). We concede that some phyla (e.g., Mycophycophyta) are merely form taxa in which the members are grouped together based upon their symbioses rather than a common phylogeny. However most of the others probably are monophyletic in the sense that monophyletic hosts share the same symbiotic ancestors.

Formation of stable symbiotic associations involve many analyzable processes including the following: partner surface recognition, behavioral and metabolic interaction, control of relative population growth (e.g., the numbers of each partner in the association), gene product (RNA, protein) interaction, or even genic (RNA, DNA) integration (Margulis, 1976). Instances in which natural selection reduces metabolic or structural redundancies rendered superfluous by the symbiosis (e.g., cell walls, amino acid synthetic pathways) have been reviewed (Ahmadjian and Paracer, 1986; Smith and Douglas, 1987). Analysis of several well-known cases of symbioses suggests there is a general role of symbiont integration in the formation of some new semes leading to new species and, with refinement and adaptive radiation, to higher taxa (Table 2). Symbiotic processes have led to fundamental or defining characteristics of these taxa. We believe the general role of symbiosis as a mechanism in the origin of protoctist, fungal, plant, and animal species has been inadequately recognized. The concept of symbiosis and subsequent partner integration as a major mechanism of innovation in evolution needs to be revived and given thorough discussion.

As early as 1921 Buchner recognized the potential of symbioses to lead to speciation (translated and cited in Wallin, 1927, p. 146). In his extensive review (1953) Buchner wrote:

> Symbiosis research has provided zoological science with the knowledge of abundant devices previously unknown or misunderstood. It has discovered the multiple sites of the symbionts and the organs and devices serving transmission, and it has shown that the two partners are already intimately related during embryonic and larval development. Symbiosis research can also furnish a basis for evaluating related questions, and it already has various criteria to assist in explaining the phylogeny of the individual symbioses which sometimes have deep-reaching effects on the formation of the hosts and their mode of life (Buchner, 1965 translation, p. 828).

Although neoseme acquisition in prokaryotes (monads and polymonads) may be explicable by DNA accumulation and transfer phenomena, we believe that, in the origin of species to higher taxa of many well-studied eukaryotes from all four eukaryotic kingdoms, neoseme appearance leading to speciation has been directly due to symbiont acquisition followed by partner integration. The general processes of formation of stable associations listed above can be correlated with the appearance of new taxa defined by new semes. This analysis has been applied to acquisition of phototropic behavior (Lindholm, 1985). It also can be applied to the following neosemes comprising tissues and organs: **light organs** of teleost fish (such as those in the genera *Monocentris* and *Kryptophaneron*) containing luminous bacteria (for example *Photobacterium fischeri* in *Monocentris* and *Vibrio harveyi* in *Kryptophaneron*, Haygood and Cohn, 1986; Nealson et al., 1981); **cavities** in the dorsal surface of *Azolla* leaves for harboring nitrogen fixing cyanobacteria (e.g., *Anabaena*, Grilli Caiola and Albertano, in press); and complex **thalli** and **soredia** of lichens composed of the green alga *Trebouxia* with fungal symbionts (Honegger, in press) (Table 4).

Table 4. Selected examples of symbiotic-induced organ or tissue differentiation

Partnerships		Tissue
Kryptopharenon^{a}	*Vibrio harveyi*^{b,1,2}	flashlight organ
Azolla^{pl}	*Anabaena*^{b,1,2}	dorsal leaf cavities
Cladonia^{f}	*Trebouxia*^{pr,1,2}	thalli, soredia
Glycine^{pl}	*Rhizobium*^{b,1,2}	root nodules
Paraspondia^{pl}	*Rhizobium*^{b,1,2}	stem nodules
Kalanchoë^{pl}	*Agrobacterium*^{b,1,2}	crown galls
Macrozamia^{pl}	*Anabaena*^{b,1,2}	coralloid roots

Key: a = animal, pl = plant, f = fungus, pr = protoctist, b = bacterium

[1] See Ahmadjian and Paracer, 1986

[2] See Smith and Douglas, 1987

MICROBIAL COMMUNITY ECOLOGY, NEW SEMES AND NEW SPECIES

> The nature of the exact responses of microsymbionts in symbiosis, remains to be determined. One thing appears certain, namely, that if the evolutionary origin of a specialized cell were dependent upon a microsymbiont, then the differentiation of the specialized cell in ontogenetic development must, primarily, be dependent upon the microsymbionts (mitochondria) associated with that cell (Wallin, 1927, p. 128–129).

Ecology is the interaction of populations of organisms forming communities. Changes in both population numbers and structure (which includes the introduction of new members) may have profound ecological effects. Ecological factors subject to alteration by changes in population numbers and community structure include rates of energy flow and utilization, carrying capacity, population, age, structure, and many others.

Animals, plants, protoctists and fungi can be considered communities of microbes. These eukaryotes are communities in the sense that they are individual cells composed of populations of various organelles (formerly microbes) and entire organisms composed of populations of cells. In special cases referred to here (those in which speciation is directly correlated with changes in the number or type of microbes comprising a distinctive community) speciation becomes equivalent to an identifiable change in community ecology. Population phenomena, especially introduction of new members into communities, are fundamental aspects of symbioses.

The origin of Darwin's genetic variation that leads to speciation and origin of even higher taxa — at least in the examples presented — correlates directly with symbiont acquisition and integration. The concept that *all* eukaryotes are co-evolved symbionts, furthermore, has important implications for ontogeny (i.e. embryonic development). Embryonic development in plants and animals is the emergence of entities with distinctive morphologies composed of large numbers of differentiated cells organized into tissues and organ systems. The symbiosis view developed here mandates that the formation of such multicellular entities results from the reproduction, growth, metabolic and genetic interactions of its components — former free-living organisms now partners. A corollary of this viewpoint is that the analysis of embryological development and its associated cell and tissue differentiation is the analysis of a specialized kind of ecological community. The comprehension and description of ontogeny will require the methods of ecological community analysis: the various populations, their genetic systems, metabolic interactions, growth, and numbers must be assessed. We recognize, then, that ecological descriptions of the component populations and their changes through time are homologous —not merely analogous — to descriptions of embryonic development. The implications of the symbiosis view are clear: although molecular biological methods are indispensable, the nonsymbiotic model (i.e., genes determine proteins which determine the development of embryos) is simplistic and untenable. The current "molecular biology of embryo development" approach must be reoriented and expanded. It must be replaced with a "molecular biology of microbial-community analysis" in which "the community" is recognized to be a highly confined, tightly integrated, co-evolved complex that undegoes cyclical (successional) changes in a biotic habitat (symbiotrophisms; Lewis, 1973).

Summary

We reject the gradualist tenet that accumulation of mutations is primarily responsible for neoseme appearance. The worm not only fails to strive to become man, he does not mount through any spires of form. Rather we support the three major claims of Wallin (1927): the origin of mitochondria (and plastids) from respiring bacterial symbionts, the importance of symbiosis in the appearance of evolutionary novelty (origin of neosemes), and the essential role of integrated microbial symbionts (e.g., mitochondria, plastids) in ontogeny. The first assertion we consider proven, the second we have tried to argue here, and the third, we feel, warrants further discussion and investigation.

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