Darwinian Evolution and Discontinuous Evolution

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We wish to propose a mechanism for evolution of major phyletic differences above the species and genus level and give an explanation for the rapid radiation of species complexes. The Synthetic Theory of Evolution [1] states that speciation proceeds by the addition and modification of genes and their integration into the population's gene pool. The Synthetic Theory fails to explain many important aspects of the evolution of specific and phyletic groupings. More precisely, there is "the problem of explaining macroevolutionary changes in terms of microevolutionary steps" [2].

The earliest and most primitive known members of the every order of mammals already have the basic characteristics of the order. In not a single case is there a continuous sequence from one order to another or to a presumed ancestoral form [3].

New phyletic groups in the fossil record invariable represent new major ecological adaptations [3], and the greatest taxonomic gaps and major morphological changes in the fossil record seem to correspond to major ecological changes in the earth's environment. (By major morphological changes we mean evolutionary novelties allowing major adaptive radiations and development of distinct phyletic groupings.)

How can a new structure be acquired gradually when the intermediate steps have no selective advantage? Bird feathers, the tympanal membrane in amphibia, the mammilian middle ear, wings in insects are just a few of a large number of unique structures which appear suddenly in the fossil record.

The keystone of our theory is that speciation can proceed by the "turning off" (with a mutation) of gene complexes--specifically those which determine developmental pathways. This would be followed by the modification and addition of genes. Major phyletic changes could occur with the turning back on of these gene complexes.

Our theory can explain a number of seemingly unrelated but in reality closely intertwined facts:

1. Williston's Rule [4]. Williston's Rule is the taxonomic rule of thumb that as a group radiates and specializes from its ancestors a, series of similar parts tend to be reduced in number while the remaining parts become more differentiated from each other. For example, in most arthropod groups the number of body segments and appendages is reduced through evolutionary time. In plants, fern leaves have gone from a primitive large, compound leaf to a derived small, simple form [5].

2. The widespread existence of homeotic mutants [6]. Homeosis refers to the replacement of an organ of one segment by the homologus organ of another segment [7]. A well known example of a homeotic mutant is the tetraltera mutant of Drosophila melanogaster which transforms the wings into halteres [8]. Homeotic mutants can easily be explained as the turning on of a previously turned-off developmental pathway.

3. Rapid rates of evolution. There are a multitude of examples of very rapid rates of speciation or explosive radiation of species groups. In the Phillipine Lake Lanao, within a period of less than 10,000 years, 18 closely related species of cyprinid fish have evolved from a common ancestor, Barbus binotatus [9]. (Also see [10, 11, 12, 13]) Major genetic differences between populations can arise exceedingly rapidly with the turning off of gene complexes.

4. The decreasing amount of DNA with increasing specialization. DNA amounts have increased greatly during general evolution. Yet within a taxon there is a significant decrease in DNA content with increasing specialization ([14, 15, 16, 17]). Our model explains this with the following time course: (1) Highly specialized species would have relatively large amounts of heterochromatic material representing turned off genes. (2) These turned off genes could be discarded through time, resulting in a

smaller content of DNA.

5. The ubiquity of gene duplication [18]. Individuals with duplicated critical genes would have a large selective advantage and therefore come to predominate in a given species population, if the turning off of genes and developmental pathways was a common evolutionary occurance.

Rapid Radiation of Gene Complexes

The foregoing observations can be understood if the process of speciation proceeds as follows: 1) turning off (with a mutation) of developmental pathways responsible for the formation of morphological or physiological characters, 2) addition of new genes by duplication and modification, and 3) modification of existing genes. The result of this process would be to increase rapidly the number of species (all descended from a common ancestor). Each of these species is progressively more specialized, and yet has a reduced functional genome [19], although not necessarily a smaller DNA content. (we define specialization as the narrowing of the species' adaptive range or zone). The reduction of the genome and the increase in the specialization and number of species continues until a climatic or other environmental change presents this highly specialized group of species with a challange to which it cannot adapt. At this point each of the highly specialized species faces two alternatives; extinction or major overhaul of its genome [20].

Genetic Control of Mutation Rates and the Evolution of Major Phyletic Differences

To understand our mechanism for evolution of major phyletic differences a small discussion of the genetic control of mutation rates is needed. Spontaneous mutation rates are under genetic control ([21, 22, 23]). The spontaneous mutation rate of an organism is controlled by the accuracy of its repair and replication enzymes. The efficiency of repair enzymes can vary over several orders of magnitude within a single population [24]. Individuals with very high spontaneous mutation rates occur every generation. Normally these individuals will be selected against, because of deleterious somatic as well as germinal effects. However, when a species has achieved a high level of specialization, and therefore has many developmental pathways turned off, and is faced with extinction due to climatic or environmental change, the individuals with a high spontaneous mutation rate offer the genetic line its best chance of survival. The species must reorganize its genome or face extinction. Among those individuals, with a spontaneous mutation rate high enough to reoragnize their genomes by turning on the developmental pathways which they carry around in a non-operative mode, are the ones most likely to survive in a changing environment.

However, the complexes of genes which are turned on are no longer the same complexes of genes which were turned off. While inoperative, these complexes were collecting mutations and duplications. At the same time changes were occurring in the organization of the functional genome and the integration of its development. It is in this new background that the newly turned on gene complexes must operate. By turning on these gene complexes against the different genetic background, a specialized organism is created that has imposed upon it a great number of generalized characteristics. This organism is our <u>new</u> version of Goldschmidt's "hopeful monster" [25], although his method for its origin was decidely different than ours. Since our "hopeful monster" contains

newly turned on gene complexes and developmental pathways against a highly changed genetic background, the possibility of major morphological or physiological changes exists. The majority of these morphological or physiological changes will be nonviable. This majority is what has disparagingly been refered to as the "hopeless monsters" [13]. Nevertheless a very small number of these major changes may have possible preadaptive value, e.g. the elaboration of paranotal lobes in insects into primitive wings, or the modification of reptilian scales into primitive feathers. The small population containing the surviving hopeful monsters may make the critical evolutionary breakthrough serving as the basis of new adaptive radiations and representing the foundation of major phyletic groups.

Viewed in this light, many of the gaps in the fossil record do not represent missing members of an evolutionary sequence. On the contrary, they are gaps! Each is the result of a major developmental change yielding organisms many jumps removed from their predecessors.

We are not so naive as to believe that "hopeful monsters" are the only (or even the major) cause of phyletic evolution. Certainly the continuous evolution of phyletic lines at the family or higher phyletic levels has been well documented in many cases. However, many major phyletic changes cannot be explained by continuous evolution. Our conception of a molecular basis for "hopeful monsters" can explain the sudden appearance of these evolutionary novelties in the fossil record.

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