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Stephen X. Arthur, scientific writer 2011  
[www.sxa-portfolio.com](http://www.sxa-portfolio.com) sxarthur@shaw.ca

*Selected excerpts*

## **Towards a Complete Synthetic Theory of Evolution**

36-page monograph by Stephen Arthur

Directed Studies in Zoology, University of British Columbia  
Supervisor: Dr. Geoffrey Scudder

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### **PROPOSAL**

Let us assume that the discontinuity of the fossil record indicates a fundamental aspect of evolution: that many transitions were not recorded because they did not exist; that these changes involved not gradual transition but sudden leaps in evolution. This, then, would be a significant factor for a complete theory of evolutionary causation to deal with.

The present Synthetic Theory of Evolution is a combination of Darwinian natural selection, Mendelian and quantitative genetics, and statistical mathematics. I propose that by the addition of knowledge of the development of organisms (epigenetics), a solution will be found. Here we may find the means by which organisms can, and have, changed non-randomly and radically, so that: "...whereas the import of the previous evolutionary theories can be sloganized in Jacques Monod's phrase 'Chance and Necessity', the fourth paradigm would substitute slogans such as 'Learning and Innovation', or 'Adapting and Improvising', or, if you like a more with-it jargon, 'Recompiling and Heuristic Search'." (Waddington, 1974, P. vi)

In the remainder of this essay I intend to show the following:

1. Evolution, according to paleontology, has involved many radical and sudden transitions to new "archetypal strategies."
2. Even according to Neo-Darwinian theory, many of the hypothesized transitional forms could not have existed.
3. The adaptability inherent (and selected for) in the developmental processes of living beings allows for—and in a sense directs—these radical changes.
4. The kind of selection involved in the survival of these new types may be quite different from that implied by the strictly Neo-Darwinian model.

## THE PROBLEM

The primary problem is the tendency toward systematic discontinuity in the record of life's history (Frazetta, 1975 see Figure 1.). Most striking is the fact that all fossilizable metazoan phyla appear in the Cambrian except for the chordata, which appear shortly after in the Ordovician. No new animals with an organization unique enough to be classed as a new phylum have evolved in the following half billion years.

By the end of the Paleozoic era the appearance of new classes has all but stopped. Two more classes appear in the next two periods—the mammals and birds. Novel organizations distinct enough to constitute new classes did not develop in the last 135 million years or so.

Orders follow a similar deceleration. For example, of the 50 or so aquatic orders almost all appear in the Lower Paleozoic, then three more in the Middle Paleozoic, and finally four more during the Mesozoic. Then, in the Cenozoic, there is a burst of new ones, the placentals. After the Eocene there are no new chordate orders.

Evolution appears to have been more rapid in the past, in terms of large scale innovation, slowing down in recent times to relatively trivial changes. As well, it seems that sometimes there have been sudden surges in the appearances of many new distinct groups. No correlation with major environmental change has been found.

To state this most clearly: evolution seems often to have proceeded from higher to lower taxonomic rank, rather than the reverse. Figure 2 shows a very simple phyletic hierarchy. It is difficult to visualize it developing through time from the bottom up, so that "the accumulation of the changes of the speciation mode tends towards segregations of higher category." (Simpson, 1944, P. 202).

A second problem for the complete theory to deal with derives directly from the implications of Neo-Darwinian theory. It is generally held that changes in phenotypic differences are always small; organisms are at an adaptive peak, so that any great or sudden alteration in phenotype will disrupt their stable position. It is thought that large scale variants will be selected out and only lesser ones will be tolerated. This implies that evolution proceeds in small steps, and builds gradually.

This view leads to certain contradictions. For one, certain properties could not have originated through accumulation. Changes in the number of segments, appendages, digits or heart chambers obviously require large all-or-none changes. Likewise it is generally accepted that the transition from procaryotes to eucaryotes was essentially instantaneous, as proposed by the endosymbiotic theory (Sagan, 1967, Margulis, 1970).

Secondly, even in many cases where the gradual origination of a property is possible, "it is unwarranted to invoke natural selection before the new function has been assumed. Thus, the small bud that would represent an incipient limb, rather than a benefit, might be a nuisance against which the selective forces would act." (Lovtrup, 1974, p. 486).

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## INTEGRATION, CORRELATION AND ADAPTABILITY

An organism is not an aggregate of "unit" traits or characters. These concepts are merely abstractions devised for communicating observations. Dobzhansky (1970) gives numerous examples of pleiotropic effects, where, for example, the drosophila mutant *vestigial*, referring to reduced wing size, also changes the balancers, the orientation of certain bristles, the wing muscles, the spermatheca shape, developmental rate, fecundity and viability. Dobzhansky cautions that talking about traits as though they were independent entities is responsible for much confusion in biological and evolutionary thought.

Frazetta (1975) emphasizes that the complex adaptations of organisms can be thought of as analogous to a machine where the performance depends upon exact cooperation among its parts. No part can be altered without changing the functioning of the entire machine. He discusses the Peaucellier straight line mechanism (Figure 3) to illustrate this point. Here the point P must always move in a straight line for the proper functioning of the machine. In order to shift the trajectory of P to one side there must be a simultaneous change in the lengths of each element, in accordance with specific rules of proportion.

The acquisition of a biological adaptation would require the same sort of integration. In fact, organisms are capable of this: ...Several people have shown that if, by some experimental means, the retina and eyeball are made larger than normal, that in itself will cause a larger lens to appear, of at least approximately the appropriate size for vision.

Frazetta discusses examples of integrated change in evolution. One comes from the work of Hampe, 1959, on the differences in hind-leg structure between modern birds and Archaeopteryx (Figure 4). By allowing the normally reduced fibula of a chick to have access to a larger supply of cells during embryonic development, it was able to grow to full length as in Archaeopteryx. As well, the ankle bones, normally fused to the tibia, remained separate. So this difference between Archaeopteryx and modern birds could have been a minor genetic mutation that restricted the amount of material available to the fibula. This then automatically influenced the factors controlling ankle development, and resulted in a new functional arrangement.

...

A third example comes from Waddington (1962). He shows that a mutant gene in drosophila can move the developing limb-buds closer together. They then interact to produce a common appendage reminiscent of a labium. Such a complex alteration as this then, can occur by the influence of one simple mutation, rather than selection of many small changes that gradually tend to form a labium structure.

There is another kind of coordinated regulation that I will call "correlation", as opposed to "integration". This is a convenience for presentation, for the two can hardly be separated. Correlation becomes apparent when studying growth (Sinnott, 1963, Frazetta, 1975). Growth is not an irregular process; the various dimensions are closely related. Though some dimensions grow faster than others, the ratio of their exponential rates is constant. Form changes progressively during development in a constant, correlated fashion. In fact, even relative chemical composition follows this relationship.

These correlated ratios are determined by simple genes (Sinnott, 1963). In fruit, for instance, there are genes which tend to flatten, elongate or otherwise distort the shape, and they show independent assortment into normal Mendelian ratios. Some have even been located on linkage and chromosome maps. Likewise such genes are recognized in drosophila that affect the form of the body, eyes and wings. Sinnott (p. 101) observes that "Genes show

their particulate character as they segregate and recombine, but not as they govern development. Once a genotype has been established it controls the entire living system as a whole."

The most striking evidence of the evolutionary significance of developmental correlation comes from d'Arcy Thompson's *On Growth and Form* (1942). Here he has shown how the shape of one species may be transformed mathematically into that of another, as in Figure 6. These shapes have not been arbitrarily re-designed; they have been evenly distorted according to simple equations. Each point retains the same coordinates but the grid has been systematically distorted. This is precisely the sort of change that we have seen can be accomplished by single genes. So we again have reason to de-emphasize the significance of random cumulative changes.

It becomes apparent that the aspects of integration and correlation just discussed provide an organism with a capacity for adjusting itself to the environment and to internal changes in an advantageous manner. I will refer to this ability as *adaptability*. Frazetta has another bone example that illustrates this beautifully:...

[quote]

...In a population of moderately sized animals, the need to possess a system of appropriate responses between weight and limb width can result in a biological organization that "recognizes" and "appreciates" pertinent physical laws.

Adaptability could be considered a major adaptation of all animals. Such capacity for adjustment is necessary for the successful "building" of an organism and would thus have high selective value. Such adaptive systems also possess potentialities for modification that to some degree determines the direction of further evolution. It should be stressed that this can also tend to promote future evolutionary change itself.

The importance of these non-random aspects of evolutionary change of organic form will become the focus of our attention in interpreting the fossil record. But there is still more to say about adaptability.

It should be made clear that adaptability can only exist by way of the hierarchical nature of developmental strategies. Koestler (1967) discusses at length how complex systems that are arranged as hierarchies can allow flexibility within stability...

...Figure 1 showed hierarchical order, where sub-wholes at each level are composed of those from the next lower level. Koestler has coined the term "holon" for a member of a hierarchy, and I think it is important to show his reasoning:

[quote]

At the base of a hierarchy, the holons show rigid, stereotyped, and specialized patterns of activity, while those toward the apex are increasingly more flexible; they have at their "command" the results of all the lower levels. The total result—the flexibility and stability of the apical holon—is far more significant than the sum of its parts. Examples of biological holons are numerous, for instance the quasi-independent nature of mitochondria, and *in vitro* isolation of functioning organs.

Anyone familiar with embryological development would immediately recognize it as a temporal hierarchy. The apex is the fertilized egg and the "branching" follows the progress of time so that the different levels represent successive stages of development. Through each level the holons (i.e. tissues) become progressively less flexible, less totipotent.

...Thus the transformations shown by D'Arcy, where variation is interdependent, would be accomplished by changes at the apex of the hierarchy, which coordinates the pattern of the whole by harmonizing the relative growth rates of the various parts.

In essence, if one truly understands the potential of hierarchical organization, then it will be recognized that all that has been said here about integration, correlation, and adaptability is equivalent to saying simply that living beings are organized as functional and

structural hierarchies. This should be a significant factor included in a complete synthetic theory of evolution.

From our understanding of the developmental hierarchy, it is easy to see that a change at an early stage of development can have a larger effect on the whole course of development, and therefore on the final form, than a change at a later stage. DeBeer's book, *Embryos and Ancestors* (1958) is based on this idea. It is a classic work in exposing the fallacy of the now universally rejected idea that ontogeny recapitulates phylogeny. He shows that evolution frequently involves alteration or reversal of developmental sequences (*heterochrony*) and is not simply the "piling up of new variations at the end of the life history, for the successional order of the pile is not necessarily respected" (DeBeer, 1965, p. 7)...

...DeBeer gives numerous examples where revolutionary revisions have occurred by such heterochrony, illustrating that the degree of change depends not on the degree of genetic change, but at what time in development the alteration first appears. The coordination and adaptability of the organic hierarchy can allow such changes to be in harmony with the organism.

The ease by which dramatic alterations can be produced is demonstrated by Lewis (1963). There are five tightly linked genes in *Drosophila* that control the appendages of the thoracic segments. Various mutations of these genes can cause wings to develop in odd locations, including the abdomen, where wings have never existed in the history of the insect lineage (but appendages have).

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What we have considered so far implies several things:

1. The fundamental steps in evolution may have been the contribution of individuals rather than populations.
2. The initial stages in these transformations were relatively imprecise.
3. We need revised ecological considerations regarding the survival of new forms in new niches.

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## CONCLUSION

Evolution has involved not only selection for adaptations, but also for adaptability. The latter then results in the non-random appearance of the former—including systematic "leaps."

A theory built mainly on genetics is insufficient; epigenetics must also be considered. This done, we should find that, to quote Lovtrup (1974, p. 412): "...the supreme creative forces of the synthetic theory, intraspecific selection and environmental pressure, assume a much more modest, if not unimportant, role in the drama of phylogenetic evolution. Rather, the real creative agent becomes the mutations responsible for innovations, particularly through interaction with epigenesis, aptly assisted by isolation."