

Evolution Is Not Mainly a Matter of Genes

(Summary of longer paper)

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The 200th anniversary of Charles Darwin's birth and the 150th of the publication of his "Origin of Species," both falling in 2009, focused the attention of scientists, philosophers, historians and substantial portions of the general public throughout the world on the phenomenon of organic evolution. Scholarly and popular books, museum and television shows, technical and public conferences, and organized pilgrimages to Darwin's country house and to the Galapagos Islands, a key venue in his scientific development, all attest to the iconic status of this thinker, and particularly to the concept of natural selection, which the philosopher Daniel Dennett has called "the single best idea anyone has ever had."¹

The theory itself can be summarized in various ways, but for the purposes of this essay it is useful to parse it into eight independent propositions: 1) Organisms present themselves as "types," perpetuating themselves (in the words of the Bible) "each according to their kind." 2) Each organismal type, however, is represented by actual individuals that are all somewhat different from one another. 3) Part of this variability is also passed on from one generation to the next; offspring are not only recognizable

¹ Dennett, D. C. 1995. *Darwin's dangerous idea: evolution and the meanings of life*. New York: Simon & Schuster, p. 21.

members of their type but also carry on some of their parents' particularities. 4) As external circumstances change, for example by a rise in the ambient temperature or depletion of a certain foodstuff, subpopulations of the group with particular quirks, or differences from the norm, will survive or thrive to a better extent than average, contributing disproportionately higher numbers of descendents to succeeding populations. 5) Later generations in these subpopulations will thus have different average properties from earlier ones. 6) After enough generations have passed the original type may no longer be recognizable in the selected subpopulations: a new type of organism will have emerged. 7) If no individuals of the new type can productively interbreed with any individuals of the originating population, *speciation*, the smallest step of evolutionary significance, will have taken place. 8) The conditions and processes described in propositions 1-7 constitute the mechanism by which new biological forms arise over time; all large-scale differences, e.g., between plants and animals or between insects and mammals, were generated by a series of many small species-level diversification events.

The observations contained in propositions 1-5 were uncontroversial in the 19th century European context in which Darwin (and his contemporary co-formulator of the hypothesis, Alfred Russel Wallace) presented the idea, and are accepted even among present-day creationists. Only with items 6 and 7 does the mechanism of natural selection emerge, and even then there are few who would disagree with its implications. Proposition 8, without which natural selection cannot explain large scale-, or macro-, evolution, is the one that has engendered the most opposition. The most prominent opponents are denialists who reject the idea that macroevolution has even occurred. But

there are also a growing number of evolutionary biologists who believe that macroevolution was the result of mechanisms other than natural selection. This disagreement with the standard model revolves to a great extent around the purported role of genes in evolutionary change.

It has been frequently noted that Darwin and his contemporaries had no understanding of the mechanisms of inheritance. To address this, mid-20th century evolutionary biologists combined Darwin's mechanism of natural selection with the then emerging understanding of the variation and transmission of genes. Since genes were conceived as the medium by which the variability referred to in proposition 3 (see above) could be conveyed from one generation to the next, the resulting Modern Evolutionary Synthesis ultimately became a theory of the dynamics of gene frequency in populations, encapsulated in the doctrine that evolution is mainly a matter of genes.

What is much more relevant to the role of natural selection in a comprehensive theory of evolution, however, is the fact that Darwin's theory in its original or modern form does not specify the mechanisms of *development*. Evolution involves changes over time in the phenotypes (i.e., forms and functions) of organisms. The phenotypes of multicellular organisms (Darwin's main concern), are generated by developmental mechanisms, formative processes that utilize the products of genes but are not coextensive with genes, their products, or their interactions.² In particular, since

² Salazar-Ciudad I. 2006. On the origins of morphological disparity and its diverse developmental bases. *BioEssays* 28:1112-1122.

developmental mechanisms shape and pattern tissues they involve the physics of materials,³ and these are in no fashion reducible to genes.

The unsuitability of tracking gene frequencies as a surrogate for evolutionary change can be inferred from considering the actual function of genes. Genes specify the sequence of protein and RNA molecules, which have only an indirect impact on phenotypes. Sometimes genetic mutation leads to dramatic phenotypic change. But often mutation or even deletion of a gene leads to little or no detectable change in the phenotype. Gregor Mendel's discovery of genes was based on genes of "large effect" – different variants associated with smooth or wrinkled plant seeds, for example. When the modern synthesis was formulated, however, it was realized that (i) genes of large effect will be rare in any natural population, and (ii) if evolution generally proceeded by utilizing such genes, proposition 8, above, the distinguishing premise of Darwin's theory, would be invalid. Since a consistent mathematical theory could be constructed by assuming Darwin was correct and genes of large effect could be ignored, that was what was done, albeit somewhat circularly.

Focusing on the transmission of genes rather than on the transmission of phenotypes via developmental mechanisms led to an impoverished evolutionary theory. Unlike genes, developmental mechanisms are frequently of large effect. Their actions, moreover, may be "plastic," that is, of variable outcome depending on external conditions. Developmental mechanisms also often lead to stereotypical or otherwise predictable morphologies, a characteristic (termed "orthogenesis") which is considered anathema to a notion of evolution based on selection of unconstrained variation. In

³ Newman SA, Comper WD. 1990. 'Generic' physical mechanisms of morphogenesis and pattern formation. *Development* 110:1-18; Forgacs G, Newman SA. 2005. *Biological physics of the developing embryo*. Cambridge: Cambridge Univ. Press..

particular, if selection merely nudges organismal form along paths that are already laid out in advance by inherent material properties, it would hardly be “the only creative force in evolution.”⁴ The recognition that phenotypes are inherited via nonlinear, plastic, orthogenic developmental mechanisms, and not simply by collections of genes, implies that some of the major conclusions of the Modern Synthesis must be incorrect.

The great selling point of the Darwin-Wallace theory was that it contained no hypotheses about how matter arrived at the point of being subject to natural selection (now encompassed under the still unsolved problem of the origin of life), nor did it depend on any knowledge of the source of variation, either inherited or non-inherited, in organismal form and function. The fact that a material object (e.g., an organism) would have properties slightly different from those of other copies of the same thing was simply the default science and manufacturing wisdom of the time. That small differences can in some circumstances be advantageous is just common sense.

The leap of mind required to turn these ordinary observations into a (materialist) theory of evolution was imagining continuous trajectories of change between present-day organisms and their ancestral forms based on the small differences that appear in each generation. While it might take a very long time, little-by-little a worm-like common ancestor could change into a lobster or a lion by gradual transformation.

Such continuous pathways of organismal change are not supported by the fossil record, however, nor, as we now appreciate, are they required for physical plausibility. Although Darwin’s theory is ostensibly concerned with changes in form over multiple

⁴ Judson, O. 2008. “Let’s get rid of Darwinism.” *The New York Times*, July 15, <http://judson.blogs.nytimes.com/2008/07/15/lets-get-rid-of-darwinism/index.html>

generations, the only way a new form can arise is if a real developmental mechanism is capable of generating it. Just as the physics of liquid water allows it to form waves and vortices, but not honeycomb structures, and (if the external conditions change), vapor or solid, the material that generates the bodies of animals – parcels of matter consisting of clusters of cells – also has preferred structural modes. These include hollow and multilayered forms, forms that are elongated and segmented, forms containing branched tubes and appendages.⁵ All the morphological motifs that characterize animal body plans and organ forms are in fact the physical manifestations of a type of substance described by physicists as soft, chemically and mechanically excitable matter.⁶ The recognition of this fact [is] a result of theoretical and experimental advances of late 20th century nonlinear dynamical systems and condensed matter physics....⁷ Furthermore, the prediction by this “physicalist” model that large-scale evolution could have occurred relatively rapidly, with only minimal change in the molecular components of the underlying developmental mechanisms, has been borne out.⁸

Many recent studies focus on the association between physical and genetic mechanisms in generating tissue structures. Gastrulation, for example, an early event in animal development, is the means by which the embryo becomes organized into distinct layers of tissue. This process has been shown to result from a combination of adhesive and mechanical forces, leading to a “sorting-out” effect between populations of cells that

⁵ Newman, S. A., G. Forgacs, and G. B. Müller. 2006. Before programs: The physical origination of multicellular forms. *Int J Dev Biol*, 50:289-99.

⁶ de Gennes PG. 1992. Soft matter. *Science* 256:495-497; Mikhailov AS. 1990. *Foundations of synergetics* I. Berlin: Springer-Verlag.

⁷ Reviewed in Forgacs G, Newman SA. 2005; see footnote 3.

⁸ Rokas A, Kruger D, Carroll SB. 2005. Animal evolution and the molecular signature of radiations compressed in time. *Science* 310:1933-1938; Newman SA. 2006. The developmental-genetic toolkit and the molecular homology-analogy paradox. *Biological Theory* 1:12-16.

is very much akin to the phase separation that occurs in a suspension of oil and water.⁹ Subtle physical differences between cells, at or just beneath their surfaces, will determine whether they act like molecules of “oil” or “water” in a particular mixture.¹⁰

Another such example is the formation of segments in the embryos of vertebrate animals.¹¹ These blocks of tissue (called “somites” in these organisms), emerge in pairs to either side of the embryo’s central head-to-tail axis, with the pair closest to the head forming first, followed in sequence by the ones increasingly closer to the tail. The somites eventually differentiate into the cylindrical vertebrae and associated muscles.

From the gastrulation and segmentation examples and others¹² it can be seen that developmental mechanisms and not genes are the means by which biological characters are transmitted across generation lines. Genes, in the usually understood form of DNA sequences,¹³ are part of all developmental mechanisms, so the heritability associated with allelic variation will enter into all traits, but often in highly complex, indirect ways. Because developmental mechanisms exhibit, variously, nonlinear, plastic and self-organizational properties, evolutionary transitions can be “saltational” (i.e., phenotypically abrupt), rapid, and influenced by environmental change in a direct (i.e.,

⁹ Steinberg MS. 2003. Cell adhesive interactions and tissue self-organization. In: Müller GB, Newman SA, editors. *Origination of Organismal Form: Beyond the Gene in Developmental and Evolutionary Biology*. Cambridge, MA.: MIT Press. pp 137-163.

¹⁰ Krieg M, Arboleda-Estudillo Y, Puech PH, Kafer J, Graner F, Muller DJ, Heisenberg CP. 2008. Tensile forces govern germ-layer organization in zebrafish. *Nat Cell Biol* 10:429-436.

¹¹ Dequéant ML, Pourquié O. 2008. Segmental patterning of the vertebrate embryonic axis. *Nat Rev Genet* 9:370-382.

¹² See Forgacs and Newman, 2005, footnote 6, for additional examples of developmental processes dependent on nonlinear and other self-organizing physical processes, and Newman and Bhat, footnote 9, for the role of physico-molecular “dynamical patterning modules” in the early evolution of the animals.

¹³ See Jablonka E, Lamb MJ. 2005. *Evolution in four dimensions: genetic, epigenetic, behavioral, and symbolic variation in the history of life*. Cambridge, Mass.: MIT Press for a discussion of some determinants that act beyond the level of DNA to influence phenotypes and their evolution, and Gorelick R and Laubichler M. 2008. Genetic = heritable (genetic ≠ DNA). *Biological Theory* 3:79-84 for an attempt, in the spirit of the present essay, to generalize the concept of the gene to include factors other than DNA.

Lamarckian) fashion and not just as a consequence of selection of marginally favorable variants. The fact that evolutionary theory became hooked on genes in the early stages of its formulation is an understandable consequence of the uneven development of the biological and physical sciences. But now that we have the means to analyze how living forms are actually produced and inherited, there is no excuse not to move on.