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BOOK REVIEW

A review of *Frozen Evolution: Or That's Not the Way It is, Mr. Darwin*, edited by Jaroslav Flegr

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Evolution: Or That's Not the Way It is, Mr. Darwin. Jaroslav Flegr, Editor, 2008, Jaroslav Flegr, Charles University in Prague, Faculty of Science, Prague, Czechoslovakia. 224 pp. Paperback ISBN 978-80-86561-73-8

Le Melodie du Gent
Blvd Emile Jacqmain
Gent
1 August, 2008

C. Darwin Esq.,
Down House

Dear Mr. Darwin
I beg your indulgence to intrude onto your valuable and jealously guarded time to bring to your attention a new book that challenges your theory of evolution by natural selection: "The driving force for the diversification of the species is quite possibly not natural selection, but an entirely different evolutionary mechanism ..." (p. 9). The book, written by Jaroslav Flegr from Charles University in Prague, was given to me at the second meeting of the European Society for Evolutionary Developmental Biology, held in Gent in July this year. I sense your surprise at hearing of the existence of such a society; yes, as you knew it would, embryology has provided a major source of evidence for the fact of evolution and has informed the nature of the transformation of organisms, although not, perhaps, the origin of species. Evolutionary embryology has matured to such an extent that there are now major societies and meetings devoted to this field.

Jaroslav Flegr is Professor of Ecology in Prague. You know that Haeckel coined the term ecology but you may not be aware that ecology has developed to the extent that chairs in this field of biology have been founded at many major universities in Europe and in the "new world." Some ecologists take a strongly evolutionary approach to their studies. Others are content to analyze an individual region (an ecosystem); curiously, the Galapagos Islands have received far less attention from ecologists than you might have predicted from your work inspired by John Gould. Others, who call themselves theoretical ecologists, are content to model ecosystems using quite complex computational and analytical approaches. Given the integrative approach Haeckel took, especially viewing ecology in relation to embryonic development, I doubt that Haeckel would approve of the subspecialization within late 20th and early 21st century ecology.

The book I bring to your attention "*Frozen Evolution: Or that's not the way it is, Mr. Darwin*," was written by someone who might be called a theoretical ecologist, but the author has background preparation in cell biology, physiology, parasitology, and classification (the latter using molecules rather than morphology to reconstruct relationships and ancestry). Jaroslav Flegr therefore brings a broad and integrative (a buzz word in 21st C biology) approach to the analysis of evolution. As the title of his book might lead you to suspect his approach is impish—rather like that of Charles Kingsley in "*Water Babies*." You may consider that the style in which the book is written goes beyond impish, verging on disrespectful, even combative; Flegr is not one who feels he should accept a viewpoint, theory, or mechanism just because it bears the name of one of the most illustrious (you might say the most illustrious) biologist of the 19th C.[1]

[1]I use the term biologist (and biology earlier in my epistle) in the way advocated by William Whewell; the term has replaced terms such as morphologist, physiologist or embryologist current in your day. A further integrative field is that of evolutionary developmental biology (known by the sobriquet of evo-devo).

I beg your further indulgence, dear Mr. Darwin, to outline the main themes in the book to make you aware of the difficulties some biologists still have with natural selection as the main driving force of evolutionary change and organismal transformation. Yes, I know, you thought you had refuted all the possible arguments in the numerous editions of "*The Origin*," and all that remained was to find the mechanism of inheritance. I regret that to that end, gemmules and pangenesis have not stood the test of time—two much blending I am afraid. August was right when he separated the germ line from the soma, although even there we find that the species in most phyla lack a germ line.

Inheritance of acquired characters, upon which you placed much emphasis, also has been ousted, although, curiously, epigenesis has revealed several modes of transmission of information from generation to generation, including substances in the ööplasm that determine such major components of the embryo as germ layers and the dorso-ventral axis. Whether these modes of transmission are mechanisms of inheritance aside from "the" mechanism of inheritance (which is encoded in a substance in the nucleus in particles known to you as determinants but to us as genes, and arranged along the chromosomes) is a subject of hot debate. Indeed it is one of the reasons Flegr wrote his book, the Czech version of which received a nomination for "Book of the Year" (yes, we have such awards now) and the Magnesia Litera award in 2007.[2]

The book is "one long argument," a phrase that will resonate with you as it does with us; some 20th C evolutionary biologists used it to their advantage in picking away at your theory. The essence of the argument is "that the vast majority of species" cannot respond to natural selection and so are "evolutionary frozen." Your immediate response will be that this must be the work of someone who does not believe in evolution—a creationist or advocate of intelligent design would be our response—evolutionary frozen being seen as a code word for designed. And if designed, there must be a designer. But no, Flegr is an evolutionary biologist, active in research, especially on evolutionary parasitology. How can an evolutionary biologist maintain that most species are not subject to change?

Evolution is change not stasis, as you demonstrated with so many examples in your magisterial book. Flegr begins by outlining your contributions, with some emphasis on the often-forgotten or unknown fact of history that you did not discover evolution. Evolutionary ideas had been circulating and becoming more generally known, even entrenched, before 1859. What you did was to provide a theory of the forces that drive evolution. Flegr claims that your theory of evolution through natural selection could not operate under the conditions of soft (Lamarckian) inheritance you advocated. We know this problem concerned you and that you spent much time after 1859 seeking a mechanism of inheritance, settling upon pangenesis as noted above. But the lack of a mechanism of inheritance did not cause you to abandon your theory. You had natural selection as verified through artificial selection; you documented variation in natural populations and within species; you were sure that a mechanism of inheritance would come.

In Chapter 3, Flegr outlines the theory of inheritance that was developed once the nature of inheritance (genes, later DNA—the substance of which genes are made and which gives them their property of storing and replicating information) had been discovered. The combination of "Darwinism" (your theory) with genetics in the 1930s produced what was and still is known as the New Synthesis. Flegr is seeking a "postneodarwinism" that includes processes other than natural selection in the generation of diversity.

One process is the occurrence of accidental events, which Flegr argues have led to some key innovations but also to random extinction of species. Accidental for Flegr need not mean nonbiological. Perhaps a better term would be random processes. Flegr presents *genetic drift* as an accidental (random) process in which some genes accumulate in a population other than in response to natural selection. Population geneticists, Mr. Darwin, have demonstrated repeatedly that genes can accumulate as a result of such a random process, especially in a species in which population size is small and generation time rapid.

A second random process is what Flegr calls *genetic draft*, a process by which a gene that has no effect or even a harmful effect, may accumulate because it is carried along by being located on a chromosome near a gene that is beneficial. Here the process seems to be accidental but not random; strong selection for the associated gene can produce a directional change, especially if the direction of selection extends over many generations.

You Mr. Darwin were concerned not to regard some creatures as higher or lower than others. Jaroslav Flegr shares your concern and so attempts to separate organization from complexity. While acknowledging that complexity and organization have both increased during evolution, Flegr posits that complexity is an evolving property and organization a fundamental property of living systems. Sponges and comb jellies, one of which is regarded as representing the ancestral metazoan condition (depending on which tree of life you support) are highly organized but come out low on the complexity scale, whether we measure complexity by the number of types of cells present or by the number of processes operating in members of each group.

With these five chapters as background, Flegr launches into speciation without natural selection. He chides you, as many have done, on devoting insufficient space in your book

[2]The book is now available free on line at http://natur.cuni.cz/flegr/frozen/index.php

to how new species arise, in part because you gave far less prominence to geographical isolation as a central mechanism in speciation, placing too much emphasis on natural selection; or so says Flegr. Now we believe that to obtain the necessary reproductive isolation within a population to initiate a new species, the population or populations must be subdivided in ways that prevent or minimize their contact with other populations. Flegr invokes a mechanism that you could not because it involves units—genes—that confer inheritance on organisms, more particularly the frequency of genes in a population. He argues that neither selection coefficients of genes—the way we assign potential input to the evolutionary process to a gene—nor biological fitness—the effect selection has on the number of offspring an individual can pass on to the next generation—adequately describe evolutionary potential. He wants to invoke an approach that allows us to determine the likelihood that a gene will be involved in (even determine) an evolutionary stable strategy (ESS). Once a particular ESS predominates in a population it will be almost impossible to replace with another strategy and so will determine or direct subsequent evolutionary change.

So you see Mr. Darwin, Flegr wants to shift the emphasis to a gene-centered evolutionary process in which genes compete for survival rather than one in which phenotypes compete for survival, with successful phenotypes dragging genes along behind them. He follows Richard Dawkins and William Hamilton in shifting the locus of selection to what has become known as the *selfish gene* in which variants of a single gene (we call them alleles) compete to pass on the greatest number of copies to the next generation. Sometimes this will coincide with survival of the fittest individuals but most of the time it will not.

This shift to the gene is but the first step in Flegr's resynthesis of the synthesis. He goes beyond Dawkins and Hamilton to make the case that competition between alleles of a single gene locus cannot work in sexually reproducing organisms. The problem is the old one of epigenesis and preformation. The genes of an organism—its genotype—are not inherited preformed from the parents. Three sources of change are documented:

(1) Some genes have two alleles one dominant over the other, but many genes have many alleles with complicated patterns of interactions. Such polymorphism makes inheritance of beneficial alleles problematic.
(2) Alleles and genes interact, genes often being inherited as integrated sets. Beneficial allelic change would have to go beyond single alleles.
(3) Consequently, any mechanisms that depends on the biological fitness of the gene being tied to its frequency in the population, is fraught with the problems of how such an allele could accumulate. The offspring inherit a new genotype created by the combination of genes from the male and female parent. As a consequence, single alleles with selective advantage cannot build up in the population. So, Flegr rejects Darwinism (natural selection) and Dawkins–Hamiltonism (selfish genes).

What, you ask, does he assert in their place?

He asserts a particular form of geographical isolation in which a small part of a population splits off—nothing controversial there—taking with it only a small part of the genetic variation present in the original population. There could a problem here; the latter need not be the case. If the original population is small and occupies a uniform environment we would not expect to find subsets with "only a small part of the genetically determined variability." If an avalanche isolated a subset of individuals it is quite likely that those individuals would represent a random sampling of the population. But Flegr is thinking of situations more like the following:

Imagine frogs that occupy different levels along the slope of a mountain at various stages of their life cycle. Suppose that a subset was isolated because of an unusual temperature increase during the breeding season, a sufficient increase that only those that could develop/survive at this higher temperature survived. Given the differential temperature tolerances of embryos, tadpoles and adults, it may only be the tadpoles that survive. This subset has become isolated by a physical change in the environment (temperature) but also because they carry genetic variants allowing survival under the conditions that forced the split. They do not represent a random sampling of the population. As envisaged by Flegr the isolated subset carries a random sampling of the genes of the population *and as a consequence of the resultant genetic similarity or even identify of the individuals in a the population, can be subject to Darwinian evolution* (p. 145). In the frog example, the former would not be true, the latter would.

This difference is important because for Flegr new variability accumulates in the population over time and the population-new species then freezes. In the frog example, a subset of genetic variation is present from the outset of the separation, thereby facilitating evolutionary change from the outset. Any freezing would reflect (i) a new balance between the genotype and the new environment, and (ii) stasis until the environment changed again, rather than the freezing of speciation because of new genetic variation arising. The difference is subtle but critical; one grounds speciation in existing genetic variation and adaptation to a new environment in response to natural selection. The other grounds speciation in the origin of new genetic variation in the absence of any phenotypic adaptation to the new environment: " . . . the basic assumption of the theory of frozen plasticity [is grounded in] 'greater evolutionary plasticity of a genetically more uniform population than of a genetically diverse population . . .'" (p. 161).

Your insistence on the gradual, step-wise nature of evolutionary transformation and the long periods of stasis that can occur between speciation events is seen as explained by frozen plasticity: "species can respond to selection pressures only for a short part of their existence, i.e. immediately after their formation" (p. 201).

Species capable of domestication and that respond dramatically to artificial selection—the species that you Mr. Darwin used as a keystone in developing your theory of evolution by natural selection—are used by Flegr as the paradigmatic examples of evolutionary plastic species. Certainly they respond to selection, often within a few generations, as you demonstrated and documented with breeds of pigeons and dogs. Just as clearly, many breeds have continued to respond to artificial selection for hundreds of generations. Whether such species are a class (type) apart from those that cannot show such responses, and/or whether the basis for their plasticity lies in the inheritance mechanisms proposed in this book, remain open questions. A key test will be of the proposal that plastic species have a greater proportion of their traits codes by a single gene and show few gene–gene interactions, while frozen species have a greater proportion of their traits codes by a large number of genes and show enhanced genetic interactions.

Now it may be that I have not provided you with a sufficient summary of the mechanism proposed to enable you, dear sir, to evaluate the book fully. I urge you to read it closely to form your own opinion. I know that you do not like to respond to critiques of your theory in person but perhaps you could encourage Thomas Henry to promulgate a rebuttal for you, as he has done so successfully in the past.

I remain, as always, your most humble and obedient servant.