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How the tree of life became a tangled web: A glimpse at the history of a powerful metaphor

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Abstract

Analogical reasoning, clothed in the garments of metaphors, diagrams and models, has been one of the most important engines of discovery and conceptual innovation throughout the history of science. Here I concentrate on one analogical device of great import to evolutionary biology, the metaphor of the tree of life.

Two years ago in my contribution to this forum (Midwest Junto 2009), I traced the vicissitudes of the concept of directed evolution from Darwin to the present, putting special emphasis on the role of analogies and thought experiments. I examined those issues starting with the Notebooks that preceded the *Origin* and followed their development down to current revaluations of the arguments and tenets of orthodox Darwinism.

This essay continues this exploration of the heuristic power of analogical thinking in evolutionary biology by focusing on the metaphor of the tree of life, from its paramount role in the discovery of the mechanism of natural selection to its later bearing on the development of twentieth century conceptions of species and the mechanisms of speciation. Finally, I consider the outcome of the present destabilization of this metaphor since the discovery of the widespread occurrence of horizontal gene transfer among phylogenetically distant organisms.

I conclude with some reflections on the evolution of metaphors and some attendant consequences for the history and the philosophy of science and their mutual interactions.

Introduction

The last three decades have witnessed an extraordinary renewal of interest on the functions of analogical thought in several domains of inquiry, including the history and philosophy of science, and the teaching and popularization of scientific ideas. Such notable authors as Evelyn Fox Keller and George Lakoff have rescued metaphors and other analogical devices from the limitations of purely linguistic treatments that frequently approached them as mere rhetorical figures. These

authors have brought to the fore their essential and indispensable role in the discovery, consolidation and promotion of new ideas and patterns of reasoning.

Two years ago in a contribution to this forum (Midwest Junto 2009), I traced the development of the concept of directed evolution from Darwin to the present. Starting with the Notebooks that preceded Darwin's *Origin*, I went on to sketch some salient steps in the history of this conception and its role in the growth and transformation of evolutionary thought in the twentieth century. Finally, I reviewed some related ideas and discoveries that have led to current revaluations of the arguments and tenets of orthodox Darwinism. Throughout that exposition, I placed special emphasis on the role of analogies and thought experiments in the discovery and unfolding of the main lines of argumentation. As I wrote then,

Darwin was an exceptional thinker and scientist in manifold ways. Besides his extraordinary powers of observation, in going through his writings one is struck by his capacity for bringing together a variety of apparently unrelated examples through a marvelous knack for exploiting recondite analogies and metaphors. Another original but seldom noticed novelty of Darwin's argumentation is his use of thought experiments. (Fernández 2009).

On this occasion I would like to revisit the subject of analogical reasoning in the discovery and historical development of ideas in evolutionary theory, starting with the seminal image of the tree of life and tracing its career up to the present. But first, it would be desirable to review a few basic notions concerning images, diagrams and metaphors and some current views about their role in the discovery, reception and furtherance of conceptual and theoretical novelties in science and philosophy.

Analogical thinking

My treatment of analogical devices is informed by the insights of Peircean semiotics. Under this view, signs (and combinations of signs) fall within three main categories according to their relations to the objects they represent: signs can be **icons**, **indexes** or **symbols**. Iconic signs represent their objects through a resemblance, indexical ones through a causal connection, and symbolic signs through a rule, often conventional. Here we are interested in iconic representations, but since the word "iconic" has diverse connotations for non-semioticians I use instead the expression "analogical," which —although somewhat technically incorrect— may be more readily understood.

Peircean semiotics distinguishes three types of iconic signs: **images**, **diagrams**, and **metaphors**. This is not the place to dwell upon the different characteristics of these types of signs, and since scientists and historians tend to use those terms more or less interchangeably I will use the expression "analogical device" as an umbrella designation (if you excuse the metaphor) for any or all of them. In Peirce's view analogical devices are logical instruments for the type of inference he called "abduction" (in contrast to deduction and induction). He considered abduction to be

the only inference that may lead us to new ideas in general and to scientific hypotheses in particular. In this brief communication I cannot expound upon the philosophical issues surrounding these conceptions and will instead highlight some historical developments that illustrate how in fact analogical reasoning leads to conceptual novelties in scientific practice.

From the tree of life to the coral of life

It is well known that the iconography of the tree of life is ancient and occurs quite often in religious and mythical writings. Even in evolutionary biology there are several instances of pre-Darwinian use, most notably by Lamarck.¹ The unique characteristics of Darwin's tree seem to stem from its pronounced diagrammatic nature. Diagrams ignore the "pictorial" aspects emphasized by other analogical devices to concentrate instead on exhibiting the relations that bind together a set of highly schematized elements, usually represented as featureless dots (nodes). Such relational patterns achieve great generality and can thus be instantiated by concrete structures that bear little resemblance to each other in their non-relational aspects. Darwin's tree can equally well represent a wide range of different structures, including some types of river deltas, the bifurcating trails in Borges' famous story of *The Garden of Forking Paths*, and the branching histories of the universe in the Many Worlds interpretation of quantum physics.

I think that the heuristic power of Darwin's tree rises from the fusion of two previously distinct interpretations of the diagram: the tree of genealogy and the classificatory tree of taxonomy.² Genealogical trees representing biological descent, such as the pedigree of horses or dogs, were in use at least since the European Middle Ages, and were not drawn with purposes of classification. On the other hand, classificatory trees for the sorting of biological taxa without reference to common descent had been around since the eighteenth century. In Darwin's tree of life, classification and descent became melded aspects of a single conception. Because of its analogical construction the tree is able to represent those different ideas simultaneously, becoming a single and integrated generalization of both. This synthesizing capacity is a special case of a more general feature that partly accounts for the heuristic fertility of analogical devices: they bring forth a previously unsuspected similarity between hitherto unrelated ideas.

In the history of science analogies may evolve, may become utterly transformed, and occasionally collapse and become extinct. In a recent paper Burnet has pointed out that the most crucial of Darwin's analogies, the similarity between the culling operations of animal breeders (artificial selection) and the selective actions of nature (natural selection), evolved in his later writings into a complex spectrum of intermediary similarities (see Burnet 2009).

Darwin himself found an improvement to the tree of life in his depiction of the "coral of life." He was concerned that extinct species were not represented in the tree. In Notebook B [Transmutation of species (1837-1838)] p.25, Darwin wrote: "The tree

of life should perhaps be called the coral of life, base of branches dead; so that passages cannot be seen". While a tree is alive from its roots to the tips of its leaves, corals grow on top of their calcified dead branches. These branches represent past organisms, species, and lineages that no longer exist. In a beautifully illustrated book, Horst Bredekamp considers Darwin's description of a coral. It was reminiscent of a specimen Darwin found in Patagonian shores, and which later turned out to be an alga. Bredekamp argues that this image of a coral was the inspiration for a peculiar diagram that Darwin carefully designed and chose as the single illustration to grace the pages of the *Origin* (Bredekamp 2005).

Architectural analogies in evolutionary disputes

The development of evolutionary theory throughout the twentieth century was marked by a series of polemical episodes in which metaphors and analogies played a major role. Here we must limit our considerations to a single one.

After a short partial eclipse in the last decade of the nineteenth century and the first two decades of the twentieth, the Darwinian view of evolution became solidly established in scientific circles. During the late thirties and early forties it was gradually amalgamated with Mendelian genetics to form what we still call the Modern Synthesis. The main tenets of the Synthesis included the primacy of natural selection as the explanatory mechanism for evolution and the belief in phyletic gradualism (no evolutionary jumps). These theses were integrated into a well-entrenched orthodox position, usually referred to as Neo-Darwinism.

Developmental biology had been closely associated with evolutionary thought in Darwin's times, but during the primacy of Neo-Darwinism it became dissociated from evolutionary theorizing and almost irrelevant to its development. In contrast, during the last three decades this situation has been radically reversed with the rise of evolutionary developmental biology (evo-devo). Some earlier polemical attacks on orthodox positions had paved the way to this and other recent developments. A brief consideration of one of these challenges, which was based on the notion of **evolutionary constraints**, offers a good opportunity to examine a different epistemic role for metaphors in evolutionary thought.

Following a distinction introduced by Robert Boyd (Boyd 1993, p. 485), scientific metaphors may be divided into two categories: theory-constitutive (or constructive) and pedagogical (or exegetical). Theory-constructive metaphors are used to introduce new conceptions and at the time of their inception they cannot be readily paraphrased. On the other hand, pedagogical metaphors serve as instruments of persuasion and illustration, and can be easily eliminated in favor of expressions drawn in literal terms. In the attacks against Neo-Darwinism, we confront a type of metaphor we find difficult to associate with either side of this dichotomy. We shall call them **confutational metaphors**. They are close relatives of confutational thought experiments, such as Newton's rotating bucket or Galileo's *gedanken* experiments with falling bodies. The purpose of these devices is not so much the

introduction of new ideas but rather the demise of well-established ones, by revealing internal inconsistencies or contradictions with other, well-entrenched, beliefs.

In the evolutionary polemics we have a good example of confutational metaphor in the architectural analogy employed by Stephen Jay Gould and Richard Lewontin in their famous paper “The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme” (Gould and Lewontin 1979).³

In renaissance architecture some curved masonry structures, known as “spandrels” were used for supporting a dome. Structural constraints of a physical nature, alien to the esthetical demands of the design, dictated the need to incorporate them. By analogy, Gould and Lewontin used the term *spandrel* to designate phenotypic traits that arise because of structural constraints in the *bauplan* of an organism, and not as a result of evolutionary adaptations. In their polemic against what they called “the Adaptationist Program,” they proceeded to show that many phenotypic features that had been previously considered adaptations were in fact evolutionary spandrels.

From the coral of life to the tangled web of life

Rapid advances in molecular biology have made it possible to reconstruct early segments of the tree of life by the application of new methods, such as the sequencing of genes that encode short subunits of ribosomal RNA. In the 1970’s, as a result of the work of Carl Woese and other researchers, the universal phylogenetic tree was reconfigured as a diagram starting from three principal branches called domains, comprising Bacteria, Archaea, and Eucarya. The first two include the unicellular organisms usually called prokaryotes. Eucaryans, having complex cells with a separate nucleus and several organelles, include some unicellular organisms and all of the major branches of multicellular ones, i.e., plants, fungi and animals.

In the traditional taxonomic hierarchy, the branchings of the tree of life proceed from domains to kingdoms, kingdoms to phyla, phyla to classes, classes to orders, orders to families, families to genera and genera to species. The lowest rank in this hierarchical order, the species, is traditionally defined as a group of organism capable interbreeding to produce fertile descendants. There are several mechanisms that explain speciation, i.e. the production of new species. The most common of these, allopatric speciation, accounts for the rise of new species as a consequence of geographic separation (e.g., birds migrating to different islands). Separate ecosystems impose different selection pressures on the individuals, resulting in genotypic and phenotypic variations. After many generations the organisms become reproductively isolated and the members of separate enclaves can no longer interbreed and interchange genes.

The traditional definition of *species* is based on a model of sexual reproduction that is most common in multicellular organisms. However in addition there are at present conflicting definitions of *species*, based on genomic similarities. In all cases

the mechanisms of speciation are conceived in terms of vertical gene transfer, i.e. the exclusive transfer of genetic material from individual progenitors to their offspring.

During the last two decades the application of new methodologies have increasingly brought to scientists' attention the high frequency and widespread occurrence of horizontal (lateral) gene transfer (HGT) between distantly related organisms. This is found most frequently among prokaryotes, but it also occurs among some eukaryotic lineages. The free interchange of genomic materials by HGT, together with other mechanisms (e.g., symbiosis and hybridization), could not have failed but to accelerate the pace of biological evolution, especially during its earlier stages.

The lateral transfer of genes and concomitant evolutionary novelties between parallel branches has short-circuited the whole scheme of the tree of life. This has rendered questionable its future application, both as a constructive and as a pedagogical metaphor. All the same, this image is remarkably useful and remains closely associated to many ideas in the history and philosophy of biology. Consequently, practitioners are naturally reluctant to dismiss it or radically alter it.

Biologists have increasingly voiced concerns over the future of the tree of life since the 1990's. An influential article by W. Ford Doolittle "Uprooting the Tree of Life" in *Scientific American* did much to bring these matters to the attention of a wider audience. In a subsequent article co-authored with Eric Baptiste (Doolittle and Baptiste 2007) Doolittle upholds the view of "pattern pluralism":

Pattern pluralism (the recognition that different evolutionary models and representations of relationships will be appropriate, and true, for different taxa or at different scales or for different purposes) is an attractive alternative to the quixotic pursuit of a single true TOL [tree of life].

An entire recent issue of the journal *Biology and Philosophy* (September 2010) was dedicated to these matters and featured articles by Doolittle and sixteen other biologists and philosophers. These papers go deeply into the biological, historical and philosophical problems arising from a total or partial demise of the tree of life metaphor, and examine issues far beyond the confines of this presentation. Although no consensus has been reached so far, it seems clear that many authors embrace one form or another of pattern pluralism, and yet at the same time they strive to retain as much as possible the use of the tree of life metaphor. They now tend to view the tree as a structure discernible as part of a wider and non-arborescent relational network, variously referred to as the web, the mosaic, the thicket, and even the forest of life (see e.g., Swithers *et al.* 2009, Olendzenski and Gogarten 2009, Puigbo *et al.* 2009). The situation is aptly summarized in a recent paper (Valas and Bourne 2010):

The tree of life is alive, but not well. Construction of the tree of cells has been viewed as the end goal of the study of evolution, where in reality we need to consider it more of a starting point. We propose a duality where we must consider variation of

genetic material in terms of networks and selection of cellular function in terms of trees. Otherwise one gets lost in the woods of neutral evolution.⁴

Whether the image of the tree of life is retained, transformed or abandoned, it seems likely that the study of its historical trajectory will afford further lessons in the investigation of analogical thought and its role in the creation of cognitive novelty.

Notes

¹ For the history of pre-Darwinian uses of the tree of life image and its relations to that of the *scala naturae* see e.g., Archibal 2009 and Ragan 2009.

² This is in agreement with observations made by Luke Jostins, in his blog “Genetic Inference” on August 17, 2009:
<http://www.genetic-inference.co.uk/blog/2009/08/on-lamarck-and-trees/>

³ According to Google Scholar this paper has been cited more than 3000 times.

⁴ Neutral evolution is brought about by random, non-selective, genetic drift.

References

- Al-Zahrani, Abdulsalam (2008). Darwin’s metaphors revisited: Conceptual metaphors, conceptual blends, and idealized cognitive models in the theory of evolution, *Metaphor and Symbol*, 23:50-82.
- Archibald, J. David (2009). Edward Hitchcock’s pre-Darwinian (1840) tree of life, *Journal of the History of Biology*, 42:561–592.
- Barahona, Ana and Martínez, Sergio F. (eds.) (2000) *Historia y explicación en biología*. México: UNAM.
- Bapteste, Eric, et al. (2009) Prokaryotic evolution and the tree of life are two different things, *Biology Direct*, 4:34.
- Boyd, Richard (1993). Metaphor and theory change: what is ‘metaphor’ a metaphor for? In: Ortony, Andrew (Ed.), *Metaphor and Thought* (2nd ed.). Cambridge, Mass.: Cambridge University Press, pp. 481–533.
- Bredenkamp, Horst (2005). Darwins Korallen: Frühe Evolutionsmodelle und die Tradition der Naturgeschichte. Berlin: Klaus Wagenbach Verlag.
- Burnett, D. Graham (2009). Savage selection: analogy and elision in *On the Origin of Species*, *Endeavour*, 33 (4): 120–125.
- Cornell, John F. (1984). Analogy and technology in Darwin’s vision of nature, *Journal of the History of Biology*, 17(3): 303-334.

Darwin, Charles R. (1837–38). *Notebook B. Transmutation of Species*. <http://darwin-online.org.uk/manuscripts.html>.

Darwin, Charles R. (1859). (1st ed.) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.

Depew, David and Weber, Bruce (1995). *Darwinism evolving: System dynamics and the genealogy of natural selection*, Cambridge, Mass.: The MIT Press.

Doolittle, W.Ford (2009). The practice of classification and the theory of evolution, and what the demise of Charles Darwin's tree of life hypothesis means for both of them, *Philosophical Transactions of the Royal Society of London B Biological Sciences*, 364:2221-2228.

Doolittle, W.Ford and Baptiste E. (2007). Pattern pluralism and the Tree of Life hypothesis, *Proceedings of the National Academy of Sciences U S A*, 104:2043-2049.

Doolittle, W.Ford and Zhaxybayeva, O. (2009). On the origin of prokaryotic species, *Genome Research*, 19: 744–756.

Dupré John, and O'Malley Maureen A. (2007). Metagenomics and biological ontology, *Studies in History and Philosophy of Science C: Biological and Biomedical Sciences*, 38: 834–846.

Evans, L.T. (1984). Darwin's use of the analogy between artificial and natural selection, *Journal of the History of Biology*, 17(1): 113-140.

Fernández, Eliseo (2009). Directed evolution: Pruning the tree of life from Darwin's demon to nanobiotechnology. Available at <http://www.lindahall.org/services/reference/papers/fernandez/juntofinal.pdf>

Gildenhuis, Peter (2004). Darwin, Herschel, and the role of analogy in Darwin's *Origin*, *Studies in History and Philosophy of Science C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 35(4): 593-611.

Gould, Stephen Jay and Lewontin, Richard C. (1979). The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme, *Proceedings of the Royal Society of London, B* 205:581-598.

Keller, Evelyn Fox (1995). *Refiguring life. Metaphors of twentieth-century biology*. New York: Columbia University Press.

Keller, Evelyn Fox (2002). *Making sense of life: Explaining biological development with models, metaphors, and machines*. Cambridge, Mass.: Harvard University Press.

Knudsen, Susanne (2003). Scientific metaphors going public, *Journal of Pragmatics* 35:1247–1263.

Koonin, Eugene V., Wolf, Yuri I. and Puigbò, Pere (2009). The phylogenetic forest and the quest for the elusive tree of life, *Cold Spring Harbor Symposia on Quantitative Biology*, 74: 205-213.

Largent, Mark A. (2009). Darwin's analogy between artificial and natural selection in the *Origin of Species*, in Ruse, Michael and Richards, Robert J. (eds.), *The Cambridge Companion to the "Origin of Species,"* Cambridge: MA: Cambridge University Press, pp. 14-29.

Lakoff, George and Johnson, Mark (1980). *Metaphors we live by*. Chicago: University of Chicago Press.

O'Malley, Maureen A. (2010). Construction and deconstruction: The influence of lateral gene transfer on the evolution of the Tree of Life. In Oren, A., and Papke, T. (Eds.), *Molecular Phylogeny of Microorganisms*, Norwich: Horizon, pp. 151-166.

O'Malley, Maureen A. and Boucher Y. (2005). Paradigm change in evolutionary microbiology, *Studies in History and Philosophy of Biology and Biomedical Sciences*, 36:183-208.

O'Malley, Maureen A., Martin, William, and Dupré, John (2010). The Tree of Life: Introduction to an evolutionary debate, *Biology and Philosophy* (special issue on the tree of life), 25(4): 441-453.

Puigbò, Pere, Wolf, Yuri I. and Koonin, Eugene V. (2009). Search for a "Tree of Life" in the thicket of the phylogenetic forest, *Journal of Biology*, 8(6): 59.

Puigbò, Pere, Wolf, Yuri I. and Koonin, Eugene V. (2010). The tree and net components of prokaryote evolution, *Genome Biology and Evolution*, 2: 745-756.

Ragan, Mark (2009). Trees and networks before and after Darwin, *Biology Direct* 4(1): 43.

Regner, Anna Carolina (2003). O papel da metáfora no longo argumento da "Origem das espécies". Available at http://www.triplov.com/mesa_redonda/anna_carolina/retorica.html

Ruse, Michael, Richards, Robert J. (eds.) (2009) *The Cambridge Companion to the "Origin of Species,"* Cambridge: MA: Cambridge University Press.

Spivak, Eduardo (2006). El árbol de la vida. Una representación de la evolución y la evolución de una representación, *Ciencia Hoy*, 16(91): 10-24.

Sterrett, Susan G. (2002). Darwin's analogy between artificial and natural selection: how does it go?, *Studies in History and Philosophy of Biological and Biomedical Sciences*, 33 (1): 151-168.

Valas, Ruben E. and Bourne, Philips E. (2010). Save the tree of life or get lost in the woods, *Biology Direct* 5: 44.

Voss, Julia (2010). *Darwin's pictures: Views of evolutionary theory, 1837-1874*. New Haven, CT: Yale University Press.

Woese, Carl R. (2004). A new biology for a new century, *Microbiology and Molecular Biology Reviews*, 68 (2): 173–186.