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BIOLOGY'S LAST PARADIGM SHIFT. THE TRANSITION FROM NATURAL THEOLOGY TO DARWINISM

1. The evolution of evolutionary theory

The theory of evolution, which provides the conceptual framework for all modern research in organismal biology and informs research in molecular biology, has gone through several stages of expansion and refinement. Darwin and Wallace (1858) of course proposed the original idea, centering on the twin concepts of natural selection and common descent. Shortly thereafter, Wallace and August Weismann worked toward the complete elimination of any Lamarckian vestiges from the theory, leaning in particular on Weismann's (1893) concept of the separation of soma and germ, resulting in what is sometimes referred to as "neo-Darwinism".

The theory then experienced a period of "eclipse" (Bowler, 1983) during which many biologists accepted the idea of common descent but either rejected or greatly diminished the importance of natural selection as an evolutionary mechanism. This situation was exacerbated by the rediscovery of Mendel's work, given the apparent incompatibility of inheritance particles affecting discrete characters with the type of continuous quantitative variation necessary for natural selection to produce gradualistic evolutionary change.

Famously, the crisis was overcome with the reconciliation of Mendelian and statistical genetics made possible by Fisher, Haldane and Wright (Fisher, 1930; Wright, 1931; Haldane, 1932), among others, and that later on culminated in the Modern Synthesis (henceforth, MS) to which several additional authors made important contributions, including but not limited to Dobzhansky, Huxley, Mayr, and Simpson (Dobzhansky, 1937; Huxley, 1942; Mayr, 1942; Simpson, 1944). The MS is still the version of the theory largely accepted by the scientific community, and it is what graduate students in the discipline are trained on (Futuyma, 1997).

More recently, several authors have pushed for an Extended Synthesis (henceforth, ES) in evolutionary biology, initially from a variety of individual perspectives largely rooted in particular fields of inquiry, such as Evo-Devo

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(Muller & Newman, 2005; Love, 2006), or phenotypic plasticity (Pigliucci, 2001; West-Eberhard, 2003), and now with a more concerted effort aimed explicitly at the formalization of a broader conceptual framework for evolutionary biology (Pigliucci & Muller, 2010). The ES is very much a work in progress, but the idea is to accomplish a number of goals that have so far proven somewhat elusive: first and foremost, to finally bring developmental biology – famously left out of the MS – into the fold. Second, to provide a coherent way to reconcile the "holistic" tendencies of organismal biological research with the decidedly more reductionist approach of molecular biology and its most recent products, the various "-omics" (genomics, proteomics, metabolomics, etc.). Third, to incorporate as primary players a number of biological phenomena and processes that had been either discarded or minimized within the context of the MS, e.g., phenotypic plasticity, genetic accommodation, epigenetic inheritance, etc. Fourth, to expand the standard theoretical toolkit of the MS – which is primarily grounded in population and quantitative genetic theory (Pigliucci, 2006, 2008a) – to include elements from computational biology (Gavrilets, 2007) and complexity theory (Newman *et al.*, 2006). Fifthly, to incorporate in evolutionary theory new concepts that have emerged from theoretical research during the past several years, chief among them the triad constituted by evolvability, modularity and robustness (Pigliucci, 2008b).

In this paper I will address the question of whether any of the above amounts to something akin to Kuhn's paradigm shifts (1962), i.e. whether evolutionary biology has ever undergone anything like what Kuhn describes as a moment of revolutionary science. I will argue that it has not, and that it will not, even if the ES will succeed in establishing itself. Rather, I think the only time in the history of biology when such a transition has occurred was during the 19th century, when Darwin's original theory replaced the dominant "paradigm" of the day, Paley-style natural theology.

2. Back to the beginning: Paley vs. Darwin

William Paley is responsible for the most articulate defense of the idea that living organisms are the result of a special creation by supernatural forces. In his Natural Theology (Paley, 1802) he famously introduced the metaphor of a watch and its watchmaker:

> In crossing a heath, suppose I pitched my foot against a stone, and were asked how the stone came to be there: I might possibly answer, that for any thing I know to the contrary, it had lain there for ever: nor would it perhaps be very easy to show the ab-

surdity of this answer. But suppose I had found a watch upon the ground, and it should be inquired how the watch happened to be in that place; I should hardly think of the answer which I had before given, that for any thing I knew, the watch might have always been there. Yet why should not this answer serve for the watch, as well as for the stone? Why is it not as admissible in the second case as in the first? For this reason, and for no other, viz., that when we come to inspect the watch, we perceive (what we could not discover in the stone) that its several parts are framed and put together for a purpose (…) This mechanism being observed (…) the inference, we think, is inevitable, that the watch must have had a maker; that there must have existed, at some time, and at some place of other, an artificer or artificers, who formed it for the purpose which we find it actually to answer; who comprehended its construction, and designed its use (Paley, 1802, p. 5).

Paley argued by analogy from the watch/watchmaker inference to the complex living organism/supernatural intelligent designer inference, despite the fact that such inference had been dealt a devastating philosophical blow by Hume, writing several decades before Paley (Hume, 1779). Contrary to what has been assumed for a long time, Paley appeared to have been familiar with Hume, though he was obviously unconvinced by the latter's arguments. Darwin was initially persuaded by Paley's reasoning, but eventually of course provided the decisive counterpoint that was missing in Hume: an alternative mechanism (natural selection) to generate both biological complexity and the pattern of common descent that was denied by Paley's natural theology.

It behooves us to briefly examine Darwin's answer, so that we may then proceed to compare Paley's and Darwin's "paradigms" in view of Kuhn's ideas to see whether we can sensibly talk of a paradigm shift occurring at the very onset of evolutionary biology as an independent discipline.

Although Paley is mentioned by name only once in The Origin (on p. 201 of the first edition in the chapter on "Difficulties on Theory"), Darwin mounts a concerted and sustained attack on natural theology in chapters VI and XIII of his magnum opus. Here are some relevant citations to establish the case. First Darwin explicitly contrasts the type of "explanation" provided by natural theologians with a naturalistic explanation typical of the new science:

He who believes in separate and innumerable acts of creation will say, that in these cases [of organisms' behavior that have changed in response to a new environment, without – yet – an accompanying change in the structure of the proper organs] it has pleased the Creator to cause a being of one type to take the place of one of another type; but this seems to me only restating the fact in dignified language. He who believes in the struggle for existence and in the principle of natural selection, will acknowledge that every organic being is constantly endeavouring to increase in numbers; and that

if any one being vary ever so little, either in habits or structure, and thus gain an advantage over some other inhabitant of the country, it will seize on the place of that inhabitant, however different it may be from its own place (Darwin, 1859, p. 186).

Then he proceeds to directly criticize Paley's use of analogies to draw a parallel between the inference to human design and the inference to supernatural design:

It is scarcely possible to avoid comparing the eye to a telescope. We know that this instrument has been perfected by the long-continued efforts of the highest human intellects; and we naturally infer that the eye has been formed by a somewhat analogous process. But may not this inference be presumptuous? Have we any right to assume that the Creator works by intellectual powers like those of man? (Darwin, 1859, p. 188).

Immediately afterwards, he goes so far as laying out the criteria for the falsification of his hypothesis, in sharp contrast of course with the natural theologian's ideas, which cannot be falsified:

If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down. But I can find out no such case (Darwin, 1859, p. 189).

Natural selection will never produce in a being anything injurious to itself, for natural selection acts solely by and for the good of each. No organ will be formed, as Paley has remarked, for the purpose of causing pain or for doing an injury to its possessor. If a fair balance be struck between the good and evil caused by each part, each will be found on the whole advantageous (Darwin, 1859, p. 201).

To summarize, then, the idea of intelligent design – which had been around at least since Plato's Timaeus – had been severely crippled on philosophical grounds by Hume in the 18th century. Still, Paley was able to mount a spirited and detailed defense of it at the onset of the 19th century, while Darwin provided the final blow to it (except of course for the modern resurgence of creationism, which is not an intellectually meaningful movement) for the first time on scientific grounds during the second part of the 19th century. It is on the latter transition that I wish to focus now from the perspective of Kuhn's paradigm shifts.

3. The Paley-Darwin transition as a paradigm shift

According to Kuhn (1962), change in science is comprised of two distinct and alternating phases: during "normal science" scientists use the dominant

theoretical and methodological tools to solve "puzzles", i.e. problems arising within a particular theory. However, from time to time the number of such problems that cannot be resolved within the dominant framework ("anomalies") becomes large enough to trigger a crisis, which is then resolved if a new "paradigm" is arrived at to replace the old framework and provide new guidance for further normal-puzzle solving science.

Typically, one of the problems with the Kuhnian approach is that Kuhn did not define exactly what he meant by paradigm, which means that it is not entirely clear what may constitute a paradigm shift. For the purposes of my argument, I will use the commonly accepted interpretation of paradigms as encompassing the "disciplinary matrix", which means not just the dominant theory or theories within a given field, but also the accompanying methodologies, training strategies for the next generation of scientists, and – no less important – the pertinent metaphysical and epistemological assumptions.

Kuhn, notwithstanding the accusation of constructivism that has been hurled at him, and from which he defended himself in later writings, suggested five criteria for comparing competing paradigms and for theory choice: 1) Accuracy; 2) Consistency, both internal and with other theories; 3) Scope, in terms of how widely the explanatory reach of a theory extends; 4) Simplicity; and 5) Fruitfulness, in terms of further research. Roughly speaking, then, the comparison between the two paradigms is striking:

Kuhn's Criterion	*Natural Theology*	*Darwinian Theory*
Accuracy	All explanations are ad hoc, since God's will is inscrutable	It can explain some surprising facts about the biological world, like the complexities of the flower structure in some orchid species, or the intricacies of the life cycles of some parasites
Consistency	Internally inconsistent with the idea of an all-powerful, all-good God (the problem of natural evil)	As internally consistent as any major scientific theory; external links to other sciences, particularly Darwin's prediction that the age of the earth had to be greater than what commonly thought by geologists and physicists of the time (turns out, he was right)

Kuhn's Criterion	*Natural Theology*	*Darwinian Theory*
Scope	Allegedly all-encompassing, but supernatural "explanations" are epistemologically empty	New facts about the biological world that are explained by the theory have been consistently uncovered for one and a half centuries
Simplicity	Deceptively simple, if one neglects the obvious question of the origin and makeup of the Creator	In its original form invokes a small number of mechanisms to explain biological history and complexity; more recent versions invoke more mechanisms, but still a relatively limited number
Fruitfulness	Did not lead to any research program or discovery	Has maintained a vigorous research program for one and a half centuries

According to the above summary, then, the Darwinian paradigm is definitely preferable to Paley's natural theology – not surprisingly. More interestingly, if we were to repeat the exercise while comparing the original Darwinism with either neo-Darwinism or the MS, the results would be quite different (I defer a comparison to the ES to the end of this paper). Neo-Darwinism is a trivial extension of the original idea, so it hardly counts as a new paradigm; as for the MS, it retains the two foundational ideas of Darwinism – natural selection and common descent – and adds more mechanisms of evolutionary change (random drift, mutations), which actually go a long way toward solving Darwin's problem of the origin of the variation necessary for selection to operate. While biologists have, rightly, made a big deal of the power of drift to counter selection pressure (Millstein, 2007), it seems universally agreed that the MS was an expansion of, not a shift from, Darwinism.

Kuhn's theory of paradigm shifts famously included another controversial notion: incommensurability. It is again far from being clear to what extent Kuhn's concept of incommensurability leads one on a slippery slope toward constructivism – something to which Feyerabend came infamously close. Here I will take Kuhn's later assurances that he never meant to be a constructivist and analyze instead the degree of incommensurability between natural theology and Darwinism. In order to do so, however, we have to recall that Kuhn actually invokes three distinct notions of incommensurability: methodological, observational and semantic.

Methodological incommensurability refers to the notion that different paradigms lead scientists to pick different "puzzles" as objects of research, as well as to the idea that scientists then develop distinct approaches to the solution of those puzzles. Obviously, natural theology and Darwinism are methodologically incommensurable: while they both rely on observation and comparative analyses, their goals are entirely different. For Paley, the focus is on the intricate complexity of living organisms, constantly interpreted as an obvious indication of the will and omnipotence of the Creator. Darwin, instead, pays particular attention to precisely those biological phenomena that are troubling to the notion of intelligent design, as in this famous passage: "I cannot persuade myself that a beneficent and omnipotent God would have designedly created the Ichneumonidæ with the express intention of their feeding within the living bodies of Caterpillars" (Darwin F., 1887, p. 312). More broadly, the sort of "puzzles", to use Kuhn's terminology, that Darwinists began to pay attention to concern the historical relationships between different species of organisms (something that is defined out of existence within the natural theological paradigm, since species are specially created), as well as the kind of ecological settings that bring about different adaptations (again, a problem ruled out within natural theology, where adaptations are the direct result of an intelligent act). It is worth noting, of course, that the subsequent move from Darwinism to neo-Darwinism and then to the MS has expanded the number and types of puzzles (most importantly with the inclusion of questions related to heredity), but has retained the core ones distinctive of the original Darwinism – again pointing to my conclusion that no (further) paradigm shift has occurred in evolutionary biology after Darwin.

Observational incommensurability is tightly linked to the idea that observations are theory-dependent: what is considered a "fact" within one theoretical context may not be such in a different theoretical context. This is perhaps one of the most controversial of Kuhn's notions, famously illustrated with images from Gestalt psychology, where the same pattern of lines on paper can be interpreted in dramatically different fashions (e.g., a vase or two faces, an old or a young woman, a rabbit or a duck, etc.). The problem, of course, is that if we take the Gestalt metaphor seriously, we are led to the position that there is no true or even better way to interpret the data, which in turn leads to the constructivist temptation (any theory is just as good as any other, and there really is no way to measure progress in science). Kuhn, as I mentioned earlier, disavowed such an extreme interpretation of his ideas, and the notion of theory-dependence of observations is now commonly accepted

in philosophy of science and embedded in textbook treatments of the subject (Ladyman, 2001). Be that as it may, it is hard to imagine examples of observational incommensurability between natural theology and Darwinism, in part no doubt because no sophisticated way of gathering data was accessible – beyond direct observation and rudimentary experiments – to proponents of the two paradigms. Later on, with the development of the MS view of evolution, the scope of observational and experimental approaches increased significantly, culminating in the molecular revolution of the latter part of the 20th century. But since the broad theoretical structure remained fundamentally the same, solidly anchored in the original Darwinism, it would be futile to look there for instances of observational incommensurability.

Finally we get to semantic incommensurability. This has to do with shifts in the meaning of terms used by scientists, one of Kuhn's examples being the concept of "mass", which is a conserved, static quantity in Newtonian mechanics, but becomes interchangeable with energy within the framework of Einstein's relativity. For the purposes of our discussion, one could make the argument that a similar situation holds for the shifting concept of species between natural theology and Darwinism. Both paradigms do refer to "species", but the meaning of the term is entirely different. For Paley, species were fixed entities set in place by the action of the Creator – in that sense not far from Newton's own conception of the physical world, and particularly of the laws governing it. For Darwin, however, species are ever changing entities with no sharp boundaries, which are altered by evolutionary processes in a continuous, gradualistic fashion. Interestingly, this is one of the few areas where the original Darwinism differs sharply from the MS: within the latter context, species are characterized by natural boundaries, i.e. they are more than just arbitrary, human imposed discontinuities on an underlying seamless continuum (which is what Darwin thought). Which is why, rather ironically, if there is one topic that Darwin's original book is not about is precisely "the origin of species". Contrariwise, the study of the nature of species and of the process of speciation has been a central one for the MS.

So far I have argued that natural theology and Darwinism are indeed different paradigms sensu Kuhn (it goes without saying that the Darwinian was obviously the more successful one), and that there was a degree of methodological incommensurability, a lesser degree of semantic incommensurability, and no discernible observational incommensurability between the two. I now turn to the further question of what happens when we examine the emerging ES against the background of the MS by the same tools of paradigm comparison and incommensurability measures.

4. Moving toward an Extended Synthesis

The ES in evolutionary biology is still very much a work in progress (Pigliucci & Muller, 2010), so the analysis that I am presenting here will need to be amended according to how theoretical biology will develop over the next several years. Nonetheless, we can attempt the same kind of comparison that I made above between natural theology and Darwinism, this time concerning the shift from the MS to the ES (I have argued above that the moves from Darwinism to neo-Darwinism to the MS did certainly not constitute a paradigm shift).

Specifically, let us consider again Kuhn's five criteria for paradigm comparisons, namely, accuracy, consistency, scope, simplicity and fruitfulness:

Kuhn's Criterion	*Modern Synthesis*	*Extended Synthesis*
Accuracy	In addition to what was said of the original Darwinism, it can produce quantitative accounts of the change over time of the genetic makeup of natural populations	It incorporates the same methods and results of both Darwinism and the MS, adding the explanation of developmental and other self-organizing biological phenomena
Consistency	As internally consistent as any major scientific theory; explicit external links to genetics, molecular biology, and ecology	Same degree of internal and external consistency as the MS, with the addition of external links to developmental biology, genomics, and complexity theory among others
Scope	New facts about the biological world that are explained by the theory have been consistently uncovered for the past several decades	Further expands the scope of the MS by explicitly including questions about the origin of evolutionary novelties, the generation of biological form, and the problem of genotype-phenotype mapping
Simplicity	It uses a limited number of mechanisms (natural selection, genetic drift, mutation, migration, etc.) to account for evolutionary change over time	It makes use of all the mechanisms of the MS, adding a number of others such as epigenetic inheritance, evolvability, facilitated (i.e., self-emergent) variation, etc.

Kuhn's Criterion	*Modern Synthesis*	*Extended Synthesis*
Fruitfulness	Has a history of 70+ years of vigorous research programs, building on the previous fruits of the original Darwinism	It builds on the ongoing research program of the MS, has already led to empirical (e.g., emergent properties of gene networks and of cell assemblages) and conceptual (e.g., evolvability, evolutionary capacitors) discoveries, though of course it is very much a work in progress at the moment of this writing

It should be obvious from the table that the ES is just what the name implies, an extension of the MS (which was itself a synthesis of various theoretical and empirical results within the original Darwinian framework). Hence, no paradigm shift appears to be on the horizon. Indeed, we would be hard pressed to find any example at all of any of the three types of incommensurability, be it methodological, observational, or semantic.

Ironically, if any concept might change in a more or less radical form during the transition from MS to ES it may be – once again – the concept of species. Although there is as yet no consensus about this among researchers involved in the ES (just as there hasn't been much of a consensus about it within the MS, Mayr's famous statements to the contrary notwithstanding), the prevalent mood is for some sort of pluralistic (Brigandt, 2003) or multifaceted (Pigliucci, 2003) species concept. In the first instance, species would be thought of as a heterogeneous category, with the term acquiring a different meaning when applied to different clades of living organisms (e.g., mammals vs. bacteria). In the second case, species would be thought of as a family resemblance concept (along the lines of Wittgenstein's treatment of concepts like "game'), i.e. concepts whose boundaries are intrinsically fuzzy, and that do not admit of a small set of necessary and sufficient conditions for their definition. These two solutions are significantly different from the prevalent ideas within the MS literature of species as either a set of organisms reproductively isolated from other such sets (Coyne & Orr, 2004), or a unit defined according to phylogenetic criteria (Nixon & Wheeler, 2008). Even though this could be construed as a type of semantic incommensurability, the situation is surely no worse than the difference in species concepts between Darwin and the MS, and it certainly does not rise to the same level of shift that we saw going from Paley to Darwin.

If the analysis I presented above is correct, the picture of the history of evolutionary theory that emerges is one of an initial paradigm shift, from natural theology to Darwinism, followed by a series of expansions building on the Darwinian foundations: first the small tweaking represented by neo-Darwinism, then the major shift that gave origin to the MS, and possibly currently a second major shift toward an ES. After Darwin, therefore, the sequence of changes in theoretical evolutionary biology does not follow Kuhn's model, but rather more closely approximates Gould's (2002) view as expressed in *The Structure of Evolutionary Theory*. There Gould talks about three criteria with which to compare different versions of evolutionary theory, in terms of the degree of agency, efficacy and scope of natural selection, which – together with common descent – is a fundamental pillar of all versions of the theory.

Agency refers to the locus of action of natural selection. This was the individual organism in the original Darwinism, but was expanded to include genes during the MS and the subsequent period of normal science. The ES aims at further expanding the agency of selection, adding group and species selection (Okasha, 2006). Efficacy is the causal power of natural selection relative to other evolutionary mechanisms. In this case, both the MS and the ES have resulted in a decreased efficacy: the MS introduced genetic drift, mutation and migration as additional evolutionary mechanisms, while the ES is bringing in the evolvability of evolutionary mechanisms themselves, as well as facilitated variation and self-organization, to mention but the major new players. Of course, natural selection still remains the only mechanism capable of generating adaptation, thus confirming the original Darwinian insight. As for scope, for Gould this is the degree to which natural selection can be extrapolated to macroevolutionary time scales. Famously, the MS initially flirted with the possibility of different types of macroevolutionary change (Simpson's distinction between bradytelic and tachytelic evolution), but ended up reasserting Darwin's dictum that all evolution is gradual. The ES, on the other hand, includes the strong possibility of partial decoupling between micro- and macroevolution, as first suggested by Eldredge and Gould (1972) and more recently upheld by the best available evidence (Jablonski, 2005).

If Gould is correct, as I maintain here, then truly the only paradigm shift in evolutionary biology took place when natural theology was abandoned in favor of naturalism. But that shift, one can reasonably argue, really represented a transition from proto-science to mature science. Contrary to some recent attempts to redefine the epistemological boundaries of science (Boudry *et al.*, 2010), science does not have epistemic access to the supernatural – a

potentially intrinsically incoherent concept – for the simple reason that science needs certain metaphysical assumptions to get started, naturalism being one of the most fundamental of them. This implies that going from Paley to Darwin one goes from a pre-scientific (though science-like) to a scientific view of biology, and that the corresponding paradigm shift did not really happen within the confines of an established science.

Several of Kuhn's own original examples – most famously the transition from Ptolemaic to Copernican astronomy, which he describes in detail – may be amenable to the same criticism of being not examples of paradigm shifts within science, but rather of transitions between proto- and full fledged science. This way of thinking, incidentally, may go a long way toward making sense of Kuhnian issues such as incommensurability. Whether this suggestion can rise to the level of a general criticism of Kuhn's ideas and to their reformulation in terms of describing the shift from proto- to full science rather than intra-science revolutions, of course, remains to be seen.

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