Darwinism in the Twentieth Century: Productive Encounters with Saltation, Acquired Characteristics, and Development

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Abstract Darwinism is one of several research traditions in evolutionary biology. I identify it, both before and after its unification with genetics, with Darwin's theory of descent by natural selection from a common ancestor. Other traditions include saltationism/mutationism, Lamarckism, and evolutionary developmentalism ("evo-devo"). I argue that Darwinism's continued dominance in evolutionary science reflects its proven ability to interact productively with these other traditions, an ability impressed on it by its founder's example. Evolution by sudden leaps (saltations) is alien to the spirit of Darwinism, but Darwinism advanced its own agenda by incorporating and subverting saltationist themes. Similarly, Lamarckism's belief in the heritability of acquired characteristics has been discredited, but some of the facts to which it seems congenial reappear in genetic Darwinism as phenotypic plasticity and niche construction. These examples help assess challenges to Darwinism's hegemony currently arising from the role of regulatory genes and epigenetic factors in development. Rather than executing already entrenched genetic programs and relying on chance mutation to initiate evolutionary change, the developmental process appears to generate heritable variations that ab initio respond to environmental factors in an adaptive way.

Keywords Baldwin effect • Darwin(ism) • Evo-Devo • Mutation(ism) • Natural selection • Lamarck(ism) • Niche construction • Phenotypic plasticity • Punctuated equilibrium • Saltation(ism)

1 Darwinism's Three Persisting Challenges

In this chapter, "Darwinism" will refer to Darwin's claim that gradual natural selection is the primary (but not the only) cause of evolutionary diversification. It will not refer to Darwin's insistence that all organisms on earth have descended with modification from a common ancestor. In the latter sense, Darwinism was a success from the start.

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Theories of evolution with multiple starting points disappeared almost overnight. Admittedly, popular culture still identifies Darwinism with denial of species fixism, that is, repudiation of "transformism" as such. "Darwinism" as evolution in general permeates the transcript of the 1925 Scopes Trial in Dayton, Tennessee, and persists to this day in American evangelical circles through the continued rhetorical resonance of that trial (Larson 1997). By the turn of the twentieth century, however, professional biologists were already using "Darwinism" to refer to natural selection's ability (or inability) to explain descent from a common ancestor. After its marriage to population genetics in the 1930s, Darwin's theory of evolution by natural selection acquired a new and improved interpretation that since the end of World War II has organized the space of inquiry in evolutionary biology. This theory or, better, family of related theories is called the Modern Evolutionary Synthesis (Huxley 1942).[1]

From the time of their youthful studies, professional evolutionary biologists have been so deeply immersed in the neo-Darwinian paradigm (as the Modern Synthesis is also called, albeit misleadingly[2]) that they are sometimes surprised to learn that at the turn of the twentieth century Darwinism was widely rumored to be on its "deathbed" as a general theory of evolution (Dennert 1904; Kellogg 1907). Where, we may ask, did these challenges to the power of natural selection come from? Sometimes in combination and sometime as rivals, they came mostly from three generative ideas about evolutionary process that preceded the *Origin of Species*, affected it, and survived it:

Evolutionary developmentalism: the idea that evolution takes place in and by means of inner-driven change in the ontogenetic or embryological process, a historical record of which is preserved in the pattern of phylogeny that ontogeny leaves behind or, as evolutionary developmentalists once believed, recapitulates.

Inheritance of acquired characteristics: the notion that evolution's causal grindstone is the adaptation of competing organisms to resource-scarce environments, but that its driver is not natural selection, as Darwin held, but the adaptive effects of impinging environments on embryos or the direct transmission to offspring of habits acquired postnatally.

Saltationism: whether its causal locus is ontogenetic or takes place at the environment–organism interface, the notion that evolutionary novelties do not result from a gradual process of adaptation at all but from sudden leaps or saltations (from Latin saltus, leap).

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[1] Biology, evolutionary biology, evolutionary theory, and philosophy of biology differ but form a continuum. The center of gravity in this chapter is between the second and the third of these forms of inquiry, with glances at the fourth.

[2] "Neo-Darwinism" originally referred to August Weismann's (1834–1914) belief that natural selection working exclusively on germ-line heritability is the sole cause of evolution. "Hard heredity" is a necessary condition for the Darwinism of the Modern Evolutionary Synthesis, but the Synthesis rejects the "all-sufficiency (*Allmacht*) of natural selection" and takes a population-level view of evolutionary processes.

Darwin himself took these ideas seriously. His theory was persuasive in part because the "one long argument" of the *Origin* respectfully reported their attractions, provided evidence against their prowess, and sometimes reformulated them in ways that assigned them auxiliary roles (Darwin 1859: 459). Later editions of the *Origin* eventually swelled to almost twice the size of the first because Darwin persisted in this simultaneously accommodative and refutative process (Depew 2009).

In this chapter, I will protract Darwin's discursive strategy into the history of twentieth-century Darwinism by arguing that:

1. The same *leitmotivs* that presented themselves as challenges to Darwin's Darwinism also presented themselves to neo-Darwinians, but this time coming mostly from the new field of genetics. For example, the recovery and reanalysis of Mendel's experiments on peas in 1900 turned saltationism into genetic mutationism.
2. The Modern Synthesis acquired its hegemony by responding to these three sorts of challenges in ways that were as persuasive, if not always as polite, as Darwin's. Since its consolidation in the 1940s, the Synthesis has maintained its dominance by simultaneously refuting and co-opting new forms of saltationism, Lamarckism, and developmentalism.
3. In attaining and retaining its primacy, the Synthesis has from the start fused empirical discoveries with conceptual adjustments, a process more common in scientific inquiry than is sometimes recognized, and more legitimate. Since the end of the 1960s, conceptual adjustments have played an especially prominent role in containing threats carrying traces of other approaches. Examples of potential threats include supposedly directional, and so far forth Lamarckian, mutation in bacteria; the "punctuated" pattern of macro-evolutionary diversification, in which the production and retention of variation is clustered around sudden, and in an attenuated sense saltational, speciation events; and the increasingly widespread perception that the regulatory sectors of metazoan genomes are highly conserved across taxa and respond to environmental variables in ways that appear to revive the prospects of evolutionary developmentalism.

Some of these threats have waned, by either empirical reanalysis or conceptual accommodation or both. In recent years, however, evolutionary developmentalism ("evo-devo") has been issuing especially strong challenges to the Modern Synthesis. The responsiveness of regulatory genes to environments seems to be the proximate cause of variations that exhibit adaptive characteristics as soon as they appear (Pigliucci 2017). One implication is that heritable factors resemble less and less the rigid genetic programs envisioned by early molecular biologists. What gives this perception an even greater *frisson* or air of danger, however, is that it comes close to contravening a rock-solid conceptual principle of the Modern Synthesis in all of its versions: that organisms and their traits can be said to be adapted only if they evolve from a multigenerational, and so far forth gradual, process in which natural selection, working on nondirected (chance) variation in conjunction with other evolutionary factors, amplifies the frequencies of some genotypes in a population and diminishes or eliminates the frequency of others

(Dobzhansky 1937). It comes as no surprise that recent work on gene expression and related topics has precipitated a debate among respected evolutionary biologists about whether “all is well” with the Modern Synthesis or whether it needs a “rethink” (Wray et al. 2014; Laland et al. 2014). By the end of the chapter, my view will be clear: All is not well, but if it can be made well it will by conceptual adjustments no more or less radical than those the Darwinian tradition has already undergone in its discursively polymorphic and polytypic career (Weber and Depew 2003; Depew and Weber 2017).

To many Darwinians the successes I chart will seem more continuous and cumulative than I portray them. In taking the part of other traditions in evolutionary thought I am not throwing cold water on Darwinism’s past triumphs or doubting its ability to rise to new occasions. Rather, I am drawing attention to the contingency of this process. It could have failed if conceptual innovations such as the probabilistic revolution, and not just empirical discoveries and methodological innovations, had not pointed the way forward. Hence, in considering current challenges to Darwinism, it is both sobering and salutary to consider, with the help of many of the essays in this volume, just how tough things looked for Darwinism at various points in its career.

2 Saltation, Old and New

The idea of “biology” construed as a unified science of life that would integrate the natural-historical fields of systematics, comparative anatomy, paleontology, and biogeography with functional studies of morphology, inheritance, physiology, embryology, and biochemistry is no older than the turn of the nineteenth century. The term “biologie” was first used in 1800 in an unpublished manuscript by Lamarck.[3] Göttingen’s Gottfried Reinhold Triviranus wrote a multi-volume work called *Biologie* in 1802. No more important site for the flourishing of biology in this sense or its cautious embrace of transformism existed than the Museum of Natural History and Jardin des Plantes in Paris. Its three titans—George Cuvier, Étienne Geoffroy Saint-Hilaire, and Lamarck—lived, worked, and argued there for over 40 tumultuous years during which France changed from an absolute monarchy—the Jardin des Plantes was originally the Jardin du Roi—to a democratic republic, a military dictatorship, and in 1830 a constitutional monarchy in whose shadow their most famous debate was conducted (Appel 1987).

Cuvier, a comparative anatomist, presumed that the parts of organisms are functionally adapted to each other in ways that fit species for life in particular environments. [His phrase “conditions of existence” refers not to these environments, as it does in Darwin, but to the tight internal organization that equips

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[3] Lamarck used the term publicly for the first time in 1802. In Latin, “biologia” occurred in the 1760s in the philosophical works of Christian Wolff and his disciples but with a different meaning.

organisms to live in and from them (Grene and Depew 2004; Reiss 2009).] So axiomatic did Cuvier regard this heuristic principle that he bragged that from a single bone he could reconstruct the entire anatomy and way of life of the extinct species he and his colleague Alexandre Brogniart unearthed in the Paris chalk. Geoffroy challenged Cuvier's conviction that animal kinds fall into four distinct, primordial phylum-level body plans: *vertebrata*, *mollusca*, *articulata*, and *radiata*. Cuvier's functionalism, Geoffroy argued, obscures structural elements whose transformations run across all body plans. The same elements recur in the most unlikely places, sizes, and combinations. The gill cover in fish, for example, shows up as the tiny bones in the mammalian inner ear. Still, even if Geoffroy was not a functionalist like Cuvier or an evolutionist like Lamarck, he was enough of a holist to maintain that all the parts of an organism must be in balance with each other. If a new species arises, accordingly, it must result from a sudden fracture followed by a more or less simultaneous rebalancing of parts. In this way, "Monstrosities could become the founding fathers (or mothers) of new species by instantaneous transition from one form to the next" (Hallgrímsson and Hall 2011: 18). This is classical saltation.

When Darwin's *Origin* was translated (poorly) into French in 1860 it entered a conceptual field prestructured by Cuvier, Geoffroy, and Lamarck's disputations. In 1864, Albert von Kölliker embraced Darwin's case for unity of descent but, seeing it through Geoffroyian eyes, discounted his gradualist and selectionist etiology. Something like this happened closer to home as well. In embracing descent with modification from a common ancestor, the comparative anatomist Thomas Henry Huxley, Darwin's polemical champion, warned him, "You have loaded yourself with an unnecessary difficulty in assuming [the ancient principle] that *natura non facit salta* [nature does not make leaps]" (Huxley to Darwin November 23, 1859, #2544).[4] Huxley's opinion reflects an anatomist's appreciation of organic unity. This led him to discount Darwin's declaration that, "My theory [of evolution by natural selection] would break down if it could be demonstrated that any complex organ existed which could not possibly have been formed by numerous, successive, slight modifications" (Darwin 1859: 189).[5]

Huxley was not alone in failing to accept, or perhaps even see, what Darwin called "the paramount power" of natural selection (Darwin 1868; Gayon 1997). Like many others he implicitly construed natural selection more as eliminating the antecedently unfit than as gradually evolving the adapted, as Darwin believed. Puzzles about how eliminative selection could possibly drive evolutionary progress were important sources of what Peter Bowler has called "the non-Darwinian

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[4] Texts from letters to and from Darwin are cited by their identifying numbers in the Darwin Correspondence Project, https://www.darwinproject.ac.uk/letters

[5] For Darwin, adaptations evolve by natural selection in order to and because they perform biological functions. He included the functionalist but anti-evolutionist Cuvier on his short list of heroes but not the incipiently evolutionist but structuralist Geoffroy (Darwin to Ogle January 17, 1882, #13622). His other heroes, Aristotle and Linnaeus, were also non-evolutionary functionalists.

revolution" that took place after Darwin's death and persisted in some biological (and social scientific) fields into the 1930s (Bowler 1988, 2013, 2017; Gayon 1995, 1998; Stocking 1968). During this period, evolutionary developmentalism was ascendant. Descent with modification was construed as ontogeny writ large and ontogeny as phylogeny writ small. Like the passage from embryo to adult, phylogenic diversification was thought to clamber up a ladder of progress by inner-driven ("orthogenetic"), not contingent environmental, causes. Human races, unfortunately, were graded the same way.

To be sure, toward the end of the developmentalist interregnum faithful Darwinian gradualists in Great Britain pioneered the use of statistics to show that character gradients correlate with identifiable environmental changes in effecting subspecific evolution by directional natural selection (Provine 1971). It wasn't until the middle decades of the twentieth century, however, that the makers of the Modern Synthesis extended this "biometrical" approach to traits to the evolution of species and higher taxa in an empirically plausible way (Dobzhansky 1937; Mayr 1942; Simpson 1944). This temporary failure, together with the prestige germ-line-only heredity had recently acquired through August Weismann's polemics, made it almost inevitable that when Mendelism appeared in 1900 orthogenetic developmentalism would be displaced not by natural selection but by genetic mutationism and hence by a new form of saltationism.[6] Henry de Vries in the Netherlands, Gregory Bateson in Great Britain, and later the German-trained geneticist Richard Goldschmidt in America all championed the anti-Darwinian idea that genetic mutations of large effect—macromutations, in later parlance—are the creative factor in evolutionary change.[7] If Goldschmidt was mocked and pilloried for this view, it was because he had the misfortune of defending it after the Modern Synthesis had gained a foothold (Goldschmidt 1940; Mayr 1980). From the perspective of the recent turn to evolutionary developmentalism, Goldschmidt appears more as a prophet before his time than as a saltationist born too late (Gould 1980b, c).

It would be wrong to call Thomas Hunt Morgan, discoverer of the chromosomal locus of genes and father of transmission genetics, a saltationist in the sense(s) that Geoffroy, Bateson, and Goldschmidt were. Still, until the end of his life Morgan retained enough of their presuppositions to believe that mutation is the creative factor in evolution (Morgan 1935; Beatty 2016). By the 1930s, he had come to see that populations contain a great deal of standing genetic variation. Assuming, however, that only "the more extreme individuals of the population" can effect a novel redistribution of genotypes, Morgan concluded that no matter how much variation may collect as recessive alleles in heterozygotes or how widely distributed

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[6] "New ideas about [germ-line or hard] heredity emerged in part out of an enthusiasm for the concept of evolution by jumps or saltations, reflecting an anti-adaptationist position" (Bowler 2013: 195, 2017).

[7] The phase "factors of [organic] evolution" was first used in Herbert Spencer (1887); the list of candidates is still growing. "Creative factor" was probably due to the influence of Henri Bergson's *Creative Evolution* (1907), even if Morgan, Dobzhansky, and others ascribed evolutionary innovation and direction to factors other than Bergson's inner-driven, intuitively apprehended source of change (*élan vital*) (Loison and Herring 2017).

through a population this variation may be, evolutionary advance will not resume until a variant powerful enough to trigger a new spasm of differential reproduction happens to arise (Morgan 1935: 130; Beatty 2016). A variant may take a while to spread, but there is at least a whiff of saltation in the discontinuity with which the evolutionary process as Morgan saw it starts and stops.

The Modern Synthesis undermined Morgan's model of evolution by capitalizing on the statistically ingenious population geneticist R. A. Fisher's refutation of de Vries and Bateson. Fisher demonstrated mathematically that the probability of a macro-mutation spreading through a population is very low, even under selection, but surprisingly high for mutations with small but continuously additive effects on comparative reproductive output (Fisher 1930). For this reason, Fisher cast natural selection, not the mutations that are its necessary condition, as the creative factor in evolution. Over trans-generational time it gradually evolves adaptations, evolution's leading edge.

In the late 1930s, Theodosius Dobzhansky, who during the decade he spent as a guest researcher in Morgan's lab apprised his host of the extent of variation his Russian mentors had uncovered in natural populations, developed a theory of raciation and speciation that made empirical use of population-genetic theorems derived by Fisher's American rival, Sewall Wright (Adams 1994a, b on Dobzhansky's Russian background; Provine 1986 on his use of Wright). Wright and Dobzhansky argued that genetic drift—the mathematically predictable tendency of genetic variation to spread indiscriminately, and hence by chance, to new generations in small populations—allows useful variations to get a toehold that natural selection can ramp up to the point of species-defining genetic isolation (Wright 1932; Dobzhansky 1937). The idea bore fruit. Mayr's evidence that speciation takes place at the periphery of a species' range is its biogeographical expression (Mayr 1942, 1963). Simpson argued that the process is extrapolable to the evolutionary genesis of higher taxa (Simpson 1944; Pigliucci 2017).

The paleontologist Stephen Jay Gould maintained that by its heyday in the 1950s and 1960s, the Mayr–Dobzhansky–Simpson version of the Modern Synthesis had become, regrettably in his view, less chancy and more selectionist, gradualist, adaptationist, and so far forth Darwinian than its Wright-inflected prototype (Gould 1983). Although the original theory was never as non-selectionist as Gould made out, the claim remains true for at least two reasons. First, Fisher's followers at Oxford proved that many species-marking traits hitherto taken by naturalists to be selectively neutral (because they stay constant enough to serve the classificatory purposes of museum taxonomists) are finely adapted to specific environments (Lack 1947; Kettlewell 1955, 1956). This led to an expectation, soon called "adaptation*ism*," that traits should be presumed to have selectionist etiologies until proven otherwise (Gould and Lewontin 1979).

A second factor in what Gould called "the [adaptationist] hardening of the Modern Synthesis" was that in 1947, a decade after the publication of his Wright-influenced account of speciation, Dobzhansky began finding evidence that natural selection evolves not just adapted traits tied to specific environments but mechanisms for adapting that make the evolution of new races and species more probable in the face of persistent but variable environmental change (Depew 2011). Diploid (and polyploid) chromosomal structures, for example, favor what was later called "evolvability" because they retain variation in heterozygotes that may prove adaptive under new conditions. Indeed, Dobzhansky maintained that heterozygotes are often selectively favored because in rapidly changing environments they are inherently adaptive.[8] Later editions of *Genetics and the Origin of Species* expand on what he told his Columbia University colleague L. C. Dunn in 1947: In natural populations, the higher reproductive rate of variation-preserving heterozygotic chromosomal loci diminishes when not yet fully reproductively isolated local races of fruit flies are crossed, but goes up again when they have become genetically isolated species (Dobzhansky 1951, 1970). This result, Dobzhansky informed Dunn, offers "one of the most elegant proofs of natural selection known," since it shows that natural selection does not depend on mutation, haphazard migration, or genetic drift but by itself can induce hybrid sterility between races-turning-into-species even as it maintains hybrid vigor within them once they are genetically closed (Dobzhansky to Dunn, April 26, 1947, Dunn Papers, American Philosophical Society).

Gould lamented the eclipse of Wright's "pluralism" about evolutionary factors because he was on the lookout for non-selective processes to account for the "punctuated" pattern he and his collaborator Niles Eldredge had spotted in phylogenetic history, according to which gene frequency changes are concentrated around nodes of speciation instead of being smoothly distributed across an ongoing process of adaptive improvement ("phyletic gradualism"), as Simpson postulated (Eldredge and Gould 1972). Gould took the punctuated character of phylogenesis as evidence that organisms are internally integrated in ways that constrain the work of natural selection. Stasis is the norm (Turner 2017). When change occurs it comes in sudden bursts of speciation. This echo of Geoffroy-like saltation and hint of regression to Morgan's start-and-stop theory of evolution led protectors of orthodoxy to point out that gradual does not mean constant. Simpson himself had allowed, indeed required, natural selection to work at different rates (Simpson 1944). Moreover, a paleontologist's "instantaneous" is consistent with a population geneticist's "gradual." "One hundred thousand years," wrote Mayr,

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[8] Fisher proved mathematically that under certain conditions natural selection can favor heterozygotes, but, unlike Dobzhansky, he did not assign an evolutionary function to this scenario (Fisher 1930). Dobzhansky's encounter with French evolutionists may have been a source of the distinction he drew between adaptations to specific environments (which can be traps) and heterotic adaptations for adapting (Loison and Herring 2017). As a young man, Dobzhansky read Bergson. He devoted his career to showing that natural selection can explain tendencies that Bergson's followers ascribed to an inner drive that can be philosophically intuited but not experimentally proven. When he argued that, "Nothing in biology makes sense except in the light of evolution," Dobzhansky's overt target was creationism, but his point has wider significance (Dobzhansky 1973). In contrast to traits that evolutionary and non-evolutionary observers alike can agree are adaptive—the differently shaped beaks of the finches Darwin found on neighboring islands in the Galapagos, for example—evolutionary history's most important adaptations cannot even be seen by pre- and anti-evolutionary biologists, let alone be explained by them.

> would be instantaneous for a species experiencing a 10-million-year stasis. The semantic problem is evident when we consider that all population evolution … is gradual. It is obvious from the recent controversy that the chronology of speciation events cannot be established by paleontological analysis. Rather, it will have to be inferred from an analysis of currently living speciating species … In freshwater fishes it may take less than four thousand years (Mayr 1992).

This was not telling Gould anything he did not know or had not already said, albeit without Mayr's implication that no revision in the general direction of saltation is required, that "all is well." Gould's aim was not to refute the Modern Synthesis, but to free it from constraining assumptions, most harking back to the context in which Darwin was arguing, by "expanding" the ways in which its full explanatory toolkit can be put to work. Evolutionary factors—mutation, migration, drift, selection (of various sorts on various objects), and sheer stochasticity—are allowed to combine differently at different levels of a hierarchy of biological structuration ranging from proteins below to higher taxa above (Gould 1980a). Gould proposed to accommodate his own brand of paleontology to his "expanded Synthesis" by liberating the Synthesis from the Procrustean box of Darwinian gradualism and adaptationism in which it had confined itself. *Pace* its founders, he maintained that macroevolution is sufficiently discontinuous with evolution at and below the species level to exhibit a kind of selection process—species selection, which ranges over differences in the fecundity and longevity of clades—that is more open than evolution at the organismic level to survival and extinction by sheer accident (Gould 1980a, 1989; Delisle 2017; Shanahan 2017; Pigliucci 2017).

Among the attractions of Gould's expanded Synthesis is that it was consonant with, and may have helped catalyze, the mass conversion of systematists to Willi Henning's "phylogenetic systematics," which began in the 1970s (Eldredge and Tattersal 1975; Delisle 2001). More commonly called "cladism" (after the Greek word for branch), phylogenetic systematics stipulates that only points where lineages split should count in classifying (Hennig 1950). By contrast, Mayr, Simpson, and especially Huxley insisted that taxonomic practice must take into account gradual phyletic evolution to higher grades as well as the splitting off of new clades. From the cladist perspective, this view seemed to harbor a prejudice that Linnaeus, for one, inherited from the medieval Great Chain of Being. Science, Darwinism, and a fortiori what passes as common sense are still having trouble freeing themselves from this "higher-lower" metaphysical picture.

The idea of expanding the Synthesis also helped slow an anti-Darwinian tendency in molecular biology. By the late 1960s, molecular geneticists, whose intellectual roots more often lay in biochemistry than natural history, had shown that the genetic code for amino acids, and hence for the proteins they compose, substitutes mutated nucleotides at a constant rate without affecting biological function. This theorem is called "neutral mutationism" and sometimes "non-Darwinian evolution" (Kimura 1968; King and Jukes 1969; see Pigliucci 2017). Even a protein as functional and deeply entrenched in evolutionary history as cytochrome c, which in its long career has presumably been subjected to a wide range of environmental pressures, shows a mutation rate constant enough to reveal the ticking of a "molecular clock" that tracks evolutionary time's branching pathways (Zuckerkandl and Pauling 1965). Gould's proposal was simple. This might be true of protein evolution, but only philosophical reductionism implies that what goes for proteins goes for everything else. In admitting a variety of evolutionary factors, multiple levels and units of selection, and rates of change, Gould was defending the Darwinism of the Modern Synthesis by expanding its conceptual framework to include semi-saltationist scenarios and developmental constraints.

This is not, however, the end of the story. It has since been shown that molecular clocks tick at different speeds in different lineages and that the occurrence of neutral or nearly neutral mutations is not as random as defenders of "non-Darwinian evolution" have assumed, since the third position of each codon, on which functioning depends least, does most of the mutating (Lee and Ho 2016; Moorjani et al. 2016).[9] Discoveries of this sort have encouraged adaptationists to believe that, far from saving the Modern Synthesis, downplaying Darwin's gradualist and adaptationist axioms undermines it. The paleontologist Simon Conwy Morris is among those who see natural selection, adaptation, and gradualism permeating the biological hierarchy. He has resisted Gould's effort to enlist him as a supporter by appealing to convergent adaptation by natural selection to restore the continuity between micro- and macroevolution postulated by Dobzhansky, Mayr, Huxley, and Simpson (Gould 1989; Morris 2003).

To be sure, many evolutionary biologists remain as convinced as Gould that important facts do not fit the adaptationist paradigm. If they also happen to believe that the Modern Synthesis is inseparable from that paradigm, their resentment in being asked to choose between up-to-date evolutionary biology and the pretensions of the adaptationist worldview to be the premier *defensor scientiae* in our time can take the form of rejecting not just the Modern Synthesis but the Darwinian tradition generally. Part of the difficulty arises from identifying Darwinism with a rigid paradigm rather than seeing it as a historically evolving research tradition with a core set of principles that is often confused with a shifting periphery of replaceable working assumptions (Lakatos 1970; Laudan 1977). Levit and Hossfeld (2017) as well as Delisle (2017) also invoke this historiographical heuristic. Interpreting Darwinism's gradualism as constancy of rate may be one of those confusions.

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[9] Intelligent design creationists have glommed on to neutral mutation and evenly ticking molecular clocks as reasons for disputing not just natural selection but evolution itself. Not surprisingly, they have been loath to take note of complications suggesting the workings of natural selection after all (Hofmann 2017).

3 Lamarckism and Darwinism: A Dialectical Relationship

Lamarck, an invertebrate biologist, was an evolutionist who did not embrace unity of descent. On the contrary, he held that evolution from the simple sorts of organisms he studied began from several points. From spontaneously generated origins, it moves toward complexity on its own steam but also relies on the direct effect of environments and the heritability of habits acquired by repeated use to adapt organisms and their offspring to particular environments.

Lamarck's theory of evolution is called *transformisme* for a good reason. His evolutionary process implies that species do not (always) go extinct but instead are slowly transformed into descendant species. Darwin's youthful voyage on the *Beagle* solidified his belief in extinction, and lots of it, and set him searching for an evolutionary mechanism far more under the sometimes lethal influence of external circumstances than the blend of Lamarckism and neo-Geoffroyean unity of descent retailed by his foil, the [then anonymous] "author of the *Vestiges of Creation*," Robert Chambers (Darwin 1859, Introduction; Chambers 1844; Secord 2000). Darwin retained use inheritance as a secondary cause of adaptation, but it played second fiddle because Darwin was sure that only his theory of natural selection could explain both the extent of wreckage in life's history and the beautiful "co-adaptations of organic beings to each other and to their physical conditions of life" (Darwin 1859, Introduction). It is no accident that Darwin did not use "transformism" in the *Origin* and used "evolving" only once.

The late nineteenth-century "non-Darwinian revolution" studied by Bowler made inner-driven complexification evolution's primary driver, reversed the primacy Darwin assigned to natural selection over the heritability of acquired characteristics, and treated the direct effect of environments on embryos and neonates as a more important form of Lamarckian adaptation than use inheritance. Natural selection was accepted as a factor, but it was largely relegated to the task of weeding out organisms that fail to adapt to the exigencies of the Malthusian scarcity under which all living beings were thought to labor (Spencer 1887). Accordingly, August Weismann was flying in the face of a widespread consensus when he insisted that acquired characteristics of every stripe come too late in the developmental process to be heritable and that only gradual natural selection working on chance variation in the germ line (not identified as genetic mutations for another decade) could cause evolution (Weismann 1889).

It is a myth that Weismann's neo-Darwinism—so called because it did away with Darwin's pluralism about inheritance and embraced the "all-sufficiency" of natural selection—was universally accepted as soon as he reported that chopping off the tails of a few generations of mice failed to show the heritability of taillessness. On the contrary, the Paris Municipal Council funded France's first chair of evolutionary biology, at the Sorbonne, with a view to supporting Lamarck. The University of Paris's interest in so arcane a topic sprang in part from the association of neo-Darwinism with eugenics at a time when France was preoccupied with raising its birth rate so that its military would be in a position to take revenge on the Germans for their occupation of France in 1870 (Cook 1999; Burian and Gayon 1999). The chair's first occupant, the zoologist Alfred Giard, urged funding an "*institut transformiste*" whose reliance on the high standards of French experimentalism established by Claude Bernard would demonstrate Weismann's errors. When Mendelism bolstered the fortunes of Weismann's hard inheritance, a graduate student in a French university was charged with proving that Morgan's work on Mendelian ratios in fruit flies was compromised by improper laboratory methods and safeguards. When he proved instead that Morgan was right, his Ph.D. supervisor disowned him (Burian and Gayon 1999: 317). After the heritability of acquired characteristics proved resistant to experimental validation, French Lamarckians turned to its inner-driven side (Loison and Herring 2017). It was not until 1946 that France established a university chair of genetics.[10]

The French were not the only latter-day Lamarckians. At the turn of the twentieth century, American biologists, especially paleontologists and botanists, had an even more pronounced neo-Lamarckian bent.[11] The biological research stations at Woods Hole, Massachusetts, and Cold Spring Harbor, New York, were initially funded with the aim of opposing Weismann. Fearing that his pan-selectionism would undermine the very possibility of evolutionary and social progress—after all, genes adapt organisms only to local, evanescent environments—and regarding as inconclusive a recent high-profile debate on this subject between Weismann and Spencer, Henry Fairfield Osborn, paleontological curator at the American Museum of Natural History, challenged the Marine Biological Laboratory at Woods Hole to conduct experiments in which:

> . . . [A]n organism with an environment or habit A is transferred to environment or habit B, and after one or more generations exhibits variation B. This organism is then re-transferred to environment or habit A. If it still exhibits, even for a single generation or transitorily, any of the variations B, the experiment is a demonstration of the inheritance of ontogenetic variations (Osborn 1895: 97).

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[10] A caveat. In the interwar period, a talented circle of French geneticists, many with training in and funding from other countries, began experiments in physiological genetics. This work, conducted in research institutes, positioned Boris Ephrussi, André Lwoff, Francois Jacob, and Jacques Monod (who with Jacob discovered the *lac* operon, the first regulatory genetic mechanism to be understood) to take the lead in studies of gene regulation in the 1960s, in the process restoring the decisive importance of experiment (Burian and Gayon 1999; Loison and Herring 2017). At that time, molecular geneticists in America were still preoccupied with nailing down the genetic code and finding the mechanisms and pathways of protein production.

[11] American neo-Lamarckism, prominent in the nineteenth century, did not last far into the twentieth. Unlike their French counterparts, American evolutionary biologists in the interwar period embraced genetic determinism and negative eugenics—eugenics aimed at preventing the supposed unfit from reproducing in contrast to the positive eugenics that flourished in the United Kingdom, which aimed at breeding a fitter governing class—in ways that tended to support the racism with which the United States still struggles (Kevles 1985). Dobzhansky worked with American anthropologists to develop a version of the Modern Synthesis that opposed all three: genetic determinism, eugenics, and racism (Jackson and Depew 2017).

Two years later, in 1896, the Welsh ethologist Conwy Lloyd Morgan and the American child psychologist James Mark Baldwin appealed to Osborn's experimental design to propose a "new factor in evolution" that Baldwin called "organic selection" (Baldwin 1896; Lloyd Morgan 1896). Habits acquired through instruction—in songbirds as well as humans, Lloyd Morgan pointed out—can be protracted by Lamarckian inheritance across an indefinite number of generations until genetic variations independently arise to support them, as Darwin and Weismann required. The reasoning was that, while variation in any and all directions is constantly arising, variants other than adaptive will either be selected against or have no effect at all (Depew 2003). Osborn jumped on the bandwagon. Why not? Organic selection saved evolutionary progress and made social progress almost axiomatic (Osborn 1896; Rainger 1991). In ascribing the concept of adaptedness to social inheritance, Obsorn predictably put the accent on the Lamarckian side. By contrast, in publications after 1896, Baldwin predicated organic selection and adaptation of the genetic changes that on his hypothesis eventually support initially learned and socially transmitted behaviors.

There the issue lay until the early 1950s, when the developmental geneticist C. H. Waddington likened his experiments in producing genetic change by heat-shocking fruit flies to Baldwin's scenario (Waddington 1953). This comparison suggested that genetic variation is both environmentally inducible and incipiently oriented in a favorable direction. Accordingly, what Waddington called genetic assimilation imposed a burden on supporters of "the Baldwin effect," as Simpson dubbed it, to show that it was not Lamarckian (Simpson 1953). The burden proved increasingly hard to meet, especially after the "central dogma of molecular biology" set germ-line inheritance and Mendel's "laws" in stone, thereby further hardening the Modern Synthesis by conceiving of DNA sequences as "coding for" particular traits and seeming to require that random mutations in the genetic code must initiate evolutionary change. The three musketeers of the Modern Synthesis, Dobzhansky, Mayr, and Simpson, had from the start predicated adaptation of gene frequency changes but had not stipulated that mutation or recombination must come first. Because they were worrying about Lysenko's Lamarckism in the Soviet Union, however, and did not want to put the Synthesis at odds with Crick and Watson's discovery of the ultimate (albeit not proximate) source of genetic variation, they distanced themselves from the phenomena to which Waddington and before him Baldwin were pointing. They regarded them as expressions of previously fixed genes with "wide norms of reaction" and "phenotypic plasticity" (Dobzhansky 1970; Levins and Lewontin 1985: 94–95, with specific reference to Waddington; Gilbert 1994: 153). That the environment in Baldwin's effect is cultural and Waddington's genetic assimilation is induced by violence contributed to the sense that even if they do occur these phenomena are unnatural and infrequent.

This is not an unreasonable interpretation. Dobzhansky's theme had always been that wherever it can natural selection fixes genotypes in populations that express themselves differently, and adaptively, in a wide range of environments, thereby enhancing the ability of lineages to ride over environmental contingencies. In a sense, the phenotypic plasticity that informs the mid-century Synthesis reconstructed Lamarckian themes by turning what Lamarck regarded as the *explanans* of a transformational process into an *explanandum* well explained by Darwin's model of chance variation and selective retention (Dobzhansky 1951; Levins and Lewontin 1985: 95). "When a trait becomes plastic," Dobzhansky wrote, "it exhibits more and more 'Lamarckian' modifications without thereby altering the [inherited] trait in the offspring" (Dobzhansky to Montagu, July 20, 1947, Montagu Papers, American Philosophical Society).

Richard Lewontin, Dobzhansky's former student and Gould's sometime coauthor, was even more forthright. In the 1960s, Dobzhansky began fancying that trans-generational natural selection uses genetic variation to solve "problems" posed to populations by environmental "challenges" (Dobzhansky 1962: 17). Lewontin saw this trope as complicit with the adaptationist and deterministic hardening of the Synthesis that Dobzhansky himself had scorned when he began viewing natural selection as favoring genotypes with wide norms of reaction. He proposed to liberate his mentor's earlier thought from his challenge-response conceit by throwing cold water on the very concept of adaptation. He portrayed organisms as making their own niches, not passive products of, because reacting to, genetic and environmental pressures. They are agents in their lived worlds because, far from merely obeying internal and external forces, they tailor developmental resources to their needs. "The environment of an organism," Lewontin writes,

> is not an independent, preexistent set of problems to which an organism must find solutions, for organisms not only solve problems, they create them in the first place. There is no organism without an environment, and no environment without an organism. 'Adaptation' is the wrong metaphor and needs to be replaced by 'construction' (Lewontin and Levins 2007: 231; see also Levins and Lewontin 1985: 99–104; Lewontin 1982).

Niche construction, as it has come to be called, has made the quasi-Lamarckian theme of agency in the unhardened Synthesis, including the Baldwin effect, more salient (Odling-Smee et al. 2003). Its advocates have been prominent among those calling for a "rethink" of the Modern Synthesis (Laland et al. 2014). Their case has profited from a sea change in genetics. The image of a genetic program running recursively, irreversibly, and autonomically through a fixed sequence from DNA to RNA to protein until a potentially useful mutation in the genetic code happens to pop up emerged in the immediate wake of Crick and Watson's great discovery in 1953. In the schools and popular press, this picture still passes as the sum and substance of genetics and as the cornerstone of trait-adaptationist, genetic-determinist versions of the Modern Synthesis, in which we are told that there is a gene for this and a gene for that. But progress in understanding gene regulation since the pioneering work of Jacques Monod, Francois Jacob, and André Lwoff has rendered this picture not just incomplete but misleadingly upside down. In turning genes on and off in the ontogenetic process, regulatory sectors of the genome slice and dice RNA as the dynamic interaction between an organism's development and its environmental circumstances requires—so much so that it is difficult to identify a particular chunk of DNA as "the gene for x," or even as a gene at all (Burian and Kampourakis 2013).[12]

Nor is DNA a splendidly isolated molecule. It often comes wrapped, sometimes loosely, sometimes tightly, around proteins and encrusted with chemical side chains, such as methyl groups. These affect whether DNA is transcribed into RNA and RNA is translated into protein. At least in single-celled organisms, these effects are "epigenetically" heritable enough to affect evolution. What is in question is whether they do so merely by providing pluralistic Darwinism with another source of naturally selectable variation or, in their openness to external influence, circumvent this process by forging a more immediate link between organism and environment. DNA's advantages as an information bank are inseparable from its chemical stolidity, to be sure, but it can be modified by tricks microbes learned long ago and that genetic biotechnicians are becoming increasingly skilled at mimicking and exploiting. When combined with revitalizing phenotypic plasticity as developmental plasticity (Schlichting and Pigliucci 1993; Pigliucci 2007; Schlichting 2008), the environmentally sensitive "epigenome"—genes in combination with other factors involved in transcription, translation, and protein folding—now coming into view has made life easier for niche constructionists, Baldwin boosters, and latter-day Lamarckians. Mary Jane West Eberhard refers to her extensively documented claim that genes are following not leading indicators of evolutionary change as Baldwinian (West-Eberhard 2003). In discussing epigenetics, Eva Jablonka and Marion Lamb speak of a "Lamarckian dimension" (Jablonka and Lamb 1995). Even genetic assimilation has been getting another look (Pocheville and Danchin 2017).

In framing one-way information flow from DNA to RNA to protein as molecular biology's "central dogma," Watson helped turn evolutionary inquiry into a well-institutionalized techno-scientific discipline, in part by creating an impression of straight-line progress in genetics from Mendel to Weismann to Morgan to his and Crick's decoding of DNA to the Human Genome project to gene therapy.[13] A strongly trait-adaptationist view of evolutionary dynamics, and a corresponding view of organisms as decomposable assemblies of parts and their functions, lurks in the background. Ironically, however, this program has rained on its own parade by turning up facts suggesting that neo-Darwinians have falsely generalized from the metazoa that served them as model organisms. Neo-Darwinian principles apply well enough to lineages whose modes of generating variation, differentially retaining it, and patterns of phylogenetic diversification depend on rigid command and control of somatic cells by sequestered genes (Keller 2000; Newman and Müller 2000). Things are more fluid, however, in other biological kingdoms.

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[12] "It takes an enormous amount of biological machinery for genes to be expressed; exactly which parts of the genome are processed depends on specific settings and structure of that machinery" (Burian and Kampourakis 2013: 613).

[13] Crick pointed out in 1970 that his 1956 version of the central dogma was not as dogmatic as the (unnamed) Watson's insistence that information must flow unidirectionally in temporal order from DNA to RNA to protein. See Burian and Kampourakis (2013: 616, n. 27).

Evolutionary bacteriologists and botanists recognize in the systems they study phenomena such as endosymbiosis, horizontal gene transfer, and strategies that enhance evolvability by biasing variation in directions from which organisms or colonies will benefit and may even anticipate (Margulis 1992; Kutschera 2017; Doolittle 1999; Cairns 1988; Foster 2007; Goldenfeld and Woese 2007; Woese and Goldenfeld 2009). It is doubtful whether the very notion of species applies to microbial systems, let alone the "biological species concept" favored by the founders of the Modern Synthesis.

It is common for Darwinians of the Strict Observance to dismiss these notions as "Lamarckian." By using it as a term of abuse, the enforcers of the central dogma broadened "Lamarckian" to include anything even hinting of violations of the formula "random genetic variation plus [and before] natural selection." However, the growing realization that there are more living things on earth than Weismann, Morgan, or Watson dreamed of has prompted Jablonka and Lamb to suggest that Lamarckism construed as broadly as it has come to be has a better claim to theoretical generalizability than the Darwinian tradition (Jablonka and Lamb 1995, 2005). The suggestion is that the explanatory range of the Modern Synthesis is biased toward organisms to which our own size and senses have adapted us. Its command over the range of living systems is no wider than the command of classical (Newtonian) physics over the full range of physical systems.

Jablonka and Lamb's suggestion can be tempting when the Modern Synthesis is viewed in terms of "selfish" chunks of DNA that "create" organisms as assemblies of optimally adapted traits (Dawkins 1989). It is less tempting, however, when "Lamarckism" is liberated from its status as a junk category and the Synthesis is made even more pluralist than Gould proposed. In adaptationism, the conflict between Lamarckism and Darwinism is categorical. In Darwinian pluralism, they are dialectically intertwined in ways I have tried to sketch in this section.

4 Evolutionary Developmentalism, Lost and Found

The fact that organisms are beings that develop was central to Aristotle's (384–322 BCE) seminal studies of biology. The creationists and materialists of his day thought of living beings as assemblies of parts. They differed on whether these parts aggregate by design or chance (Sedley 2007). Aristotle simultaneously refuted both by adducing facts showing that the commingling of male and female seminal elements triggers off a self-propelled, end-oriented (*teleios*) process in which an originally indeterminate matter forms itself into a progressively more differentiated and individuated whole of hierarchically organized parts. These parts carry out the morphological, physiological, behavioral, and cognitive functions that in concert allow members of each species to flourish in the environment that affords it appropriate resources (*Generation of Animals* 2.1.735al0-25; 2.4.740al-24). For Aristotle, the process of ontogeny (normally) culminates in the act of reproduction, thereby setting off a new round of a cycle that for each lineage shows no sign of beginning or ending, creation or extinction (*On the Soul* 2.4.415a26-30).

Aristotle's "epigenetic" view, as it came to be called, was preserved in medical schools (with accretion of creationist and corpuscular elements) from the time of Galen (129–216 CE), who was physician to the Roman emperors Marcus Aurelius and his heir Commodus, to that of William Harvey (1578–1657), who treated James I of England. In the eighteenth century, Caspar Friedrich Wolff (1733–1794) called on epigenesis to help him refute preformationism, which accommodated the end-oriented and functional aspects of organisms to Enlightenment mechanism by sleight of hand. On the sixth day of creation, according to preformationists, God placed in the egg or sperm—there was a dispute about which—a nested series of miniature little humans (*homunculi*) which thereafter come mechanically rolling out (evolving in the original sense of the term) generation after generation (Richards 1992).[14]

In the transformism stirring within the new science of *Biologia* at the end of the eighteenth century, there lurked a notion that the complexification of individual development mirrors and recapitulates phylogenetic history. Darwin accepted Karl Ernst von Baer's weak recapitulationism, which conceded that the embryos of advanced species resemble the adult forms of more primitive kinds (Darwin 1859, Chap. XIII; Nyhart 2009). For this reason, many early readers interpreted the *Origin* as restating "the development hypothesis." The strong recapitulationism of Darwin's self-proclaimed disciple Ernst Haeckel, in which organisms in the course of their development are said to run though the *adult* stages of earlier forms, gave them precious little reason to think otherwise. For Haeckel, there was a time when each human passed through a fish-like stage. This background helps us see why it was easy for Darwinism, or rather Haeckel's *Darwinismus*, to give way to the orthogenetic ontogeny–phylogeny parallelism of the later nineteenth century (Gould 1977).

The geneticist Morgan was trained as an embryologist. Aware as he was, however, that efforts to find inherited factors supporting recapitulation had so far been in vain, he set development aside to focus experimentally on the chromosomal mechanism of Mendelian inheritance. He always meant to get back to embryology armed with new insights (Allen 1979; Maienschein 2016 doubts he ever left it). Instead, his "transmission genetics" was taken up into population genetics and the

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[14] Classical epigenesis and contemporary epigenetics do not refer to the same thing but do have historical connections. Neo-Darwinism reduced the scope of nongenetic forms of heritability, such as cytoplasmic inheritance, almost to zero. Those who defended the latter, notably C. H. Waddington, referred to all aspects of inheritance as "epigenetic." The epigenome includes genes but goes beyond them. By stressing the ontogenetic locus in which an array of reproductive factors interact as "developmental resources," current advocates of the evolutionary significance of epigenetic modifications contest whether DNA is the sole carrier of biological heritability. Seeing residues of preformationism lurking in the notion of molecules that carry and transmit "information," they sometime call for a new form of preformationism's ancient antagonist, epigenesis (Oyama et al. 2001).

Modern Synthesis. No one associated with these research programs denied that organisms develop, but they did sense that viewing the evolutionary process from the perspective of "population thinking" yields insights that focusing on the development of individual organisms casts into shadow (Mayr 1980). Organisms develop but don't evolve. Spatiotemporally bounded populations don't develop, but they do evolve—by gradual shifts in the distribution of genotypes in interbreeding populations over trans-generational time. It is true that life cycle strategies are naturally selected in accord with ecological circumstances. It is also true that, following his Russian colleagues I. I. Schmalhausen and I. M. Lerner, Dobzhansky incorporated development into the Modern Synthesis by distinguishing modes of natural selection—diversifying, stabilizing, balancing—that reflect ontogeny (Dobzhansky 1970; Gilbert 1994; Depew 2011). But in both unhardened and hardened versions of the Synthesis, these phenomena bear only on how variation is differentially distributed in populations, not on how it becomes available for selection in the first place. It is the latter process that after a century of separation has brought evolutionary developmentalism into dialogue with Darwinism again, minus the red herring of recapitulation. By making ontogeny the cause of phylogeny rather than the other way around, developmental biology revealed its experimental prowess until well into the twentieth century (Esposito 2017). The maturation of developmental genetics in our own time is helping evolutionary developmental biology emerge from its eclipse by population genetics—and helping the latter come to terms at last with development.

Since the 1980s, the debate about "evo-devo" has rotated around three successive ways of envisioning "the return of the organism." In protesting the adaptationist fractioning of organisms into aggregates of separate traits, the "process structuralist" Brian Goodwin insisted that species are self-organizing natural kinds, not (just) historical lineages (Goodwin 1994). A second approach was no less opposed to adaptationism but more open to Darwinism. In Gould's "punctuated equilibrium," genetic change clusters around speciation events for the same reason one cannot presume that natural selection can or will always come up with optimally adapted traits. The many-layered structuration organisms acquire in the developmental process constrains both the availability of genetic variation and the scope and path of adaptive natural selection, thereby showing why lineages are as vulnerable to fortune as Gould took them to be (Maynard Smith et al. 1985).

A third, more recent approach has caused Darwinians to pay more attention to evo-devo, in part because it highlights empirical discoveries more than conceptual revisions or metaphysical theorizing about what organisms or species (really) are. The fundamental insight is that in controlling the developmental process, regulatory sectors of the genome turn structural, protein-specifying genes on and off only with a great deal of help from other "developmental resources." In doing so, regulatory genes do not constrain genetic variation, as Gould had it. On the contrary, they make it available in the form of shifts in the timing, placement, and rate of gene expression which almost immediately affect adaptedness to particular environmental conditions (Alberch and Alberch 1981; Newman and Müller 2000; Carroll 2005; Gilbert and Epel 2009; Pigliucci and Müller 2010; Pigliucci 2017).

Two linked observations support this claim. The first is that regulatory genes are highly conserved across lineages. HOX genes, for example, which control bilateral symmetry, are as ancient as the first metazoa. The second observation concerns the source of ontogenetic differences if genes aren't. DNA works in conjunction with epigenetic mechanisms such as the methylation of DNA, RNA in its multiple roles, enzymatic transcriptases, and hormones, to open the developmental process to organismic and environmental signals. These processes are not so much violations as evasions of the central dogma of molecular biology. Still, in conjunction with the fact that it can be spliced in many alternate ways, they suggest that DNA does not contain a code that encrypts the information for making traits in a quasi-preformationist way, but is one of a number of developmental resources that interact dynamically in the reproductive cycle (Moss 2003; Oyama et al. 2001). The resulting view is more than a return of the organism in Aristotle's substantialist sense. It is a re-conception of organisms as developmental processes that are more deeply embedded in their ecologies than even niche constructionists typically envision.[15]

From the perspective of evo-devo, setting development aside as population-genetic Darwinism does, if only for tactical reasons, forecloses the very possibility of understanding evolutionary dynamics. That is why the degree of continuity and discontinuity between the Modern Synthesis and evo-devo, especially in the third sense I have discriminated, currently divides advocates of an "extended Synthesis" from those who would replace it, either with a post-Synthesis form of Darwinism or with a resolutely post-Darwinian form of evolutionary developmentalism. Having surveyed the impressive ability of the Modern Synthesis to maintain its continuity by incorporating insights that initially seemed to threaten it, I would be the last to discount its ability to adjust. Still, I hazard to guess that whatever emerges just inside or just beyond the conceptual boundaries of the Modern Synthesis will affect how adaptation, speciation, and the origins of higher taxa are interpreted.

To be sure, the Synthesis has done better on the topic of speciation than Darwin, who merely hoped that adaptive natural selection combined with geographical isolation would eventually be shown to lead to lineage splitting. The Synthesis furthered his cause by using its characteristic "population thinking" to identify genetic, not just environmental, isolating mechanisms as marking off the boundaries of species (Dobzhansky 1937, 1951; Mayr 1963). The molecular-genetic revolution of the mid-twentieth century gave the Synthesis new tools for tracking gene frequencies but didn't affect its fundamental approach to this

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[15] Embedding organisms in ecological systems brings into view the lawful thermodynamic imperatives to which ecological systems must conform. In thermodynamically open, far from equilibrium systems, variation and selection of efficient dissipative pathways is inevitable. These physical and chemical imperatives permit, or even encourage, the emergence of developmental systems in which variation and selection take specifically biological forms. A lesson favorable to integrating evo-devo and Darwinism is that adaptive natural selection properly so called can take place only in developmental systems, which in turn are entrained with the environments by which they are co-defined.

topic.[16] Point mutations in protein production have little to do with the speciation process and so throw little light in. By contrast, switching regulatory genes on and off is so closely linked to phylogenetic branching that it validates the sweeping homology Darwin saw in the history of life by making visible the architecture of diversification (Carroll 2005).

Evo-devo highlights the unexpected speed with which speciation can occur. Earlier, I quoted the gradualist Mayr as conceding that, "In freshwater fishes [speciation] may take less than four thousand years." In fact, even without benefit of gene flow from a "founder" population, it has been reported that speciation occurred in ten generations in certain freshwater sticklebacks, a genus of sub-arctic fish (McKinnon and Rundle 2002). It is a good guess that the same or similar genetic shifts were in play in the transition of sticklebacks from their ancestral ocean-going habitat to bays, streams, and lakes as glaciers receded. These include but are not restricted to reduction or full elimination of the protruding dorsal spines that give these fish their name by deletion of specific base pairs in the HOX gene *Pitx1* and a range of associated shifts in the frequency of gene sequences coding for proteins (McKinnon and Rundle 2002; Colosimo et al. 2004, 2005; Chan et al. 2010; Jones et al. 2012). Experiments show that dorsal spine expression is affected almost as soon as the diet of saltwater sticklebacks has been changed (Wund 2008; Pfennig et al. 2010). One can readily see in the parallel evolution of species in isolated environments the plasticity of genotypes previously fixed in ancestral populations. Recasting phenotypic plasticity as developmental plasticity may allow extended versions of the Modern Synthesis to accommodate stickleback speciation without undue strain (Schlichting and Pigliucci 1993; Schlichting 2008; Pigliucci 2017). Still, this case study, if properly attested, makes it temping to cast gene regulation in the developmental process, which recruits supportive genetic changes in dynamic interaction with environment, as the creative factor in evolution, not gradual natural selection (Gilbert and Epel 2009). If so, continuity with the Modern Synthesis may demand amending, and not just extending, what counts as its core and what is peripheral. If this cannot be done in a way that preserves and further illuminates the vast amount of knowledge that has been accumulated under the aegis of the Modern Synthesis, even as new knowledge about the role of developmental genetics is added, evolutionary theory may escape the gravitational field of the Modern Synthesis, and perhaps of the Darwinian tradition more generally. I wouldn't bet on it. But it is important to acknowledge the current situation of debate in evolutionary biology without prejudging or foreclosing it.

Evo-devo's effect on genetic Darwinism's conception of adaptation may be more challenging than its effect on speciation. Earlier, we noted the Modern Synthesis's insistence that gradual natural selection is the proper cause of

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[16] Coyne and Orr (2004) summarize the methods and results of speciation research. That Coyne is an opponent of expanded, extended, or new syntheses is not unconnected with his understandable desire to defend real achievements of which he is a direct heir and contributor (Coyne and Orr 1989; Coyne 2009).

adaptation. The first occurrence of a useful genetic variant is by definition not an adaptation. On this view, natural selection cannot be restricted to eliminating the already unfit or to merely retaining mutations that happen from day one to have beneficial effects. The Modern Synthesis makes it a matter of principle that the adaptedness of populations and the adaptations acquired by members of these populations evolve over a number of generations by a cumulative process in which genotypes having a positive effect on a population's rate of reproduction are differentially propagated, and in which in consequence the mean distribution of chance variation bends in the direction of the adaptive process (Beatty 2016).[17] This is why Dobzhansky said, "Selection is . . . much more than a sieve retaining lucky and losing the unlucky mutations" and why Julian Huxley remarked, "The statement that selection is a destructive agency is not true if it is meant as merely destructive . . . It has a share in evolutionary creation. Neither mutation nor selection alone is creative of anything important in evolution; but the two in conjunction are creative" (Dobzhansky 1962: 430–431; Huxley 1942: 28; see also Mayr 1980: 2, 18).

Here, too, issues of timing come to the fore. Earlier, we reviewed the question of how many generations it takes to evolve an adaptation. This issue arises for and within the orthodox framework of population genetic Darwinism, not in opposition to it. It concerns the minimal conditions necessary for abiding by Darwin's gradualist axiom. Directed mutation, organisms rather than genes as initiators and beneficiaries of adaptive change, environments eliciting evolutionary novelties by modifying genetic material, and other controversial claims that have agitated the scene of inquiry since the 1970s pose different, potentially more heterodox questions. Recent suggestions "that variation is not random, that there is more to inheritance than genes, and that there are multiple routes to the fit between organisms and environments" have challenged not just adaptationism but the idea of adaptation as construed by the Modern Synthesis (Laland et al. 2014).

Lewontin has proposed disarming the question by deconstructing adaptation as an ideologically suspect residue of natural theology allowed to live an undeservedly beatific afterlife in many versions of modern Darwinism. Once this illusion has been dispelled, Lewontin implies that the slow steady dialectic between experimentation, observation, and theorizing in a truly scientific evolutionary science may resume (Levins and Lewontin 1985). Advocates of evo-devo have a different solution. The concept and reality of adaptation are to be retained but transferred from gene frequency changes that meet certain criteria back to organisms considered as developmental processes (Nicholson 2014; Walsh 2015). It is not populations that adapt to environmental contingencies but organisms that adapt environmental resources to their needs. Tracking gene frequencies is useful, even indispensable, in bringing evolutionary biology's *explananda* into view, but it cannot identify evolutionary causes, which are to be found in the dynamic interrelation between ontogeny and ecology (Ariew and Matthen 2002; see Millstein et al. 2009; Hodge 2016 to the

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[17] Lamarkism co-opted by Darwinism yet again!

contrary). This perspective threatens the conceptual coherence of the Modern Synthesis. Waddington seems prophetic when, following the lead of the embryologist Wilhelm Roux, he proclaimed that the problems of evolutionary biology would never be solved until biologists come back to development (Needham 1984; Gilbert 1994). What this entails remains to be seen.

5 Conclusion: Intertwined Traditions in Evolutionary Biology

Bowler has provocatively contributed to the current debate by using the genre of counter-factual history to make an informed guess that nineteenth-century evolutionary developmental biology would probably have arrived somewhere close to where it is now even if Darwin had never lived (Bowler 2013). The very existence of Bowler's thought experiment testifies to the seriousness with which evo-devo is currently being received. Bowler does not mean that natural selection would not have been discovered along the way. Weldon and other biometricians, he says, would have found their way to it in the course of applying advanced statistical-probabilistic analysis to shifts in trait distributions in species under identifiable environmental pressures (Bowler 2013 199). But in their hands natural selection would have taken its place in a continuous research tradition with Lamarckian, saltationist, and developmentalist features. In fact, Bowler argues that the current state of knowledge would have been reached earlier because it would not have been delayed by the ideological fireworks set off by Darwin's *Origin.* Descent with modification from a common ancestor and natural selection as an evolutionary agent would long since have acquired secure places in the common sense of modernity because, never having had to endure the rise of literalism about *Genesis* I, neither would we have had to endure Dawkins's atheistic provocations or Daniel Dennett's testimony that in Darwin's hands natural selection is the "best idea that anyone ever had" because it "eats like a universal acid" through religious illusions (Dawkins 2006; Dennett 1995). This is theology more than science.

In Bowler's book what counts as Darwinism is not far removed from what Gould called "Darwinian fundamentalism" (Gould 1997). It is true that in recent decades gene-by-gene, trait-by-trait adaptationism, especially applied to animal and human behavior, passes as Darwinism's highest achievement, final justification, and hence defining mark. In this chapter, I have tried to suggest that Darwinism is better identified as a research tradition whose unifying thread is not just natural selection but natural selection viewed as its founder was the first to view it: as the creative factor in evolutionary change. I have argued that its continuity has been achieved by following Darwin's lead in attempting to meet challenges arising from competing orientations in evolutionary biology. In contrast to Dawkins' and Dennett's, my Darwinism is far from triumphalist. I have acknowledged that whether it can retain its conceptual integrity and dominance in evolutionary studies in the face of challenges from evo-devo is at least as problematic as whether it could survive mutationism or revitalized forms of Lamarckism once were.

My account raises the question of whether the rival traditions that Bowler pictures as making continuous progress under the sober impulse of ideology-free inquiry may actually have reached their present condition by interacting with each other and with Darwinism in much the same way Darwinism interacted with them. These interactions would have found their way toward reliable facts and explanations by working through, not ignoring, ideological pressures that affect them all. Historians of biology who wish to pursue research along these lines will find a clue through the maze in the lively disputes about the "creative factor" in evolution that began in the 1880s and continue to this day.[18]

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