



Evolutionary Theoretician Edward D. Cope and the Extended Evolutionary Synthesis Debate

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Abstract

The Modern Synthesis (MS) gene-centered population model of evolution is currently being challenged by the Extended Evolutionary Synthesis (EES) organism-centered developmental model of evolution. The predictions of the EES are here examined with respect to the arguments of Edward Drinker Cope (1840–1897) for an organism-centered evolutionary process in which organisms both shape and are shaped by their environments such that the activities of the organisms themselves play a role in their own evolution.

Keywords Edward Drinker Cope · Developmental biology · Epigenetics · Extended Evolutionary Synthesis (EES) · Horizontal gene transfer · Niche construction · Lamarckism

Introduction

Edward Drinker Cope ... was America's first great evolutionary theoretician.

—Stephen Jay Gould (1977, p. 85).

Today, over 120 years after his death, Edward Drinker Cope's theoretical ideas continue to be studied and debated by scientists, philosophers of science, and science historians (Gissis 2011; Gliboff 2011; Ceccarelli 2019; Rieppel 2019). At a very early age Cope became fascinated with science—his first scientific paper was published at age 19 (describing a revolutionary reclassification of salamander evolutionary relationships; Cope 1859). At age 26 he described his first dinosaur, the tyrannosaurid *Dryptosaurus (Laelaps) aquilunguis*, discovered in the Cretaceous marl beds of New Jersey. He is best known as a vertebrate paleontologist, a professor of zoology at Haverford College and later at the University of Pennsylvania, but in reality he is difficult to characterize due to his incessant curiosity with all aspects of biology and geology.

Of Cope's work, Ceccarelli (2019, p. 170) wrote:

During his short life he contributed nearly 1,400 papers to scientific literature on herpetology, ichthyology and mammalogy (Frazer 1902) and described 1,282 fossils of vertebrates, about half of the total amount found in America in the years between 1846–1897 (Osborn 1931, pp. 19–20). ... At the age of 28, Cope published his first detailed formulation of an evolutionary process in *On the Origin of the Genera* ... Cope turned toward a new account of evolution in the 1870s with the publication of the essays *The Laws of Organic Development* and *The Method of Creation of Organic Forms*. . . .

Cope's final book, *The Primary Factors of Organic Evolution*, was published in 1896. He died early in the next year, at the age of 56.

Aside from the astonishing breadth of field and quantity of his scientific works, Edward Cope was unusual in other ways as well. He was almost entirely informally trained, as a young man volunteering and working part-time with the zoological collections at the Academy of Natural Sciences of Philadelphia under the direction of the great anatomist Joseph Leidy. He attended Leidy's lectures in comparative anatomy at the University of Pennsylvania and many years later was appointed to Leidy's position of chair of Zoology and Comparative Anatomy following Leidy's death. Cope's

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two academic degrees—an A.M. (Master of Arts) from Haverford, a private Quaker college in Pennsylvania, and a Ph.D. from the University of Heidelberg in Germany—were both honorary.

Cope was also raised as a Quaker, trained to live a life of simplicity and pacifism. And yet at Penn he was embroiled with Othniel Charles Marsh at Yale in one of the greatest scientific feuds in American history, the fossil-hunting Bone War rivalry (Osborn 1931; Lanham 1973; Krishtalka 1989; Wallace 1999; Jaffe 2000).

Evolution in the 19th Century

Having reviewed the reasons why the doctrine of evolution should be received as truth, I desire to give attention to the laws which may be made out by reference to its phenomena.

—Cope (1887, p. 225).

Evolution is a fact, not a theory. What exactly is evolution? In Charles Darwin's time—and Edward Cope's—a general definition was “descent with modification.” And that is not a bad definition. It means that one generation of animals or plants produces the next generation of offspring, which in turn produces the next generation, and so on. That is the descent part of the definition. Upon close observation, however, it can be seen that each generation of organisms is different from the one preceding; that is, the generations are not exact copies of each other. That is the modification part of the definition. And that modification is an empirical observation, not a theory.

Note however that this general 19th-century definition of evolution was organism-centered—it refers to modifications in the form of specific organisms. In the 20th century, one gene-centered definition of evolution was “any change in the gene frequencies of a population with time” (modified from Wilson and Bossert 1971). And that change in gene frequencies is an empirical observation, not a theory. Life is constantly changing, is constantly undergoing genetic modification, with time. Life evolves.

Why does life evolve? This is where theory comes in, and there are several theories of what might cause the modification of life with time. The most widely subscribed-to theory of how evolution takes place is Darwin's theory of natural selection. What is natural selection? A 20th-century, rather pithy definition is “the differential change in genotypic frequencies with time, due to the differential reproductive success of their phenotypes” (modified from Wilson and Bossert 1971). The first part of the definition is simply a restatement of the definition of evolution itself—the observation that

the gene frequencies present in successive generations of organisms change. The real heart of the theory is differential reproductive success. If certain variants in a population with certain phenotypes—their forms and traits—reproduce at a higher rate than other variants with other phenotypes, then the next generation will contain more of their genes than the previous one. And that change in gene frequencies, from generation one to generation two, is by definition evolution. Thus natural selection could clearly drive evolution. The next question is obvious: what determines differential reproductive success? Why do different variants reproduce at different rates? Darwin's genius was in proposing that differential reproduction was a function of differential *adaptation*.

Evolution does not take place in an ecological vacuum. Organisms must function in their environments, and they must interact with other organisms. If certain variants in a population possess forms and traits that are better adapted to their ecological setting then those variants function well in that setting—they are healthy, well fed, and potentially able to devote more time and energy to reproduction. If other variants possess phenotypes that do not allow them to function as well in that ecological setting—they are less well adapted—then they may have to spend more time simply trying to escape predators and find food, may be generally less healthy, and have less time and energy to devote to reproduction. Darwin thus proposed a mechanism that could not only produce differential reproduction, but that also could produce organisms that appeared to have been designed to function in their environments in the absence of a designer.

Cope and Natural Selection

Cope was not convinced by Darwin's argument. To Cope, the phenomenon of biological evolution consisted of two parts: one, an unknown process that produced biological variants, and two, a process that caused certain variants to reproduce more successfully than others. Cope argued that Darwin's theory of natural selection only covered part two, and thus that it was an incomplete theory as to how evolution occurred. Cope thus set out to create a complete theory on the causation of evolution and eventually published his first book, *The Origin of the Fittest: Essays on Evolution*, in 1887. The best-known evolutionary essayist of the 20th century, the Harvard paleontologist Stephen Jay Gould, wrote in his book on evolutionary development, *Ontogeny and Phylogeny*, that, “Cope was more interested in the mechanics of evolution He did not accept Darwin's emphasis on natural selection, for, although he saw how selection eliminated the unfit, he could grant it no role in the creation of

the fit—hence the sardonic title of his 1887 work” (Gould 1977, p. 85). In Cope’s own words in *The Origin of the Fittest* (Cope 1887, p. 225):

Before the excellence of a machine can be tested, it must exist, and before man or nature selects the best, there must be at least two to choose from as alternatives. Furthermore, it is exceedingly improbable that the nicely adapted machinery of animals should have come into existence without the operation of causes leading directly to that end. The doctrines of “selection” and “survival” plainly do not reach the kernel of evolution, which is, as I have long since pointed out, the question of the “origin of the fittest.” ... The law by which structures originate is one thing; those by which they are restricted, directed, or destroyed is another thing.

That is, Cope accepted natural selection is a sorting mechanism that preserves the better adapted variants in populations via the differential reproductive success of those variants. But where did the different variants—both the best adapted and the worst adapted—come from?

Neither Darwin nor Cope knew anything about the actual genetic processes of inheritance, hence they never knew the role of genetic mutations in producing new variants, new morphological forms or phenotypes (during this same period of time the Austrian monk Gregor Mendel (1822–1884) was quietly working with his plant-breeding experiments. Although he published his work in 1866 its significance would only be realized some 34 years later, when it was rediscovered and replicated in 1900). Cope was entirely right—the origin of new variants is essential for the process of natural selection to continue for, without new variants, there are no adaptive differences to select—no differential reproductive successes and no further evolutionary change. To Cope, Darwin seemed to simply accept the empirical observation that variants occur in nature without rigorously trying to discover how those variants arose.

Cope and Biological Development

There are, it appears to us, two laws of means and modes of development: I. The law of [developmental] acceleration and retardation. II. The law of natural selection. It is my purpose to show that these propositions are distinct, and not one part of another: in brief, that, while natural selection operates by the “preservation of the fittest,” [developmental] retardation and acceleration act without any reference to “fitness” at

all; that, instead of being controlled by fitness, it is the controller of fitness.

—Cope (1887, p. 43).

One profound source of variation in form and traits that was obvious to all pre-Mendelian-genetics biologists were those modifications seen in the growth and development of a single organism. Cope argued that biological developmental processes were the major creative factor in evolution, not natural selection (Cope 1887, p. 350; emphases are Cope’s):

To explain the origin of variation in animal structure is, par excellence, the object of the doctrine of evolution. There can be little doubt that the law of natural selection includes the cause of the preservation of certain modifications of pre-existent structure, in preference to others, after they have been brought into existence. In what manner or by what process the growing tissues of young animals have been so affected as to produce some organ or part of an organ which the parent did or does not possess, must be explained by a different set of laws. These have been termed *originative*, while those involved in natural selection are *restrictive* only.

Cope argued that new morphological, phenotypic variants were produced by the processes of developmental acceleration and developmental retardation, and it is only after these variants have been produced that could they then be affected by natural selection. A simple, schematic view of developmental acceleration could look something like this, where generation X is the oldest and generation Z is the youngest:

Generation X: A - - - B - - - C - - - D - - - E: Adult form X.

Generation Y: A - - B - - C - - D - - E - - F: Adult form Y.

Generation Z: A - B - C - D - E - F - G: Adult form Z.

Adults of form X grow through five developmental stages, adults of form Y grow through six stages, and adults of form Z grow through seven stages. Since Y adults grow through six stages in the same amount of time that X adults grow through only five, the growth of Y adults is *accelerated* relative to the growth of X adults. The growth of Z adults is even *more accelerated* relative to X adults, as Z adults grow through seven stages in the same amount of time as X adults grow through five.

The same process works in reverse for developmental retardation, with growth stages being subtracted in each generation rather than added. This last process is termed neoteny today and is described as the “retention of juvenile traits into the adult phase.” It is one of the developmental differences that distinguishes humans from chimpanzees. This is easy to observe in that baby chimpanzees look much more like adult humans (large foreheads and eyes, small mouths, arms and legs not too dissimilar in length) than adult

chimpanzees (very small foreheads and eyes, very large and protuberant snouts, very long arms, very short legs).

Now we encounter another very important concept in 19th-century evolutionary development—the biogenetic law of the German biologist Ernst Haeckel (1834–1919). Haeckel argued that the major changes observed in the growth of an individual recapitulated the more important changes that had occurred in the evolution of the lineage of that individual in geologic time. In short, that “ontogeny recapitulates phylogeny.”

To Cope, the biogenetic law reinforced his belief that new developmental stages could be inherited and passed on to the next generation, as illustrated by the sequential addition of developmental stages F and G in the developmental acceleration schematic diagram above. As Gould summarized in his own book on the subject, *Ontogeny and Phylogeny* (Gould 1977, p. 85):

We have seen, in Haeckel’s case, how easily recapitulation fits with a belief in the heritability of acquired characters. Since this belief was the foundation of America’s first major evolutionary school—that of the self-proclaimed “Neo-Lamarckists”—it is not surprising that the school’s leaders, the paleontologists E. D. Cope and Alpheus Hyatt, exalted recapitulation to a higher status than it had enjoyed before or has achieved since.

Now we come to the famous (or infamous?) experiment of August Weismann (1834–1914) which claimed to definitively disprove the inheritance-of-acquired-characteristics evolutionary model of Jean-Baptiste de Lamarck (1744–1829). In his experiment, Weismann chopped the tails off of mice for five generations, carefully noting with the birth of each new generation if any of the baby mice had no tail, a shorter tail, or any noticeable change in tail length. No change was observed, thus disproving the inheritance of acquired characteristics ... or did it?

The Neo-Lamarckians immediately cried “Foul!” pointing out that Lamarck modelled animals that actively used a phenotypic structure for a purpose—such as Lamarck’s example of a giraffe stretching its neck to reach leaves to eat that were out of the reach of other herbivores. If the giraffe succeeded in obtaining more food it would be healthier, live longer, and have more offspring thus triggering natural selection. Even if absolute neck length were not passed on to the next generation, the phenotypic plasticity present in the original ancestor that allowed it to elongate its neck somewhat during its lifetime could be inherited by the next generation so that they might elongate their necks also.

In contrast, chopping off mice tails is a mutilation perpetrated by an external organism, not by the mouse. It has

nothing to do with the usage of the tail by the mouse and is an involuntary phenotypic change (and presumably an undesirable change, if the mouse liked its tail). More meaningful experiments in “enduring modifications” have later been conducted at the Vivarium Institute in Vienna and other institutions with numerous environment-organism interaction-focused experiments (Jablonka and Lamb 1995; Müller 2017a).

The 19th century was rapidly coming to a close, and Cope spent a great deal of this time defending Lamarckian and Neo-Lamarckian ideas in his papers (see discussions in Bowler 1977; Ceccarelli 2019) and in his last book (Cope 1896a). He had only three and one-half months left to live.

The “Modern Synthesis” of Evolution

The Modern Synthesis (MS) emerged in the first half of the twentieth century, with the integration of Darwinian natural selection, population-level thinking and Mendelian inheritance, and has provided the dominant conceptual framework for evolutionary biology.

—Laland et al. (2015, pp. 1–2)

Gregor Mendel’s work on the genetic basis of inheritance was rediscovered in 1900. The 19th-century “blending” model of inheritance was disproved and discarded, and the foundation for the Modern Synthesis of evolutionary theory was laid. Three individuals in particular were prominent in the advancement of the Modern Synthesis—the geneticist Theodosius Dobzhanski (genetics of the evolutionary process), the population biologist Ernst Mayr (population-geographic speciation models), and the paleontologist George Gaylord Simpson (application of adaptive landscape models to macroevolutionary patterns in geologic time; see discussion in McGhee 2007).

The missing piece of the evolutionary puzzle now seemed to have been discovered—phenotypic variants were the product of genetic mutation, not developmental processes. A complete theory of how evolution worked had now been produced in the Modern Synthesis. As a result, Cope’s earlier attempt to create a complete theory was abandoned. The science historian Lukas Rieppel writes of this event (Rieppel 2019, p. 223):

During the mid-twentieth century, biologists largely abandoned the orthogenetic ideas championed by [Henry Fairfield] Osborn and Edward Drinker Cope. Instead, they embraced natural selection as the primary mechanism of evolutionary change. Supplemented by Mendelian genetics and enriched by new

theoretical models, the process of evolution was recast as a numbers game, with chance variation playing a far more important role than was previously believed. Consequently, evolution came to be seen as something that happens to populations rather than individuals ...

Gould considered the Modern Synthesis to have finally explained the true relationship between changes in individual development, ontogeny, and changes in the evolution of lineages of organisms, phylogeny. Haeckel's biogenetic law, that ontogeny recapitulated phylogeny, was thought to be rendered invalid when the true Mendelian nature of inheritance was rediscovered, leading Gould to conclude (Gould 1977, p. 8):

The biogenetic law finally collapsed as Mendelian genetics repudiated the generality of its two necessary principles—terminal addition and condensation. All varieties of change in developmental timing became orthodox. The development of individual parts could be either accelerated or retarded relative to other parts. These accelerations and retardations engender the full set of parallels between ontogeny and phylogeny.

That is to say, that evolutionary development was now considered by some as an orthodox part of the Modern Synthesis, and could be fully explained by the wedding of the laws of Mendelian inheritance and the sorting of population variance by the process of natural selection (see, for example, Wray et al. 2014). In summary, the complete theory of how evolution works had been attained.

This conclusion was fully accepted in England and the United States of America. It was not accepted on continental Europe—particularly in France, Germany, and Austria. The “Modern” Synthesis—now no longer modern—began to be challenged by the continental Europeans in the early days of the 21st century (Müller 2007; Pigliucci 2007; Pigliucci and Müller 2010).

The Return of Lamarck

The cells that make up our bodies have not arisen gradually in the typical Darwinian manner of gene mutation and natural selection. ... roughly 8 percent of the human genome consists of the remnants of retroviruses that have invaded our lineage—invaded the DNA, not just the bodies, of our ancestors ... we are at least one-twelfth viral

—Jan Sapp, quoted in Quammen (2018, p. 349).

Cope's belief in the inheritance of acquired characteristics has now been conclusively demonstrated to occur, even in human evolution, but in a way he never dreamed of—horizontal gene transfer. We now know that about 8% of the human genome was acquired by horizontal gene transfer from retroviruses that have infected us.

What is “horizontal gene transfer”? Normal Mendelian inheritance takes place in a process that is now termed “vertical gene transfer,” or VGT for short. The vertical part of the term refers to time—the time between each generation of organisms producing the next generation, and so on. The gene transfer part of the term means that each generation only receives genes from the preceding generation—our parents, our grandparents before them, and so on. Those genes do not have to be the same, for we know that the genes sometimes mutate from one generation to another. But all our genes, mutated or not, are inherited only from our ancestors, vertically, yes? No, we now know that that is not true.

Horizontal gene transfer, HGT for short, refers to genes transferred at the same level in time, not between levels in time, and between different organisms that are not ancestral. HGT is rampant in bacterial populations, with bacteria commonly acquiring new genes from neighboring bacteria or viruses. It was long thought that HGT was common only in asexual-reproducing, single-cell organisms like bacteria. But each year of biological research began to find (once one knew what to look for) first evidence of HGT in single-cell eukaryote cells, then multicellular eukaryotes, then simple bilaterian animals, then complex reptiles and mammals, and finally even humans.

Not only have we acquired genes from retroviruses by HGT, some of those genes are of extreme importance to us in that they are essential to the production of the placenta in the reproduction of placental mammals. It appears that placental *syncytin* genes are modified HGT retroviral envelope genes that assist in immunosuppression, and that play a role in the placenta's buffering effect between the fetus and its mother (Heidmann et al. 2009).

A second factor in the return of Lamarckian thinking is renewed research interest in epigenetics. Epigenetics refers to mechanisms that operate “above” (hence “epi” genetics) the underlying genetic DNA code in both development and evolution (Adrian-Kalchauer et al. 2020). Epigenetic mechanisms can actually turn on or turn off the expression of the genes coded for in DNA—leaving the underlying DNA unchanged but sometimes radically affecting the development of phenotypes coded for in that DNA. Epigenetic mechanisms can also simply speed up, or slow down, a developmental process coded for in the underlying DNA—thus changing the ultimate phenotype that is developed without changing the DNA for that phenotype (Jablunka

Table 1 Contrasts of the core assumptions of the MS and the EES (modified from Laland et al. 2015, Table 1)

Modern Synthesis Core Assumptions	Extended Synthesis Core Assumptions
A. <i>Natural selection causation.</i> Organisms are shaped by their environments by natural selection.	A. <i>Reciprocal causation.</i> Organisms both shape and are shaped by their environments.
B. <i>Random genetic variation.</i> Phenotypic variants are produced by random, nondirectional, genetic mutation.	B. <i>Nonrandom phenotypic variation.</i> Phenotypic variants are also produced by directional, nonrandom developmental bias.
C. <i>Inheritance by vertical gene transfer only.</i> Acquired traits cannot be inherited.	C. <i>Inheritance by vertical gene transfer, horizontal gene transfer, and epigenetics.</i> Acquired traits can be inherited.
D. <i>Gene-centered evolution.</i> Populations evolve through changes in their gene frequencies.	D. <i>Organism-centered evolution.</i> Populations also evolve through modifications of their environments, developmental biases, and social/behavioral transmission.

and Lamb 1995; Pigliucci and Müller 2010; Gissis and Jablonka 2011). However, epigenetic research is not new—Cope wrote about it over 120 years ago (Cope 1896b).

The Return of Evolutionary Development

In the EES [Extended Evolutionary Synthesis], developmental processes, operating through developmental bias, inclusive inheritance and niche construction, share responsibility for the direction and rate of evolution

—Laland et al. (2015, p. 1)

The 20th century meets the 21st century—and the MS meets the EES (Pigliucci and Müller 2010; Laland et al. 2015). The Extended Evolutionary Synthesis (EES) is the outgrowth of extensive work in the field of evolutionary developmental biology (or evo-devo to its practitioners), work conducted by developmental biologists who did not accept Gould's (1977) judgment that the Modern Synthesis (MS) fully accounted for evolutionary development (see Müller 2020 for a discussion of evo-devo research contributions to the EES. An aside: Gould later began to question and criticize some aspects of the MS, but in the end returned to a gene-centric position; see Newman 2003 for discussion).

Cope would have been overjoyed—Cope's belief that biological developmental processes were a major creative factor in the process of evolution has returned full force in the Extended Evolutionary Synthesis. Table 1 lists some contrasts between the Modern Synthesis and the new Extended Evolutionary Synthesis, which I have modified

and condensed from the lengthier lists given in Laland et al. (2015, Table 1). Not only do the core assumptions of the EES differ significantly from the Modern Synthesis, but the resulting predictions do as well (see Laland et al. 2015; Müller 2017b).

Organisms Influencing Their Own Evolution

It has been maintained above, that environment governs the movements [activity] of animals, and that the movements [activity] of animals then alter their environment. ... The history of animal life is in fact that of a succession of conquests over the restraints imposed by physical surroundings.

—Cope (1887, p. 357).

Cope's belief that the activities and desires of animals themselves were a directing force in evolution has returned in the Extended Evolutionary Synthesis. Living organisms are not just passively at the mercy of uncontrollable environmental conditions and the uncontrollable sorting effects of natural selection. Four separate factors in the EES argument have explicit implications with regard to organisms and their evolution:

Factor 1: *Niche Construction*: organisms can either modify their given environments or construct their own entirely new environments (and hence modify natural selection and thus influence the direction of their own evolution).

Factor 2: *Developmental Plasticity*: organisms can modify their own development in reaction to environmental conditions (and hence modify natural selection and thus influence the direction of their own evolution).

Factor 3: *Developmental Bias*: organisms can produce their own nonrandom phenotypic variation (and hence influence the direction of their own evolution).

Factor 4: *Inclusive Inheritance*: organisms' nongenetic inheritance factors (parental care, social learning, etc.) can alter the differential survival of their phenotypes (and hence influence the direction of their own evolution).

I will here briefly comment on each of these EES factors with regard to Cope's views—for a broader and more detailed discussion the reader is referred to the original EES paper of Laland et al. (2015) and also to Müller (2017b). In the EES: "Niche construction [is] treated as a process that directs evolution by non-random modification of [natural] selective environments" and that in niche construction "organisms co-evolve with their environments" (Laland et al. 2015, p. 5). Cope's view of evolution, written 129 years earlier, is given in the epigraph at the beginning of this

section of the chapter. The two quotes describe the same evolutionary process.

Modern humans are considered the ultimate in niche-construction alteration and direction of their own evolution, a view also expressed by Cope (1887, p. 357): “Man has attained to a wonderful degree of emancipation from the iron bonds that confine the lower organisms.” Yet two of the most powerful niche-construction activities of humans—architecture and agriculture—are not unique human traits. No less than 29 phylogenetic lineages of animals have independently developed architecture in the process of convergent evolution (McGhee 2011) and no less than nine independent animal lineages have convergently evolved agriculture (McGhee 2022). Indeed, as Cope believed, “the history of animal life is in fact that of a succession of conquests” in influencing the direction of their own evolution.

Developmental plasticity “is the capacity of an organism to change its phenotype in response to the environment ... plasticity facilitates colonization of novel environments ... and may increase the chance of adaptive peak shifts, radiation and speciation events” (Laland et al. 2015, p. 3). The great majority of Cope’s insights came from the analysis of fossil organisms and hard tissues like teeth and bones, rather than experimentation with living organisms and soft tissue. However, Cope was clearly aware of the importance of developmental plasticity and environmental induction (Cope 1887, p. 351):

Animals have again and again been called upon to face new conditions, and myriads of species have fallen victims to the inflexibility of their organization which has prevented adaptation to new surroundings. But it is evident that if change of environment has had any influence in the progress of evolution, it has not been alone destructive. It has preceded life as well as death, and has furnished the stimulus to beings capable of change ... and the necessity for new mechanism on the part of animals has always preceded the appearance of new [organic] structure in geologic time.

Directional, nonrandom developmental bias can produce “heritable variation [that] will be systematically biased towards variants that are adaptive and well-integrated with existing aspects of the phenotype” (Laland et al. 2015, p. 10). “Developmental bias may also contribute to the many examples of convergence across the tree of life. ... Such repeated parallel evolution is generally attributed to convergent selection. However, inherent features of development may have channeled morphology along specific pathways ...” (Laland et al. 2015, p. 3; see also Newman and Müller 2006). Newman (2019, p. 12) has argued that, “Inherency clearly does much of the work attributed in the standard

model [Modern Synthesis] to trial-and-error-based natural selection” in the generation of novelty (Müller 2007) or Cope’s “the appearance of new [organic] structure in geologic time” above, and in repeated convergent evolution in independent lineages. Convergence in evolution was once thought to be a rare curiosity in the history of life, but it is now argued to be ubiquitous at all levels of life and a dominant evolutionary process—the evolutionary expectation rather than the exception (McGhee 2011, 2019)—and historically contingent evolution is now being argued to be developmentally and functionally constrained to occur within a finite number of limited convergent pathways (McGhee 2015, 2016).

Cope was greatly interested in repeated parallel development and inexact, or transitional, parallel development within and between groups of organisms for the evolution of higher taxonomic levels. He published his ideas on repeated developmental parallelisms in the essay *On the Origin of Genera* in 1868 and added his law of repetitive addition in development to his essay *The Method of Creation of Organic Forms* in 1871, an essay that won him the Walker Prize (both essays are reprinted in *The Origin of the Fittest*, Cope 1887, pp. 41–123, 173–214, respectively, with a brief summary on pp. 124–127). The EES reawakening of research into the developmental factors that produce convergence and parallelism would have greatly pleased Cope.

“Inclusive inheritance” refers to factors that are not inherited through vertical gene transmission, but rather through social and biological interactions between the generations—parents to offspring, teachers to learners, and cultural transmission from one generation to the next. These factors clearly affect the differential survival of the organisms involved and thus their inclusive inheritance affects the direction of their evolution (Danchin et al. 2011).

For example, even if humans transplant woolly mammoth DNA into the nucleus of the eggs of female elephants—removing the DNA of the elephants from the nucleus—the resultant offspring would not be true woolly mammoths. The offspring would never learn how to behave like a woolly mammoth and would never have the intestinal microbiota necessary to digest cellulose that would have been passed on from a mother woolly mammoth to her offspring (both in her milk and her feces), and so on. Instead, the offspring would learn to behave like modern elephants and digest their food with modern elephant microbiota. Thus there is more to being a real woolly mammoth than DNA-genetic inheritance—parental training and parental microbiota must also be inclusively inherited.

Even in the 19th century evolutionists were aware of, and debated, aspects of inclusive inheritance. Chief among these was the concept of “social heredity” of Baldwin (1895)—that socially acquired behavioral adaptations “even without

causing any germinal transmission of habits or acquired traits, would allow organisms to survive as long as there was a concurrence between ontogenetic modifications and congenital variations, thus triggering natural selection” and thus that “ontogenetic accommodations socially acquired could influence the direction and rate of evolutionary change” (Ceccarelli 2019, p. 181). Curiously enough, Baldwin’s concept of social heredity influencing evolution was vigorously attacked by Cope, who thought it challenged his Neo-Lamarckian view of transgenerational epigenesis (Cope 1896b; Ceccarelli 2019).

Books Still in Print

It is of note that the 1859 edition of Darwin’s *On the Origin of Species* and the 1887 edition of Cope’s *The Origin of the Fittest* are still in print. After over a century, both are vastly out of date but they still are instructive of the state of thought in the early days of evolutionary theory. For both Darwin and Cope, their first book in evolutionary theory is considered to be their best. In contrast to their later books, facsimile editions of both *On the Origin of Species* and *The Origin of the Fittest* are available for scholars so that they can cite the original pagination present in the original publications (see References).

Conclusion

Edward Drinker Cope’s organism-centered argumentation that the activities and desires of animals themselves as well as the inherent properties of their developmental systems play a directing role in the process of evolution has returned in the Extended Evolutionary Synthesis. Cope certainly would have been an enthusiastic supporter of this expanded and more inclusive view of how evolution actually works in nature. He also would have been delighted with the modern discovery that horizontal gene transfer was a significant element in the evolutionary process. And, given modern argumentation for the process of inclusive inheritance, perhaps he would have resolved his disagreement with Baldwin’s concept of social heredity.

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Declarations

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