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Revisiting Edward D. Cope's "The Relation of Animal Motion to Animal Evolution" (1878)

George R. McGhee Jr.[1]

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Abstract

In 1878 evolutionary theoretician Edward D. Cope published an eight-page paper filled with prescient ideas that clearly anticipated theoretical evolutionary topics that are actively being debated some 145 years later. An examination of these ideas and their modern counterparts is the primary objective of this essay. A proposal is also made to provide an answer to Cope's Puzzle concerning the sequences of events involved in the evolution of adaptive animal structures. This article revisits Cope's "The Relation of Animal Motion to Animal Evolution" (published in *The American Naturalist*, volume 12, number 1, January 1878, pp. 40–48) for *Biological Theory*'s "Classics in Biological Theory" collection; Cope's original paper is available as supplementary material in the online version of this article.

Keywords Edward Drinker Cope · Cope's Puzzle · Extended evolutionary synthesis (EES) · Developmental bias and plasticity · Epigenetics · Niche construction and reciprocal causation

Introduction

> Edward Drinker Cope … was America's first great evolutionary theoretician.
> —Stephen Jay Gould (1977, p. 85).

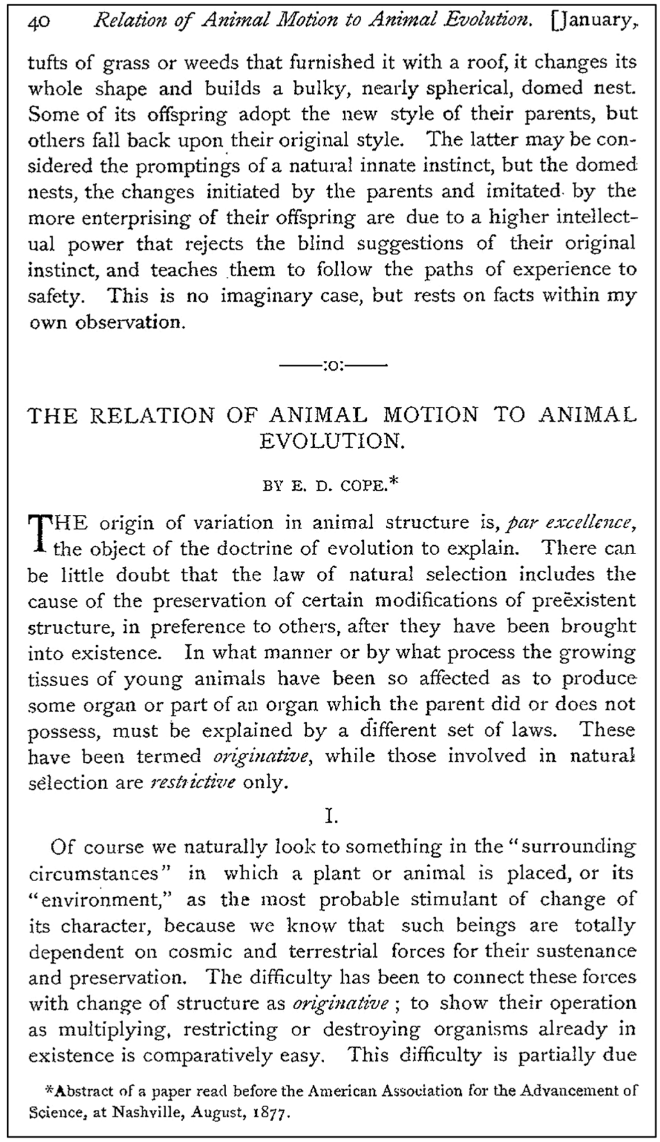
Evolutionary theoretician Edward D. Cope (1840–1897) has been lauded not only as a great theoretician but also as a genius. His first scientific paper was published at the age of 19 (describing a revolutionary reclassification of salamander evolutionary relationships; Cope 1859). He is best known as a vertebrate paleontologist, but in reality he is difficult to characterize due to his incessant curiosity with all aspects of biology and geology. Aside from the astonishing breadth and quantity of his scientific works, Edward Cope was unusual in other ways as well. He was almost entirely self trained; his two academic degrees—an AM (master of arts) from Haverford College in Pennsylvania and a Ph.D. from the University of Heidelberg in Germany—were both honorary. His first dinosaur discovery, the Cretaceous tyrannosaurid *Dryptosaurus (Laelaps) aquilunguis*, was described at the age of 26, and he was later, as a professor at the University of Pennsylvania, embroiled in the infamous "Bone War" with Othniel Charles Marsh at Yale (see the detailed biographical examinations of Cope's life in Osborn 1931, Davidson 1997, and McGhee 2023a).

Edward D. Cope (Fig. 1) lived for only 56 years, yet in that brief lifetime he authored 1,395 publications (Hilton et al. 2014, pp. 760–761), a feat that remains unsurpassed. Instead of one of the most well-known of Cope's works, the paper I have chosen to revisit is a publication that is only eight pages long. Despite its short length, this paper is packed with Cope's prescient ideas anticipating theoretical evolutionary topics that are actively being debated at the present time, some 145 years later (McGhee 2023b). This is Cope's "The Relation of Animal Motion to Animal Evolution," a paper that Cope first read in August 1877 at the annual meeting of the American Association for the Advancement of Science, held that year in Nashville, Tennessee. The paper was then published in January of 1878 in *The American Naturalist* (Cope 1878). For such an idea-packed work it was given no particular emphasis, the title merely appearing in the middle of a page in the journal (see Fig. 2). However, nine years later, Cope reprinted the paper as Chapter XII in his first book on evolutionary theory, *The Origin of the Fittest: Essays on Evolution* (Cope 1887).

✉ George R. McGhee Jr.
mcghee@eps.rutgers.edu

[1] Department of Earth and Planetary Sciences, Wright Laboratories, Rutgers University, Piscataway, NJ, USA

Fig. 1 Edward D. Cope, in an 1892 photo (from Hilton et al. 2014, Fig. 1C, in *Copeia*, published by the American Society of Ichthyologists and Herpetologists)



40 *Relation of Animal Motion to Animal Evolution.* [January,

tufts of grass or weeds that furnished it with a roof, it changes its whole shape and builds a bulky, nearly spherical, domed nest. Some of its offspring adopt the new style of their parents, but others fall back upon their original style. The latter may be considered the promptings of a natural innate instinct, but the domed nests, the changes initiated by the parents and imitated by the more enterprising of their offspring are due to a higher intellectual power that rejects the blind suggestions of their original instinct, and teaches them to follow the paths of experience to safety. This is no imaginary case, but rests on facts within my own observation.

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THE RELATION OF ANIMAL MOTION TO ANIMAL EVOLUTION.

BY E. D. COPE.*

THE origin of variation in animal structure is, *par excellence*, the object of the doctrine of evolution to explain. There can be little doubt that the law of natural selection includes the cause of the preservation of certain modifications of preëxistent 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 sèlection are *restrictive* only.

I.

Of course we naturally look to something in the "surrounding circumstances" in which a plant or animal is placed, or its "environment," as the most probable stimulant of change of its character, because we know that such beings are totally dependent on cosmic and terrestrial forces for their sustenance and preservation. The difficulty has been to connect these forces with change of structure as *originative*; to show their operation as multiplying, restricting or destroying organisms already in existence is comparatively easy. This difficulty is partially due

*Abstract of a paper read before the American Association for the Advancement of Science, at Nashville, August, 1877.

Fig. 2 Page 40 of the January 1878 issue of *The American Naturalist*; scan made by the author

This paper is but one example of Cope's prescient anticipation of ideas that would become major topics of evolutionary debate long after his death. For example, he was clearly ahead of his time in considering dinosaur energetic activity in locomotion. Cope directed the artist Charles R. Knight to illustrate the two *Dryptosaurs* shown in Fig. 3 as agilely leaping and rolling, anticipating the modern "hot blooded" dinosaurs debate. The two *Dryptosaurs* seem to be enjoying themselves, not attacking in earnest, like two young kittens practicing attack modes. Cope may have actually used kitten behavior as a model as he was very fond of cats—both the living and the extinct saber-toothed cats. He once considered bringing a jaguar home from his field work in Mexico. He decided not to because he learned that jaguars were known to prey on horses in Mexico, thus one would not make a good pet in Philadelphia (Osborn 1931, pp. 235–236).

Cope's Ideas: Then and Now

In this article I will demonstrate that Cope clearly anticipated theoretical evolutionary topics that have been proposed since his death and that are at present under active debate. These include niche-construction theory and reciprocal causation, developmental bias and non-random phenotypic variation. In contrast to the current Modern Synthesis (MS) gene-centered population model of evolutionary theory, Cope argued in his paper for an organism-centered developmental model of the 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. That view of the evolutionary process has returned in the current Extended Evolutionary Synthesis (EES) challenge to the standard MS model of evolution.

At the very beginning I must point out that when Cope used the phrase "animal motions" in 1878, his meaning was much closer to the phrase "animal activities" in current English. Cope's 1878 usage was much broader than that of just animal locomotion—swimming, walking, jumping, gliding, flying, etc.—and included such activities as parental care or

Fig. 3 Two *Dryptosaurs* illustrated as agilely leaping and rolling by artist Charles R. Knight under the direction of Edward D. Cope (Wikimedia Commons)

animal architecture. Thus I will insert the word "activities" in brackets as a reminder adjacent to Cope's "motions" in the quotations that follow.

The theory of natural selection—that natural selection was the driving force of evolution and the origin of new species—was published by Darwin (1859). 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 opened his 1878 paper with that argument (Cope 1878, p. 40; emphases in original):

> The origin of variation in animal structure is, *par excellence*, the object of the doctrine of evolution to explain. There can be little doubt that the law of natural selection includes the cause of the preservation of certain modifications of preëxistent 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 thus set out to create a complete theory on the causation of evolution by discovering the unknown source of biological variants—the *originative* drive of evolution.

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 new morphological, phenotypic variants were produced by the processes of developmental acceleration (addition of traits) and developmental retardation (subtraction of traits), and it is only after these variants have been produced that they could then be affected by natural selection (Cope 1878, p. 43). Thus Cope concluded by arguing that biological developmental processes were the major *originative* factor in evolution, not natural selection.

Cope argued 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. As noted by Hilton et al. (2014, p. 757) specifically with regard to Cope's 1878 paper:

> In his new theory, he [Cope] approached Darwin in one crucial sense: he gave the environment the main role in driving evolution. Unlike Darwin, though, he did not believe this happened through natural selection of random variations.... There was nothing random in Cope's process... now the [driving] purpose was directed by the organism itself and its interaction with its environment (Cope 1878).

Rather than being helpless in the face of environmental conditions or changes, organisms could 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. The most striking examples of this capability by animals are the convergent evolution of two major environmental modifications that were once thought to be attainable only by humans—agriculture and architecture. No fewer than 29 phylogenetic lineages of animals have independently developed architecture in the process of convergent evolution (McGhee 2011) and no fewer than nine independent animal lineages have convergently evolved agriculture (McGhee 2011, 2019, 2021).

Next, Cope advanced the argument that organisms could modify their own development in reaction to environmental conditions and hence could modify natural selection, thereby influencing the direction of their own evolution (Cope 1878, pp. 42–43; emphasis in original):

> I will now endeavor to exhibit some reasons for believing that the movements [activities] of animals affect their structure *directly*....the most direct evidence in support of the view that motion [activity] affects structure directly, is to be found in the well-known phenomenon of the increase in size and power of all organs by use.

The flip side of that observation is, of course, that animal non-activity also affects a structure directly, as seen in the well-known phenomenon of the decrease in size and power of all organs not in use—such as the atrophy and loss of eyes in fish living in dark, lightless environments and flightless, ground-dwelling birds that have atrophied, nonfunctional wings (McGhee 2011, pp. 147–154). Cope was a neo-Lamarckian, firmly believing in the transgenerational inheritance of acquired characteristics (Bowler 1977; McGhee 2023b), thus the observation of flightless birds laying eggs that hatch flightless chicks with atrophied wings did not prompt Cope to advance any natural selection mechanism to produce such a phenomenon.

Another aspect of the ability of organisms to modify their own structures is phenotypic plasticity—"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). In 1878 Cope was clearly aware of the importance of developmental plasticity and environmental induction (Cope 1878, p. 41):

> 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.

In the modern literature of evolutionary theory, Newman (2019, p. 12) has argued that, "Inherency clearly does much of the work attributed in the standard model [of evolution] to trial-and-error-based natural selection"—such as the generation of novelty (Müller 2007) or Cope's "the appearance of new [organic] structure in geologic time" above, and in the repeated convergent evolution of organic structures in independent lineages (McGhee 2011, 2019).

Cope's Summary: Then and Now

Concluding his paper, Cope (1878, p. 47) quickly summarized four main points that he wanted to make in it. I have here separated and numbered his four sentences in order to contrast them one-by-one with four sentences from the modern literature of evolutionary theory:

1. It has been maintained above [in this paper], that environment governs the movements [activities] of animals, and that the movements [activities] of animals then alter their environment.
2. It has also been maintained that the movements [activities] of animals have modified their [own] structure so as to render them more or less independent of their environment.
3. The history of animal life is in fact that of a succession of conquests over the restraints imposed by physical surroundings.
4. Man has attained to a wonderful degree of emancipation from the iron bonds that confine the lower organisms.

Now the four sentences from the modern literature of evolutionary theory. The first three sentences are from Laland et al. (2015, p. 4) and the fourth is from Arroyo-Kalin et al. (2017, p. 106):

1. The evolutionary significance of niche construction stems from: (i) organisms modify their environmental states in non-random ways, thereby imposing a systematic bias on the selective pressures they [the environmental states] generate...
2. (iii) acquired characters [of the organisms] become evolutionarily significant by modifying selective environments [that affect them]...
3. These findings have led to the claim that niche construction should be recognized as an evolutionary process through its guiding influence on [natural] selection...
4. Niche Construction theorists agree that the human species is the ultimate ecosystem engineer or niche constructor...

Comparing these two sets of sentences, it can be seen that Cope (1878) anticipated four important aspects of the current debate between the MS and EES theoretical models of the evolutionary process (Müller 2007, 2017; Laland et al. 2015; McGhee 2023b). These four aspects are (1) niche construction, (2) developmental bias and plasticity, (3) the role of niche construction and developmental biology in the evolutionary process, and (4) the recognition of human niche construction in human evolution.

One important aspect of the current MS-EES debate that is not explicitly anticipated in Cope (1878) is that of *inclusive inheritance*: the role of the nongenetic inheritance factors of organisms (parental care, social learning, etc.) in altering the differential survival of the organisms' phenotypes and hence the direction of their own evolution. A hint of this concept does exist in Cope (1878, p. 41) where he muses over *originative* developmental changes in organic structure:

> such modifications must be realized during a limited portion of the life of an animal at least; that is, during

> the period of growth, when it is not at all or but little subject to the influence of external environment, but is usually protected or supported by the parent.

Even in the 19th century evolutionists were aware of, and debated, aspects of inclusive inheritance. Chief of these was the concept of "social heredity" of Baldwin (1895) yet, 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 1896; Ceccarelli 2019).

Cope's Final Puzzle: Then and Now

In his considerations of the activities of animals in interacting with their environments Cope mused on the possible sequences of events in the evolution of adaptive animal structures (Cope 1878, p. 42):

> There are two alternative propositions expressive of the relations of structures of animals and their uses. Either the use or attempt to use preceded the adaptive structure, or else the structure preceded and gave origin to the use. The third alternative, that use and structure came into being independently of each other is too improbable for consideration in the present article. Many facts render the first of these propositions much more probable of the two.

At first glance this puzzle may appear to be of a "what came first, the chicken or the egg?" variety but it is not. In modern times it underlies as profound a question as "Is the process of evolution limited and predictable or is it unbounded and lawless?"

Hordijk (2016) outlined the modern debate between the view that the number of potential pathways available to the process of biological evolution is not infinite but in fact is limited and potentially predictable (McGhee 2011, 2015, 2016) in contrast to the view that the number of potential pathways available to the process of biological evolution is unbounded and that the process is lawless (Longo et al. 2012; Kauffman 2016). Hordijk (2016, p. 189; emphasis in original) then had the insight that the underlying assumptions of the two views of evolution were different:

> perhaps the two views are not that mutually exclusive after all. McGhee focusses on possible *forms*, presuming a particular function, whereas Kauffman focusses on possible *functions*, presuming a particular form.

Cope's Puzzle (1878, p. 42) question was framed in terms of the timing of needed usages and appearances of adaptive structures:

(1) Needed usage → Adaptive structure.
(2) Adaptive structure → Needed usage

and he stated that possibility (1) appeared to him to be *the most probable of the two*.

Hordijk's (2016) insight yields the following formulation of Cope's Puzzle to the present debate, where (1) is the thesis of McGhee (2011, 2015, 2016) and (2) is the thesis of Longo et al. (2012) and Kauffman (2016):

(1) Function → *limited number of possible* Forms *can perform that function.*
(2) Form → *unbounded number of possible* Functions *that form can perform.*

The example of Kauffman's (2) given in Hordijk (2016, p. 188) is non-biological:

Form: *screwdriver* → Functions: *screwing screws, opening paint cans, wedging a door open, using as a spear point,...*

but the point is made that the concept of screwdriver could be carried over to "biological screwdrivers" such as flagella.

One example of McGhee's (1) is:

Function: *flying* → Form: *wings*

where the same form, wings, has independently evolved four separate times in the clades of pterosaurs, dinosaurs (birds), mammals (bats), and arthropods (insects) in the past 250 million years (McGhee 2011, p. 18).

Now combining the theses of McGhee and Kauffman to Cope's Puzzle format yields the following scenario:

(1) Function: *flying* → Form: *wings.*
(2) Form: *wings* → Repurposed function: *swimming*

where it is a fact that some organisms that evolved wings for the purpose of flying have later repurposed those flying wings for a new function—that of swimming, where the wings are now modified to flipper forms. The most familiar example of that evolutionary repurposing is seen in the penguins, which no longer fly but are very agile swimmers.

In summary, the modern form of Cope's Puzzle can be stated as follows: Given a *function* it is highly *predictable* what *forms* can fulfill that function, and the ubiquitous phenomenon of evolutionary convergence—where numerous independent lineages of organism repeatedly evolve the *same form* over and over again—demonstrates that the numbers of those forms are quite *limited* for any given single function. However, given a particular *form* it is likely *impossible* to predict all of the possible *repurposed functions* that form might be used for in the future.

Thus, for Cope's original 1878 Puzzle: both his discussed pathways (1) and (2) are equally probable, not just (1) alone as Cope thought then.

In Retrospective

1. Many of Cope's original theoretical ideas concerning epigenetics and the inheritance of acquired traits in evolution are still debated by scientists, philosophers of science, and science historians to the present day, 145 years after his death (Bowler 1977; Gould 1977; Gissis and Jablonka 2011; Raia and Fortelius 2013; Hilton et al. 2014; Ceccarelli 2019; Liow and Taylor 2019).
2. In addition, Cope clearly anticipated theoretical evolutionary topics that have been proposed since his death and that are actively being debated at the present time. These include niche-construction theory and reciprocal causation, developmental bias and nonrandom phenotypic variation.
3. Cope's organism-centered argumentation that the activities of animals themselves as well as the inherent properties of their developmental systems play a directing role in their own evolution has returned in the Extended Evolutionary Synthesis of the 21st century (Laland et al. 2015; Müller 2017; McGhee 2023b). Cope certainly would have been an enthusiastic supporter of this expanded and more inclusive view of how evolution works in nature.
4. Cope's 1878 Puzzle still remains central to the debate between the seemingly diametrically opposed views that the number of potential pathways available to the process of biological evolution are not infinite but in fact are limited and potentially predictable in contrast to the view that the number of potential pathways available to the process of biological evolution are unbounded and limitless, and that the process is lawless and unpredictable (Hordijk 2016).

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Declarations

Competing Interests I declare I have no competing interests.

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