ARTICLE

Darwin's Error: Using the Story of Pangenesis to Illustrate Aspects of Nature of Science in the Classroom

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Abstract

This article discusses a number of aspects of the nature of science that can be illustrated by considering the development of pangenesis, a principle proposed by Charles Darwin to describe the rules of inheritance, explain the source of new variation, and solve other natural history puzzles. Pangenesis – although false – can be used to illustrate important nature of science ideas such as the need for empirical evidence, the use of inductive reasoning, the creative component of science, the role of bias and subjectivity, social and personal influences on science, and the notion that scientific knowledge is tentative but durable, yet self correcting.

Key Words: *History of science; Charles Darwin; heredity; nature of science.*

Accusing Charles Darwin of making an error is a dangerous strategy for those of us who support natural explanations for change through time. On the one hand, using the work "error" might be seen as heralding an attack on one of the great heroes of biology. On the other, there is the strong possibility that those who oppose Darwin and his ideas will read anxiously, looking for support in their ongoing battle with evolution. However, neither alternative will be supported here. While it is true that Darwin made a mistake when proposing a mechanism of inheritance, he remains one of the most productive scientists of all time. So, the purpose of this account is not to criticize Charles Darwin simply for having erred, as if to suggest that truly great scientists never make mistakes. Likewise, those who oppose evolution will find no solace in this account, because the "error" mentioned in the title has nothing to do with Darwin's major contribution of an account for evolution by natural selection. Darwin's many accomplishments – including natural selection – stand as testament to what the human mind can accomplish when inspired by mountains of questions surrounded by a sea of facts.

While it is true that Darwin made a mistake when proposing a mechanism of inheritance, he remains one of the most productive scientists of all time.

This article provides a wonderful illustration, rarely included in textbooks, of Darwin working as a scientist to solve a specific problem and interacting with colleagues. As the great evolutionarily biologist and essayist Steven Jay Gould was fond of saying, sometimes errors and mistakes are more revealing than another example of something expected. I began this story in the previous issue of *ABT*, in which I recounted the fascinating story of Charles Darwin and his invention of a mechanism of inheritance called "pangenesis" (McComas, 2012). Although this story is well known to historians of biology (Geison, 1969; Winther, 2000; Endersby, 2009), it is likely unknown to biology teachers and their students, but it has much to offer because of the lessons it can teach.

Of course, textbooks are not designed primarily as historical accounts but are more like encyclopedias focusing on providing conclusions rather than processes. This leaves naive readers to think that science must be a linear pursuit of the truth without dead ends, conflicts, and the impact of personalities. Such an approach in communicating science is justifiable if the goal is to present as much information as possible while preparing students for the end-of-course exams that focus only on facts and principles. Unfortunately, this picture of science inevitably dehumanizes it while making science less interesting and less accurate if the goal is to present process *and* product. Rarely do teachers and textbooks show how facts and principles are established by those whose work in the field and laboratory makes its way into the classroom. Here, rather than dwell on the fact of a Darwinian error, I will focus on why the error was made, the reactions of Darwin and his colleagues to pangenesis, and what it can teach us about how science functions. Helping students understand how science is done may open a new avenue of science instruction that communicates the facts while immersing students in the rich historical accounts of the people and processes of science.

○ Darwin's Hypothesis of Pangenesis

As discussed in more detail previously (McComas, 2012), Darwin recognized two major problems that, if solved, could make his evolutionary mechanism much stronger. These problems were related to the source of new variation and an explanation of the rules of inheritance. Although Darwin was a contemporary of Gregor Mendel, his pea plant experiments were not well known, leaving Darwin with no alternative but to develop his own explanation for inheritance. Furthermore, the production

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and transmission of new traits – the raw material of natural selection – was a mystery to Victorian naturalists. It is worth pointing out that the twin puzzles of variation and inheritance dogged Darwin throughout his professional life; he was not reluctant to share his frustration with his many correspondents and with his readers. In *On the Origin of Species* (1859), Darwin states clearly that "we must…acknowledge plainly our ignorance of the cause of each particular variation" (p. 131). Working in his study at Down House (see Figure 1), Darwin added several unique touches to the explanations for the source of variation and mechanism of inheritance available at the time and proposed what he called the provisional hypothesis of pangenesis (1868b, 1875).

Pangenesis posits that each body part and organ produces microscopic particles, called "gemmules" by Darwin. These gemmules flow from their source and unite with partially developed cells in the ovaries and testes, which, in turn, produce the gametes that go forth to form individuals in the next generation. Most interesting, Darwin believed that these gemmules would be modified in response to experiences that occurred during the life of the individual. So, if a body part were to react successfully to some environmental stimulus, the gemmules produced by that body element would be slightly different than had the stimulus not occurred. If this sounds a bit Lamarckian (i.e., use and disuse), this is correct. Darwin fully accepted the view that changes to the phenotype could result in changes to what we now call the genotype: inheritance related to the coming together of countless gemmules from the two parents. Just as importantly, pangenesis and its tiny particles could explain the source of new variants that were vital to evolution by natural selection. Without new heritable varieties, there could be no selection.

Darwin was alternately delighted and challenged by his pangenesis insights. He wrote an entire chapter in the book *Variation of Animals and Plants under Domestication* (1868b and 1875), talked extensively about the principle in *Descent of Man* (1871 and 1874), mentioned pangenesis in much correspondence with colleagues, but, curiously, failed to include mention in any edition of *On the Origin of Species*. In spite of its explanatory power, the lack of physical evidence for pangenesis may be one reason why Darwin never seemed fully able to embrace pangenesis even though the idea had great explanatory power. Consider the follwing pair of quotations. First (3 February 1868), Darwin tells colleague J. D. Hooker that "I did read Pangenesis the other evening, but even this, my beloved child, as I had fancied, quite disgusted me" (in Darwin, F., 1887, p. 75). Just a year later (21 May 1868) he says to this same colleague, "You will be surely haunted on your deathbed for not honouring the great god Pan" (Letter 6196). The two statements taken together clearly illustrate the depth of insecurity Darwin had about his own idea – pangenesis.

Figure 1. Image of part of Charles Darwin's study at Down House, located in the village of Downe, about 25 km southeast of central London. Darwin lived and worked in this house from 1842 until his death in 1882. When not experimenting in his greenhouse or hiking his "thinking path," he often worked at this special rolling chair with writing table, where he wrote most of his iconic works. (Photo by William F. McComas.)

The criticism of pangenesis from the scientific community was generally muted, probably owing to Darwin's preeminent reputation among Victorian naturalists and scholars. However, there was simply no empirical evidence that the tiny particles even existed and functioned in the way that Darwin suggested. So, except for one experimental inquiry by Francis Galton, pangenesis faded from view with the death of the master of natural selection. All that remains of pangenesis today is the name *gene*, given in 1909 by Wilhelm Johannsen to the actual heredity particle (Mawer, 2006).

○ Pangenesis: Its Legacy as an Illustration of the Nature of Science

It is widely perceived by science educators that biology textbooks have changed little in the past half century beyond their increased use of dramatic photographs, more engaging design elements, and the inclusion of ever-growing amounts of content. Although texts still remain stubbornly resistant to providing examples of the work of real-life scientists and the "story behind the story," there is a glimmer of hope for the future. Increasingly, nature of science (NOS) is recommended by science educators (Lederman et al., 2002; Osborne et al., 2003; McComas, 2004, 2008b) along with state and national content documents (National Research Council, 1996). Once end-of-course tests include items on nature of science, it is very likely that textbooks and classroom discussions will follow.

In anticipation of the increased inclusion of NOS in school science, educators have begun to converge on a description of NOS for instructional purposes (Figure 2). There is growing consensus that

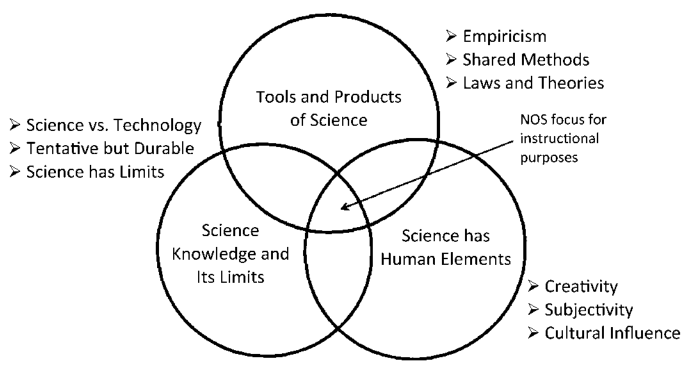

Figure 2. A summary of the three main domains of nature of science (NOS) and the accompanying subunits most appropriate for inclusion in science instruction (modified from McComas, 2008a).

students must understand something of the *tools and products of science* (including empiricism, shared philosophical principles, and the law–theory distinction), the *human aspects of the scientific enterprise* (creativity, subjectivity, and the impact of culture on science), and *elements of knowledge production in science* (the science–technology distinction; that conclusions are tentative but durable; and that there are limitations on what science can address) (McComas, 2008a). Even if we agree on what should be taught regarding NOS, we still lack pedagogical tools to communicate this important dimension of science content. This is where a story like that of pangenesis can be very helpful. The following sections will reflect on Darwin's invention to illustrate each of the three major domains of NOS to enliven and humanize science instruction.

○ The Tools & Processes of Science

This domain of the nature of science focuses on the vital issue that science is an empirical pursuit. Ideas are scientific only if they can be substantiated by facts. Empiricism is perhaps the most important of many shared practices of science, which include the use of inductive reasoning and hypothetico-deductive testing, the lack of a single step-by-step scientific method, and the distinction between laws (generalizations) and theories (explanations). Each of these elements can be illustrated by the story of pangenesis, but we will begin with empiricism and inference.

In reviewing the way in which Darwin represented the notion of pangenesis, it is clear that he may have been troubled by the fact that, although the idea appeared to solve a number of interesting natural-history problems and both addressed the source of variation and suggested rules for inheritance, there was no evidence. As critic G. H. Lewes wrote at the time (1868), "[A] very different aspect is presented by Pangenesis: all its elements are inferences; not one of them can be admitted as proven" (p. 507). Such inferences included the notion that cells throw off gemmules, these gemmules are carried through the body, they multiply by division, and they are transmitted from generation to generation in the dormant state, finally coming together in the ovaries and testes.

Unfortunately, these proposed gemmules were nowhere to be seen. This may have concerned Darwin enough that he typically referred to pangenesis as a "provisional hypothesis." His allegiance to an organized approach to conducting science is reflected in his statement that

> An unverified hypothesis is of little or no value. But if anyone should hereafter be led to make observations by which some such hypothesis could be established, I shall have done good service, as an astonishing number of isolated facts can thus be connected together and rendered intelligible. (in Barlow, 1958, p. 130)

Darwin further stated, in a letter to Charles Lyell (Letter 6023, 19 March 1868), that "an untried hypothesis is always dangerous ground" (cited in Freeman, 2007, p. 226). We gain some additional insight into Darwin's thinking about the role of hypotheses with the following:

> As Whewell, the historian of…sciences remarks: — 'Hypotheses may often be of service to science, when they involve a certain portion of incompleteness, and even of error.' Under this point of view I venture to advance the hypothesis of Pangenesis, which implies that the whole organization, in the sense of every separate atom or unit, reproduces itself. (Darwin, 1868a, p. 357)

In an interesting coincidence, it was Darwin's half cousin Francis Galton who rose to the occasion to offer an experimental analysis of pangenesis in saying "It occurred to me when considering these theories, that the truth of Pangenesis admitted of a direct and certain test…. The conclusion of this large series of experiments is not to be avoided…" (Galton, 1871, p. 395). The test he designed consisted of transfusing blood between pure-bred rabbits of the silver-gray variety and the normal or wild type. If pangenesis operated properly and the gemmules were transferred, he predicted that the offspring from those rabbits would not breed true. Following the experiment, the rabbits continued to produce offspring as before the transfusion. This led Galton to conclude "that the doctrine of Pangenesis, pure and simple, is incorrect" (1871, p. 395).

Darwin's response, discussed in detail earlier (McComas, 2012), resulted in an apology, some bruised feelings, and the apparent end to serious testing of pangenesis. In an interesting footnote to history, Galton very likely had a personal reason for wanting to engage in the experiment in the first place, a topic that will be explored later. Ultimately, pangenesis was rejected as a viable scientific idea, at least in part because of lack of evidence. This is the logical demise for unsupported notions, even those put forward by the likes of Charles Darwin.

In this example, we see inductive reasoning leading to the proposal of a hypothesis (the idea of pangenesis), followed by inferences that could be tested. Galton devised his test as the crucial experiment whereby the case could be decided one way or another. This is a remarkable example of several major NOS ideas that we should communicate to biology students. This is also a wonderful example of what Karl Popper (1963) called "conjecture and refutation," an intellectual process whereby ideas related to the underlying principle (in this case the gemmules of pangenesis) are proposed and then subjected to experiment in an attempt to reject them. The failure to reject would make the idea more reasonable to accept. This is not proof (since that cannot be offered in science), but the failure to reject is a major consideration in the acceptance of scientific ideas.

The pangenesis story provides a good example of the law–theory distinction, but before making this connection it will be helpful to provide a quick review of these terms that are often confused. In science, the term "law" is a generalization that holds true within some well-described limits, whereas "theory" is best used to describe scientific ideas that explain laws. There is no evidence that Darwin made the kind of distinction between these terms that should be made today, but in his work he often pursued answers to questions about patterns in nature and their ultimate cause. There can be no better example of this than evolution itself. Evolution, which was not discovered by Darwin, is the pattern of change through time that we see preserved as fossils and "hardwired" into the anatomy and physiology of every living thing. Darwin's contribution was to propose an explanation for how evolution occurs. To keep the principle of evolution separate from its explanation, it is best to refer to Darwin's work as the Theory of Evolution by Natural Selection.

In the case of pangenesis, Darwin proposed the underlying theoretical mechanism for how inheritance occurs and how new variants could develop. He based this theory on a great number of observations and seemingly disparate facts about the natural world. Of course, in the case of pangenesis, his proposal did not stand the test of time nearly as well as natural selection.

○ The Human Dimension of Science

This NOS domain comprises related elements such as the role of creativity in science, the lack of complete objectivity, and the cultural and social influences on the practice and direction of science. With pangenesis, creativity and subjectivity are particularly well illustrated.

Many puzzles and problems that confronted Darwin, such as regeneration and the reappearance of ancestral traits, still beg for an explanation. The creative invention of pangenesis tied all of these problems together in a common solution. Therefore, it is quite reasonable to consider the entire story of pangenesis as an illustration of creative thinking. Consider Darwin's highly creative – even flowery – explanation of how pangenesis functions:

> [O]vules and spermatozoa of higher animals must be crowded with invisible characters, proper to both sexes…yet these characters were not visible, …but lie ready to be evolved whenever the organization is disturbed by certain known or unknown conditions. (Darwin, 1868a, p. 77)

The social forces that influence science are clear in the story of pangenesis, as illustrated throughout this article by Darwin's allegiance to the accepted method of the day and by his extensive correspondence on the issue of pangenesis. Many of the letters cited earlier (McComas, 2012), along with Darwin's engagement in print with friends and critics, demonstrate how science functions. It is not enough to have a good idea. Scientific ideas – even more so today – are tested by experiment as well as debate. Students must understand that scientific work is conducted and evaluated in social contexts.

More than 100 years ago, even Darwin's critics were willing to enter the fray with a degree of generosity and concede that

> even should…[Pangenesis] prove a will-o'-wisp it is worth our following, if we follow circumspectly, for it hovers over lands where we may find valuable material. As a hypothesis it so links together wide classes of facts that it may be a clue to great discoveries. (Lewes, 1868, p. 508)

The fact that science contains an element of subjectivity should come as no surprise. Scientists, because they are human, have prior opinions about what they will discover or what their experiments suggest. Again, Darwin clearly knew that he had a problem with the lack of evidence for pangenesis and vacillated over how strongly to support it. Simultaneously, Darwin referred to his proposal of pangenesis as "stillborn" (Darwin, F., 1887, p. 78) and a "mad dream" (Letter 5649 to Asa Gray, 16 October 1867) even as he proceeded to "stick up for my poor child" (Darwin, F., 1887, p. 78). There is no doubt that Darwin wanted pangenesis to be correct. In a letter to George Bentham (22 April 1868), he expresses his relief in being able to explain his observations:

> To my mind the idea has been an immense relief, as I could not endure to keep so many large classes of facts all floating loose in my mind without some thread of connection to tie them together in a tangible method. (Darwin, F. & Seward, 1903, p. 371)

Interestingly, a useful example of the lack of complete objectivity in science comes from an analysis of the motivations behind Galton's desire to test pangenesis experimentally. Galton was interested in a variety of subjects, including fingerprints and eugenics, a branch of applied genetics held in disrepute today. As part of this work, he became interested in the idea that genius could be inherited. To set the stage, we should note that Galton was developing his own views on inheritance but with a particular interest in the inheritance of intelligence (Gillham, 2001) in an article published in 1865. His book *Hereditary Genius* (Galton, 1869) was published just before the pangenesis experiment and was well known to audiences of the time. Let us explore what a book on the inheritance of intelligence has to do with pangenesis. Basically, pangenesis was very likely seen by Galton as a threat to his idea that genius runs in families. Pangenesis suggests that new variations that might result in increased intelligence could arise spontaneously and then be inherited; this would challenge Galton's favored notion that familial genius stays in the family. The forces of prior conception and personal motivation are as alive in science today as they were in Darwin's time, and this is a fine example of scientists at work – biases and all.

○ Scientific Knowledge & Its Limitations

This NOS domain embraces issues like the distinction between science and technology, the idea that scientific knowledge is tentative but durable, yet self-correcting, and the notion that science and its methods cannot answer all questions.

The case of pangenesis makes some contribution to our understanding of the roles of science and technology but sheds little light on the principle that science cannot address all questions. At its core, pangenesis was a legitimate scientific issue that resulted in the formation of testable hypotheses, a requirement of all scientific ideas. Darwin suggested that the gemmules were physical entities and that, as such, other scientists could look for them or for their effects. The failure of others to find these tiny information-bearing "seeds" was one of the factors that ultimately helped to defeat pangenesis.

The interaction with technology is also illustrated by the story of pangenesis. Technology is the domain in which specific problems are solved, usually by creating some tool or device that makes reference to underlying scientific principles. For instance, the microscope is not science per se but uses scientific knowledge in its design. At the same time, the microscope was a technological tool developed in response to the desire to visualize tiny elements of the natural world. It is likely that pangenesis lasted longer than it might have otherwise because the proposed gemmules were thought to be too small to be seen with the microscopes of Darwin's time. The story would be wonderfully symmetrical if the desire to see the gemmules increased interest in building more sophisticated microscopes, but there is no evidence that this occurred in the relatively short life of pangenesis.

The second issue in this domain – that science is tentative and self-correcting – is very well illustrated by an exploration of the pangenesis affair. In a journal article reflecting on the pangenesis chapter, an anonymous writer says the following:

> Mr. Darwin, in his work on "Animals and Plants under Domestication," has modestly described Pangenesis as a provisional hypothesis, which might be useful until a better one should be brought forward. (J.D., 1868, p. 49)

What many students fail to understand is that this is how all scientific proposals function in the marketplace of competing ideas. All generalizations and explanations offered by science are subject to testing, reconsideration, and possible rejection if new evidence and interpretations provide reason to do so. Of course, in our haste to dismiss all science contributions as provisional, it is important to remember that science produces ideas that are durable as well. By the time that scientific conclusions are codified in textbooks, they have been argued, explored, vetted within the scientific community, and are as close to "truths" as science can manage.

Anonymous writer J.D. reminds us that

> Some of his [Darwin's] admirers, however, seem to forget that it [Pangenesis] is as yet only a supposition, and, by assuming it to be the true theory, tend to discourage the advancement of other hypotheses, and thus impede the progress of science. (J.D., 1868, p. 49)

Had J.D. understood the nature of science, he need not have worried. Scientists will always propose false ideas that may, for some time, hold forth. However, because scientific ideas are tentative and science is a self-correcting pursuit, faulty ideas will be excised from the cannon of scientific "truths."

As we have seen, Darwin was desperate to protect and defend his provisional hypothesis of pangenesis. As he said, pangenesis "is a very rash and crude hypothesis, yet it has been a considerable relief to my mind, and I can hang on it a good many groups of facts" (Letter 4837 to Huxley, 27 May 1865). Ultimately, it did not matter how relieved Darwin was or how much this hero of biology wanted pangenesis to be true, it did not survive. So, Darwin's error was overthrown just as it should have been by the principle that science is a self correcting enterprise.

To some, the fact that pangenesis is a faulty idea may warrant its exclusion from our textbooks and classrooms. However, I hope that you have been convinced that even the story of a mistake can play a role in helping students understand the complex and fascinating work of science as practiced by one of our most productive biologists. Furthermore, analyzing the account of pangenesis by considering how it might be useful in communicating a number of aspects of the nature of science should, I trust, warrant the resurrection of this and other accounts from history to provide the most complete picture of this thing we call science.

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PRESS RELEASE

NEW STUDY FINDINGS SUGGEST THAT U.S. HIGH SCHOOL SCIENCE STANDARDS IN GENETICS ARE "INADEQUATE"

Most states fail to keep pace with modern genetics in their science curricula

BETHESDA, MD – 24 August 2011 – A new study by the American Society of Human Genetics (ASHG), the country's leading genetics scientific society, found that more than 85% of states have genetics standards that are inadequate for preparing America's high school students for future participation in a society and health care system that are certain to be increasingly impacted by genetics-based personalized medicine. ASHG's study findings are being published in the September 1 issue of the CBE–Life Sciences Education journal (Citation: CBE-Life Sciences Education, Vol. 10, 1–10, Fall 2011).

"Science education in the United States is based on testing and accountability standards that are developed by each state," said Michael Dougherty, Ph.D., director of education at ASHG and the study's lead author. "These standards determine the curriculum, instruction, and assessment of high school level science courses in each state, and if standards are weak, then essential genetics content may not be taught."

According to ASHG's study, which included all 50 states and the District of Columbia: • Only seven states have genetics standards that were rated as "adequate" for genetic literacy (Delaware, Illinois, Kansas, Michigan, North Carolina, Tennessee, and Washington). • Of the 19 core concepts in genetics that were deemed essential by ASHG, 14 were rated as being covered inadequately by the nation as a whole (or were absent altogether). • Only two states, Michigan and Delaware, had more than 14 concepts (out of 19) rated as adequate. Twenty-three states had six or fewer concepts rated as adequate.

"ASHG's findings indicate that the vast majority of U.S. students in grade 12 may be inadequately prepared to understand fundamental genetic concepts," said Edward McCabe, M.D., Ph.D., a pediatrician and geneticist who is the executive director of the Linda Crnic Institute for Down Syndrome at the University of Colorado. "Healthcare is moving rapidly toward personalized medicine, which is infused with genetics. Therefore, it is essential we provide America's youth with the conceptual toolkit that is necessary to make informed healthcare decisions, and the fact that these key concepts in genetics are not being taught in many states is extremely concerning."

[NOTE: ASHG's 19 core genetics concepts are listed on page 3 of the paper. See pages 5–6 of the paper for two U.S. maps that provide a visual state-by-state summary of the quality and comprehensiveness of genetics coverage in states' standards. For a list of the individual concept scores for each state, see the supplementary data chart from the paper posted at http://www.ashg.org/education/pdf/StateConceptScores.pdf.]

"We hope the results of ASHG's analysis help influence educators and policy makers to improve their state's genetics standards," said Dougherty. "Alternatively, deficient states might benefit from adopting science standards from the National Research Council's Framework for K–12 Science Education, which, although not perfect, does a better job of addressing genetics concepts than most state standards that are currently in place."

ABOUT THE AMERICAN SOCIETY OF HUMAN GENETICS

Founded in 1948, the American Society of Human Genetics (ASHG) is the primary professional membership organization for human genetics specialists worldwide. The nearly 8000 members of ASHG include researchers, academicians, clinicians, laboratory practice professionals, genetic counselors, nurses, and others involved in or with a special interest in human genetics. The Society's mission is to serve research scientists, health professionals, and the public by providing forums to (1) share research results through the Society's Annual Meeting and in the American Journal of Human Genetics (AJHG); (2) advance genetic research by advocating for research support; (3) educate current and future genetics professionals, health care providers, advocates, policymakers, educators, students, and the public about all aspects of human genetics; and (4) promote genetic services and support responsible social and scientific policies. For more information about ASHG, visit http://www.ashg.org.