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EVOLUTION AND MEDICINE

Evolution, Medicine, and the Darwin Family

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Abstract The common scientific roots of evolution and medicine are deep, as these fields of science developed in parallel from the Enlightenment in the late 1700s to the modern genomics era. The influence of the medical sciences on the discovery of evolution in the 1700s and 1800s is typified by how the medical family of Charles Darwin, including his grandfather Dr. Erasmus Darwin and father Dr. Robert Waring Darwin, directly and indirectly guided Charles' scientific development and eventual discovery of natural selection. In particular, in the 1700s, Erasmus Darwin was a prolific writer, legendary doctor, and published extensive descriptions of both the process of adaptation and common descent among all of life (including humans). The influence began with Charles' years in medical school at Edinburgh and is recorded in Charles Darwin's own letters and notebooks. Despite scientific overlap, evolution and medicine have remained distant from each other, in part because of the same religious and political reasons that many oppose the view of a world changing via evolution. But evolution also has been limited in its influence on the biomedical sciences because of abuses and misunderstanding. The three issues discussed here are (1) typological application of medical "constitutions," (2) teleological thinking in how adaptations evolve, and (3) the misapplication of evolution during the eugenics period up to the 1940s. The modern-day surge of interest and synthesis between evolutionary biology and the biomedical sciences, medical practice, and public health can build on a long legacy that spans more than two centuries. The large role played by the Darwin family of doctors can bring this history to life, can be used to illustrate potential pitfalls as the synthesis moves forward, and may be of interest to students both as undergraduates and in medical schools.

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Introduction

The last decades have seen a surge in the application of evolutionary biology to medicine and public health, spurred by the seminal book *Why We Get Sick* (Nesse and Williams 1994) and featured in several multi-authored volumes (Stearns and Koella 2007; Trevathan et al. 2008), special issues of scientific journals (Stearns et al. 2010), and a recent textbook (Gluckman et al. 2009). The synthesis between evolution and medicine is ever-expanding; it provides insights into why humans in modern times remain vulnerable to maladies like cancer and heart disease and promises to lead to new diagnostics and therapies. The evolutionary view in medicine takes off from the point of an individual patient's disease symptoms, then looks for the cause of disease by considering interactions between the patient's ancestry, genotypic, and epigenetic variation; the evolutionary history of pathogens to which the patient has been exposed; and the environmental circumstances in which the patient and pathogens meet (Williams and Nesse 1991; Nesse and Stearns 2008; Antolin 2009). Combining ideas of ancestry with individual-level genetic variation and applying modern genomic analyses of both patients and pathogens also leads to the newly emerging approach of "personalized medicine" (Jiang and Wang 2010; Costa et al. 2010; Knight 2009).

As these linkages become clearer, it is perhaps surprising how little the biomedical field explicitly uses the language of evolutionary science, even in areas like the evolution of antibiotic resistance in microbes (Antonovics et al. 2007; Nesse and Stearns 2008). The separation between evolutionary and biomedical sciences persists in part because the two branches grew separately through the 1800s and into the modern scientific era (Porter 1998). Biologists in the mid-1800s largely accepted that evolutionary science could provide accurate explanations for the history of life and for biological diversity. Acceptance of evolution by doctors and the application of evolutionary thinking into clinical practice and biomedical research were not as steady (Richardson 1893; Desmond 1989; Desmond and Moore 1991; Porter 1998; Zampieri 2009). Before Darwin and Alfred Wallace published the ideas of evolution by natural selection in 1858–1859, "transformism" was taught in some medical schools that covered natural history and comparative anatomy. At the same time, however, such notions were actively opposed by influential and politically conservative scientists like the anatomist Richard Owen (Desmond 1989). In some ways, the divide between evolution and medicine is as old as the more general religious and political objections to the evolutionary view of life. It is the purpose of this essay to show that understanding the common historical and scientific roots shared by evolution and medicine will help students gain perspective on how the two areas of science have interacted through time. Further, these roots are clearly seen in how Charles Darwin in the 1800s was influenced by a Darwin family that practiced medicine and studied biological diversity at the same time.

Needless to say, the historical relationship between evolution and medicine is complex (e.g., see Desmond 1989; Porter 1998; Nesse and Stearns 2008; Zampieri 2009), and giving it complete coverage is a bigger job than is possible in an essay of this length. Rather, I provide here a more focused view of Charles Darwin himself and how he was influenced by his biomedical surroundings through his family. It is well known that Darwin attended medical school but never completed his studies. It is less well known that he came from a family of doctors and scientists, with many members attending medical school, and that both his grandfather Erasmus Darwin and his father Robert Waring Darwin had long-lasting and distinguished medical practices (Fig. 1). Here, I briefly describe the family, explore the influences of his brief time in medical school, and trace how ideas from his grandfather and father would have led Charles toward his synthetic view of evolution (see also Antolin 2011).

The writings by and about the Darwins is voluminous, with biographies of Erasmus Darwin (King-Hele 1999, 2003[1]), less

Fig. 1 Portraits of Charles R. Darwin's grandfather Dr. Erasmus Darwin (by Joseph Wright) and father Dr. Robert Waring Darwin (by James Pardon). Both images accessed from the Wikimedia Commons

about Robert Darwin (Meteyard 1871; Darwin 1888; Barlow 1958; King-Hele 1998, 1999), multiple biographies of Charles Darwin (De Beer 1964; Desmond and Moore 1991; Browne 1995),[2] and a restored autobiography of Charles Darwin edited by his granddaughter (Barlow 1958). Both grandfather Erasmus and Charles were prolific writers who kept extensive notes and correspondences and authored multiple books. Hundreds of their original records survive and are available for historical research online either as facsimile or as transcribed/edited versions (http://darwin-online.org.uk/: The Complete Works of Charles Darwin Online; http://www.darwinproject.ac.uk/: Darwin Correspondence Project). What emerges from this analysis of the Darwin family is that links between medicine and evolution were an integral part of Charles Darwin's discovery of natural selection.

The Darwin Doctors

Charles Darwin's grandfather and physician Erasmus Darwin used a modified family crest with a griffin and banner with three scallop shells, with the motto "*E conchis omnia*" (everything from shells; Fig. 2). The motto described Erasmus Darwin's view of transmutation: All life including humans descended and transformed from simpler forms originating from "a single living filament" (King-Hele 1998, 1999). After briefly using the emblem and motto in 1770 on his carriage in the town of Lichfield (near Birmingham), Erasmus removed the controversial motto from his carriage and public scrutiny but continued to use the crest and motto on bookplates in his library. Erasmus' transmutationist ideas, which were original to him but resembled Lamarckian inheritance of traits acquired through the experiences of life, were kept to Erasmus and his friends

[1] King-Hele (2003) is an annotated and updated edition of Charles Darwin's biography of his grandfather, originally published in 1879.

[2] A critical review of earlier C. Darwin biographies is in Colp (1989).

Fig. 2 Family coats of arms used by Erasmus Darwin as a bookplate, similar to the coat of arms painted on his carriage in 1770 (from King-Hele (1999). Reproduced with permission of the publisher Giles de la Mare, London http://www.gilesdelamare.co.uk/)

until he began publishing them more than 20 years later. The extensive writings of Erasmus Darwin in medicine and natural history are not now widely known, but during the latter half of the 1700s his influence extended well beyond his medical practice in Lichfield and Derby.

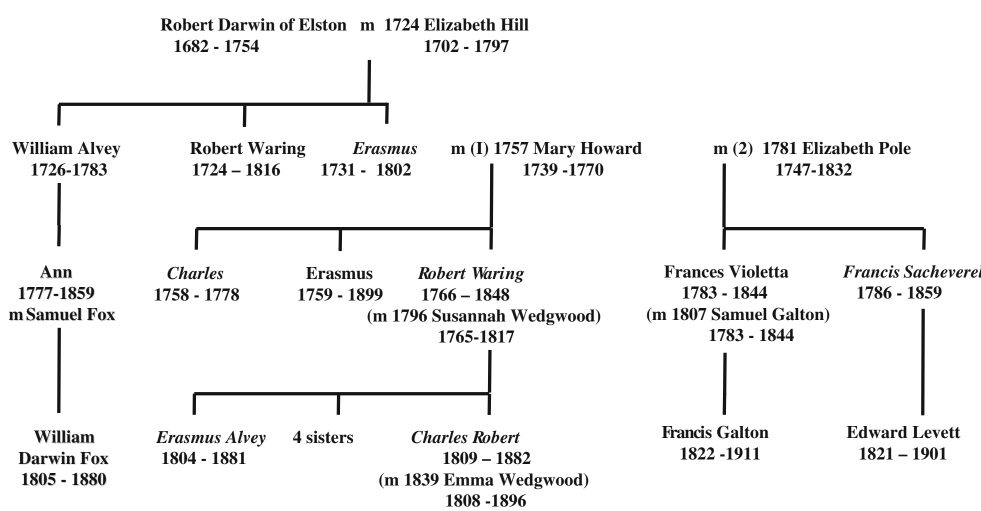
Erasmus Darwin's son (and Charles Darwin's father) Robert Waring Darwin was also a doctor practicing in central England from 1787 to the 1840s and used the same crest and motto on bookplates in his library. He never publicly proclaimed support for transmutation, but Robert had plenty of reasons to keep quiet, given how vigorously his father Erasmus was attacked after publishing his transmutationist ideas in 1794 (Garfinkle 1955; Desmond and Moore 1991). Robert Darwin did not leave a written legacy to match either his father or son but was generally supportive, despite the oft-quoted rebuke to Charles when he was a teenager, "You care for nothing but shooting, dogs, and rat-catching, and you will be a disgrace to yourself and all your family" (Barlow 1958). Robert Darwin had broad interests in natural history, kept gardens and greenhouses he shared with his children, and financially supported Charles for the *Beagle* voyage and during his subsequent work (Meteyard 1871; Barlow 1958; King-Hele 1999, 2003). This includes the post-voyage years in London and Cambridge (1836–1840) when Charles secured his scientific reputation and secretly conceived of his theory of natural selection.

Charles was raised in an extended family that included the Darwin physicians and the Wedgwood makers of fine china. Many family members attended medical school and/or were known as naturalists (Fig. 3). With liberal religious views and a deep love for science, natural history and active outdoor life, this family instilled in Charles from an early age that life's diversity has changed over eons of time under the force of natural laws. Erasmus Darwin died in 1802, seven years before Charles was born, and we have little evidence that transmutation was openly discussed by Charles with his father or the rest of the family. Nevertheless, Charles wrote in his autobiography "…it is probable that the hearing rather early in life such views maintained and praised may have favoured my upholding them under a different form in my Origin of species" (Barlow 1958).

The Celebrated Dr. Erasmus Darwin

Erasmus Darwin was the youngest of seven children who survived to adulthood. His eldest brother Robert Waring was also scientifically inclined and published a volume on plants, *Principia Botanica*, an English translation of the Linnaean classification system. The book was often reprinted, including an edition that Charles eventually read (King-Hele 1999). Also in this generation was William Alvey Darwin, a London lawyer who was grandfather of William Darwin Fox, Charles' lifelong friend—a clergyman,

Fig. 3 A partial genealogy of the Darwin family tree extending from the 1600s century to Charles R. Darwin (extracted from F. Darwin 1888; Barlow 1958; Freelan 1982). Names in *bold italic* are those who attended medical school (even if they did not practice medicine), and names in **bold** are those who were published naturalists



geologist and avid naturalist, and credited by Charles for introducing him to beetle collecting when they were students together at Cambridge (Barlow 1958). The first Darwin on this family tree is Robert Darwin of Elston, who was credited with finding in 1718 a fossilized Jurassic plesiosaur presented to the Royal Society in London by William Stukely (1719).

Erasmus Darwin was a large man, both in body and influence, known as a physician, naturalist, inventor, builder of canals, and poet (King-Hele 1999, 2003). He was called "the celebrated Dr. Darwin" because of his medical knowledge and his extensive poetic verse, especially *The Botanic Garden* (1789). His medical training at Cambridge, London, and then Edinburgh, Scotland (1753–1756) came during the period when the medical sciences in Europe discarded the notion of the human body as a series of passive hydraulic systems guided by Newton's physical laws (attributed to Boerhaave in Leiden, the Netherlands). The new view, that medicine and disease must be understood in specific biological terms, was promoted by William Cullen (1710–1790) and colleagues at Edinburgh (Richardson 1893; McNeil 1987; Porter 1998). Here, systems of the body developed by movements of internal vital powers, somewhat analogous to electricity (which was also discovered around the same time). The heartbeat, for instance, could be understood as irritability of nervous fibers and sensitivity of heart muscles for contraction (Greene 1982; Porter 1985, 1998). The human body was an economic system of interacting organs and tissues, with focus on how the parts formed and how substances move among them. In this time period, the idea of reproduction via a preformed homunculus was also overturned. Growth and development was not from a fully formed miniature but by epigenesis of more complex parts from simpler ones (Harrison 1971). This idea is in parallel with and central to the longer-term process of more complex forms arising via transmutation (evolution) from simpler forms.

As a physician, Erasmus Darwin incorporated and promoted biological thought in his practice. In some ways, he was a doctor of his times (i.e., bleeding patients to control fever), but he also pioneered oxygen therapy to treat lung disease and digitalis (foxglove) to relieve irregular heartbeat, and promoted sanitation and small pox vaccination for public health. From the early 1760s, Erasmus was also a founding member of the influential Lunar Society of Birmingham, a group of preindustrial innovators that began with friendships in Edinburgh and expanded to include others with interests in science. The Lunar Society derived its name from monthly meetings held on days with full moons so members could see their way to ride home afterwards (see Richardson 1893). Over time the group included Matthew Boulton (scientific instruments), Josiah Wedgwood (pottery), James Watt (steam power), James Keir (industrial chemistry), Richard Lovell Edgeworth (mechanical inventions), William Withering (medicine), Thomas Day (author), Samuel Galton, Jr. (armaments), and Joseph Priestly (Unitarian minister and chemistry). Erasmus Darwin attended until at least 1788. The Lunar Society typified the period of the Enlightenment in central England and Scotland, where scientific ideas were freed from religious orthodoxy and were applied to improving society, including, for instance, the workings of the Wedgwood potteries. Erasmus Darwin identified himself as a Deist who worked to understand the natural laws breathed into this world by First Causes. An important aspect of Lunar Society thinking and Erasmus Darwin's transmutationist ideas was that the world and human society were progressively and inevitably improving (Primer 1964, Harrison 1971, Bowler 1974, McNeil 1987).

Besides his own ambition and skill as a physician, Erasmus Darwin had great hopes that his sons would study and practice medicine. Like their father, three sons studied medicine at Edinburgh: Charles (the elder) and Robert Waring, and Francis Sacheverel from a second marriage. Charles died at Edinburgh at age 20, most likely from an infection when he cut his hand while dissecting the brain of a child. Robert Waring followed to Edinburgh in 1783 and Francis Sacheverel in 1804 (Shepperson 1961).[3] Francis Sacheverel did not practice medicine but maintained interest in natural history along with an assortment of semiwild animals. His son, Edward Levett Darwin, also a naturalist, gained some renown as the author of *A Gameskeeper's Manual* in the mid-1800s (Darwin 1888, King-Hele 2003). As a final note on Darwin genealogy, the Victorian eugenicist and statistician Francis Galton was Erasmus Darwin's grandson and Charles Darwin's cousin through Violetta Darwin and Samuel Tertius Galton, son of a member of the Lunar Society (see Richardson 1893).

Robert Waring Darwin

Charles' father is perhaps one of the least understood figures in Charles' life (Meteyard 1871; Barlow 1958; Kelly 1964; Desmond and Moore 1991; King-Hele 1999, 2003). Mostly, he is described as disapproving of Charles' life choices, especially after Charles withdrew from medical school at Edinburgh, but this has been exaggerated. Robert Darwin studied and practiced medicine to satisfy his father but succeeded and was known as an acute observer and diagnostician. He also had interests in natural history and maintained extensive gardens and greenhouses stocked with

[3] Three Wedgwood uncles of Charles Darwin also attended medical school at Edinburgh: Josiah II (father of Emma Darwin, Charles' wife), John, and Thomas. Apparently, none practiced medicine.

tropical plants.[4] He married Susannah Wedgwood, who herself kept varieties of fancy pigeons. Although Susannah died in 1814 when Charles was eight years old, this was a house of science and natural history, a place where belief in divine revelation was pushed to the background, and bookplates in the library bore "*E conchis omnia*." Charles was greatly fond of his father, visiting him regularly over the years. He wrote in his autobiography that "My father's mind was not scientific, and he did not try to generalize his knowledge under general laws; yet he formed a theory for almost everything which occurred" (Barlow 1958).

Charles Darwin at Medical School in Edinburgh

The importance of Charles' time as a medical student in 1825–1827, beginning when he was 16 years old, is often overlooked, most likely because Charles' disparaged his medical courses in his autobiography (Barlow 1958). Charles' time overlapped for a year with his older brother Erasmus Alvery, and they were among the most serious students at the university—the two borrowed more books than anyone from the library in the fall term of 1825 (Desmond and Moore 1991). Erasmus Alvey never practiced medicine, and a medical career was not for Charles, even though he showed early promise working with the sick in Shrewsbury with his father. Attending medical school in Edinburgh was a deep family tradition, but Charles was sickened by the sight of blood and left his surgery course never to return after witnessing a brutal operation performed without anesthesia on a child. Being several hundred miles north of home during a dark, cold and damp school year in a crowded city known as "auld reekie" apparently left a less than flattering impression on the teenaged Charles. The experience at Edinburgh was, however, Charles' first scientific training, and it set a path that led to his eventual pursuit of "the species question" (Ashworth 1935; Shepperson 1961; Sloan 1985; Desmond and Moore 1991; Browne 1995; Eldredge 2009a).

In the early 1800s, medical training was one of the only opportunities for formal studies of life sciences and natural history. Along with anatomy, surgery, clinical practice, and chemistry, Charles attended courses on *materia medica* (pharmacology), which included medicinal plants and natural history. It was expected that physicians trained in Edinburgh would serve the British Empire abroad, where they could identify new species and understand their potential medicinal value. At Edinburgh, natural history was taught by Robert Jameson, a broadly thinking scientist, curator of the Natural History Museum in the University of Edinburgh (now the Scottish Royal Museum) and editor of the *Edinburgh Philosophical Journal*. Jameson's course included practicals in the museum and field excursions, access that led to other connections for Charles.

Charles was invited to join several of the university-sponsored scientific societies that intellectually enriched Edinburgh's formal educational programs. The role of the societies was unique within Europe at the time. In his second year, Charles attended most meetings of the Plinian Society, which was organized by Robert Jameson. Further, Charles was taken as a guest by his mentor Robert Grant to meetings of the Wernerian Natural History Society, where he met the American ornithologist and painter John James Audubon and Sir Walter Scott as society president. Charles also attended meetings of the Royal Medical Society and the Royal Society of Edinburgh (Shepperson 1961).

Charles befriended and worked closely with Grant, a medical doctor and professor of comparative anatomy who was a well-known invertebrate zoologist and an ardent transformist (Desmond 1989). In his first year in Edinburgh, Charles and his brother Erasmus Alvey regularly made natural history excursions to the coast of the Firth of Forth. In the second year after Erasmus left Edinburgh, trips were often in the company of Grant, with whom Charles made discoveries of the mobile larvae of the marine bryozoan *Flustra*. Bryozoa are small branching animals, similar to corals, which may be mistaken for marine algae. This work was fundamentally important for tracing relationships between animals and plants (a topic grandfather Erasmus Darwin also speculated on) by careful studies of life stages and reproduction of each. This work was presented by Charles to the Plinian Society in March, 1827 and was eventually published by Grant. As noted in Charles' autobiography, he was confronted directly with Lamarckian ideas by Grant and at the time read both Lamarck and his grandfather's *Zoonomia* (Browne 1995). From this beginning, Charles developed skills as a field naturalist and careful observer that would serve him well in future years and likely led to his careful work on other invertebrates such as barnacles (Sloan 1985).

Fourth, isolated from the conservative center of Victorian England, Edinburgh remained a hotbed of the Enlightenment, where no topics were too radical for discussion, including metaphysics and religion in relation to scientific materialism (Shepperson 1961). The same meeting of the Plinian Society where Charles and Grant described their zoological observations of the *Flustra* ended with a raucous debate on whether consciousness arises from material causes within the mind. The question was of concern because it was feared that dissecting brains of cadavers would damn those persons for all time by destroying their souls (Desmond and Moore 1991). In contrast to conservative England, Edinburgh was

[4] His plant collection included a banana tree purchased while Charles was voyaging on the *Beagle*, so he could sit under it and think of his son similarly shading himself somewhere in the tropics.

rife with freethinkers and Lamarckian transmutatonists.[5] In his autobiography, Charles criticized some of the lectures in the medical curriculum, but the broader scientific education provided by the Edinburgh medical school was unique in its time and critical for Charles' development as a scientist.

The Darwins and Natural Selection

In Erasmus Darwin's writings and in Charles' correspondence with his father Robert Darwin, it is possible to trace some of the observations and concepts Charles Darwin built upon to discover natural selection. These are certainly not the only influences on Charles as he conceived his idea of natural selection between 1836 and 1839, immediately after returning from the *Beagle* voyage to live in Cambridge and London (Ghiselin 1986; Sulloway 1982). Besides his own observations, Charles was an avid reader and collector of biological facts through his correspondences. His first projects completed upon his return secured his position as one of England's preeminent naturalists: the zoological descriptions of specimens collected during the *Beagle* voyage, his journal from the voyage (which eventually became the *Voyage of the Beagle*), and a volume on geology of oceanic islands and coral archipelagos.

As for the grandfather Erasmus, Charles gives public credit in only two sentences in a footnote in the "Historical Notes" in later editions of the *Origin*, and in part of a paragraph in his autobiography. Nonetheless, Charles' "B" notebook from 1838 is named "Zoonomia," apparently in honor of his grandfather's major work with the same title published between 1794 and 1796. Both the "B" and "M" notebooks are filled with references to *Zoonomia*, including the description of a wasp cutting off the wings of its insect prey to make it easier to carry away on a windy day (Ghiselin 1976; Gruber 1985; Porter 1998). Some earlier oversights of Erasmus' influence were corrected by Charles Darwin's *Life of Erasmus Darwin*, which was written much later (King-Hele 2003).

Erasmus Darwin's *Zoonomia* is a massive work written over more than 20 years. It provided a systematic unification of human physiology and four shaping forces (irritation, sensation, volition, association), extension of these forces to natural history, heredity of traits in successive generations and transmutation of species, and a Linnaean classification of human diseases based on patients' symptoms (Porter 1985). *Zoonomia* was widely read and translated but eventually lost influence in medicine, possibly because of its evolutionary views. It is also likely *Zoonomia* was left behind as the medical sciences moved toward uncovering direct causes of disease, for instance with the application of germ theory. The primary focus in the *Zoonomia* on disease symptoms would make it inadequate for differential diagnosis and effective treatment (Porter 1985; Barlow 1959). Nonetheless, the evolutionary ideas in *Zoonomia* were clear enough that it was severely criticized during the anti-Enlightenment backlash in England during the early 1800s and even landed on the Vatican's list of banned books, the "Index Expurgatorius" (Garfinkle 1955; Desmond and Moore 1991; King-Hele 2003, 2004). The poetic work *Temple of Nature*, published posthumously in 1803, also made a strong case for transmutation but for more general audiences.

The attacks on Erasmus Darwin went beyond reaction to his transmutationist ideas, and he was broadly discredited for his political views during the early 1800s (Primer 1964; Desmond and Moore 1991; King-Hele 1999). His flowery poetry was criticized and ridiculed (e.g., Seward 1804), and his theorizing about the origins of man led the poet Coleridge to coin the term "darwinizing" to mean excessive speculation. Further, the liberal Whig politics of pre-industrial Birmingham were crossways to the Tory conservatism in an England lashing back against the French and American revolutions and the Napoleonic wars (Desmond and Moore 1991; Barlow 1959). It is thus not surprising that Charles, in writing in his autobiography about his experiences in Edinburgh, downplayed the importance of his grandfather's work while acknowledging that he already knew about transmutation (Barlow 1958) Lastly,

> Dr. Grant, my senior by several years, but how I became acquainted with him I cannot remember….. He one day, when we were walking together, burst forth in high admiration of Lamarck and his views on evolution. I listened in silent astonishment, and as far as I can judge without any effect on my mind. I had previously read the 'Zoonomia' of my grandfather, in which similar views are maintained, but without producing any effect on me. Nevertheless it is probable that the hearing rather early in life such views maintained and praised may have favoured my upholding them under a different form in my 'Origin of Species.' At this time I admired greatly the 'Zoonomia;' but on reading it a second time after an interval of ten or fifteen years, I was much disappointed; the proportion of speculation being so large to the facts given.

Erasmus Darwin's theorizing about Lamarckian evolution caused difficulties for his grandson. The *Zoonomia* lacked mechanisms based on observable natural forces and

[5] The *Edinburgh New Philosophical Journal*, edited by Robert Jameson, published an anonymous essay "Observations on the Nature and Importance of Geology" (vol. 1 (1826): 293–302) outlining the relationship between Lamarckian evolution and the appearance of fossils of more complex life forms in more recent rock layers. The author is thought to have been either Jameson or Grant, and the article was likely read by Charles Darwin (Browne 1995; Eldredge 2009b).

relied on general observations rather than the careful measurements and experimentation that characterized Charles' own work. Further, Erasmus Darwin had been politically discredited in conservative Victorian England and thus provided little moral support.

Nonetheless, most aspects of evolution by natural selection can be traced back to the elder Dr. Darwin's transmutation. Simply stated, evolution by natural selection depends on three conditions, leading to two outcomes:

1. traits of organisms vary among individuals within populations,
2. trait differences are inherited between generations,
3. traits provide an advantage in the struggle for existence under competition for resources and in different environmental conditions.

The results of natural selection directly follow:

(a) over time, favored traits predominate in populations (i.e., adaptation),
(b) over longer time periods, populations diverge from each other as different adaptations evolve, leading to new species (i.e., speciation).

I consider how the Darwins conceived of each of these.

Traits within Populations Vary

That traits vary within populations was well known and documented before and during the 1800s, for instance by the French naturalist Buffon, and many examples of variation in both animals and plants are recorded in Erasmus Darwin's *Zoonomia* and his other volumes on plants (*The Botanic Garden* (1789), *Physiologic* (1800)). In the *Temple of Nature*, Erasmus observed the role of sexual reproduction in generating variation:

So grafted trees with shadowy summits rise,
Spread their fair blossoms, and perfume the skies;
Till canker taints the vegetable blood,
Mines round the bark, and feeds upon the wood.
So, years successive, from perennial roots
The wire or bulb with lessen'd vigor shoots;
Till curled leaves, or barren flowers, betray
A waning lineage, verging to decay;
Or till, amended by connubial powers,
Rise seedling progenies from sexual flowers.

E'en where unmix'd the breed, in sexual tribes
Parental taints the nascent babe imbibes;
Eternal war the Gout and Mania wage
With fierce uncheck'd hereditary rage. (II 168–180)

Charles gathered together many similar observations in the Origin and later works like *The Variations of Animals and Plants under Domestication* (Darwin 1875). One wonders whether having seen at an early age the variety of fancy pigeons kept by his mother at home in Shrewsbury generated a familiarity that led Charles to experiments on pigeons as an adult.

Trait Differences are Inherited

The lack of a heredity mechanism was one of the greatest shortcomings for the *Origin*, one that would not be overcome for 70 years until the discovery of genetics and understanding of sources of hereditary variation and mechanisms that maintain variation within populations (Provine 1971). Even without a mechanism, hereditary differences among individuals (families) within populations were known, and this is where the influence of the Darwin doctors on Charles is most clear. In medical practice, both Erasmus and Robert Darwin were keenly aware of the effects of heredity on disease, for instance in their own familial tendencies for gout and alcoholism. While working on his notebooks on the species problem in 1838, Charles records a visit to his father in Shrewsbury to discuss what he knew about heredity (Bynum 1983, Colp 1986). *Zoonomia* extensively describes hereditary disease and variability between individuals and families, and Erasmus did not confine his observations of hereditary differences to human diseases. He wrote in *Zoonomia* of "sports" or monstrosities, and that "Many of these enormities of shape are propagated, and continued as a variety at least, if not as a new species of animal."

Traits Provide an Advantage in the Struggle for Existence

This critical piece of natural selection—that in most species, high natural birth rates result in more individuals being born each generation than can survive to reproduce—traces its population-level thinking to Thomas Robert Malthus.[6] Malthus' book was widely read after its publication in 1798 (Charles read the 1826 edition). The key is that specific traits will be favored in the competition among individuals within populations because the innate capacity for increase means that most populations will outgrow the supply of available resources. Erasmus Darwin did not make this connection, but he clearly grasped the notion of reproductive excess, for instance in his *Temple of Nature* (see Harrison 1971):

Air, earth, and ocean, to astonish'd day
One scene of blood, one mighty tomb display!
From Hunger's arm the shafts of Death are hurl'

[6] An *Essay on the Principle of Population*, published in several editions between 1798 and 1826.

> And one great Slaughter-house the warring world!
> (IV 63–66)
> But war, and pestilence, disease, and dearth,
> Sweep the superfluous myriads from the earth
> (IV 373–374)

Erasmus Darwin's conception came close to understanding the struggle for existence through the idea of species and extinctions, in that progressive evolution presupposes the extinction of primitive forms and replacement by more advanced ones (Colp 1985; Gruber 1985).

Over time, Favored Traits Predominate in Populations

That species adapt to meet environmental challenges was largely accepted, but before the *Origin*, the closest things to scientific explanations were those of Lamarck and Erasmus Darwin: that adaptive traits are acquired by the experience of life and passed on. In *Zoonomia* we find:

> As air and water are supplied to animals in sufficient profusion, the three great objects of desire, which have changed the forms of many animals by their exertions to gratify them, are those of lust, hunger, and security.

Further, Erasmus Darwin came close to describing sexual selection but missed because his mechanism depended on unspecified teleological life forces based on males' mental powers rather than on natural causes (Ghiselin 1986):

> The birds, which do not carry food to their young, and do not therefore marry, are armed with spurs for the purpose of fighting for the exclusive possession of the females, as cocks and quails. It is certain that these weapons are not provided for their defence against other adversaries, because the females of these species are without this armour. The final cause of this contest amongst the males seems to be that the strongest and most active animal should propagate the species, which should thence become improved.

Under Other Conditions, Over Longer Time, New Species Form

The idea of speciation depends upon both common descent and transmutation and is typified by the Darwin doctors' motto "*E conchis omnia*." The Darwins' evolutionism is unmistakable and appears in several works including the *Temple of Nature*

> First forms minute, unseen by spheric glass [microscope lenses],
> Move on the mud, or pierce the watery mass;
> These, as successive generations bloom,
> New powers acquire, and larger limbs assume;
> Whence countless groups of vegetation spring,
> And breathing realms of fin, and feet, and wing
> (IV 297–303)

and *Zoonomia*:

> From thus meditating on the great similarity of structure of the warm-blooded animals, and at the same time of the great changes they undergo both before and after their nativity; and by considering in how minute a portion of time many of the changes of animals above described have been produced; would it be too bold to imagine, that in the great length of time since the earth began to exist, perhaps millions of ages before the history of the commencement of mankind, would it be too bold to imagine, that all warm-blooded animals have arisen from one living filament, which THE GREAT FIRST CAUSE endued with animality, with the power of acquiring new parts, attended with new propensities, directed by irritations, sensations, volitions and associations; and thus possessing the faculty of continuing to improve by its own inherent activity, and of delivering down those improvements by generation to its posterity, world without end?

Moving Evolution and Medicine Forward to Modern Times

The years following publication of the *Origin* did not see broad acceptance of evolutionary thinking into the medical sciences. This is not to say that no one at the time embraced the importance of variation, evolution, and common descent in understanding hereditary and infectious disease (e.g., Aitken 1885), and over time many scientists and physicians advocated the union of evolution and medicine (Huxley 1881; Aitken 1885; Richardson 1893; Morton 1926; Bynum 1983; Porter 1998; Zampieri 2009). Medical sciences did not oppose evolutionary thinking, but neither did physicians wholly embrace evolution while other fundamental scientific discoveries were needed to propel medicine into the modern era. Further, industrialization and concentration of humanity in cities created new public health challenges that also required attention (Porter 1998).

In the late 1800s, many applications of evolution to medicine were holistic, with evolutionary thinking via "constitutions" and "diatheses" that characterized patients as being susceptible to particular kinds of diseases (Bynum 1983; Zampieri 2009). These general descriptions were thought to result from evolution, either through past natural selection or through degeneration back to atavistic traits.

Individuals, and then races, were categorized in diatheses, including propensity for mental illnesses. Unfortunately, without an understanding of the specific causes of disease and the environmental contexts like nutrition and habitation that influence them, this kind of typological thinking also led to racial and gender profiling (i.e., common descent, but not recently, and in different ways between the sexes and among races). Further, because diatheses were based on identifying symptoms, they were unable to differentiate infectious, hereditary, or epigenetic causes of disease and thus were not generally useful in developing effective therapies. Charles Darwin briefly addressed the relationship between evolution and disease in his *Descent of Man* (Darwin 1882) and in *Variation of Plants and Animals Under Domestication* (Darwin 1875), including observations of hereditary disease, similarity of diseases (and responses to medication) in humans and apes, differing disease prevalence among human populations, effects of disease on aboriginal populations coming into contact with Europeans, and sex-limited maladies like hemophilia and gout. Darwin's references to medicine, however, were in the language of constitutions and diatheses.

In many ways, the science of evolution developed in parallel with the medical sciences. In the late 1800s, medicine moved toward more science-based practice, resulting in improved diagnosis and treatment (Porter 1998). Anesthesia and aseptic methods in surgery were developed during this period, and the emergence of germ theory through work of Pasteur, Koch, and others made it possible to identify the microbial pathogens that cause common diseases like whooping cough, syphilis, and cholera (Porter 1998; Gluckman et al. 2009). As the physiological, developmental, genetic, and microbial bases of diseases were explored in medicine, so were the genetic mechanisms underlying evolution (Provine 1971; Mayr 1982). In 1910, the Flexner report, a classic of medical education, placed medicine on a foundation of human biology and experimental analysis of physiology, development, endocrinology, biochemistry, and anatomy of specific tissue and organ systems (Flexner 1910). Flexner also called for broad coverage of general science in medical training and practice. The effect was movement toward reductionist views of the causes of disease, diverging from previous holistic approaches. While medical knowledge grew rapidly, medical applications based on the similarly emerging evolutionary science were not as clear, and as a result the evolutionary viewpoint did not make inroads into medical school curricula.

Evolution was not mentioned in the Flexner report, but one response to the report was for medical schools to establish departments of anthropology to bring human natural history, comparative anatomy, and geographical medicine explicitly into medical training (Morton 1926). This period spanning 1910 through the 1940s saw the Modern Synthesis in evolutionary biology and breakthroughs in the science of evolution (Mayr 1982). But evolutionary biology still was not incorporated into medical training, in part because the successful clinical application of antimicrobial drugs promised to make infectious diseases completely manageable (Burnet and White 1972; Anderson 2004).

But even more so, as both medical and evolutionary sciences made spectacular advances, three misunderstandings and abuses of evolutionary science severely hindered synthesis between them, and some of these persist to this day (Porter 1998; Zampieri 2009). The first was the "constitutions," "diastheses," and "degeneracy" used to explain disease vulnerabilities in certain racial groups and in women. This typologically racist and sexist view of disease was wrongly tied to evolutionary principles and in some ways was deflected by Flexner's (1910) recommendation to center medicine on a scientific foundation. Even though mechanistic understanding of disease should have attenuated societal biases of race and gender and the uneven delivery of medical care, the broad strokes of "constitution" also tarred the science of evolution in the eyes of doctors. The second and more pernicious reason was the horror of eugenics as practiced during in the first half of the 1900s, culminating in the genocidal Nazi regime in the 1930s and 1940s in Europe (Zampieri 2009). Eugenics was a social malignancy that arose from misapplication of the science of natural selection in attempts to improve the human condition and was discarded by evolutionary biologists after the population genetic interplay between mutation and natural selection were better understood (Haldane 1964). But the persisting backlash has been severe enough that even today many physicians and biomedical researchers do not fully acknowledge how much evolutionary science informs medicine (Wilson 1993; Antonovics et al. 2007; Nesse and Stearns 2008). The third reason was that the reductionist scientific paradigm advocated by the Flexner report trained doctors and scientists to reject teleological notions of evolution as constantly and endlessly progressive. Teleology of this kind has been mistakenly conflated with the adaptive process of natural selection and is a common misunderstanding of evolution that still persists.

Currently, few medical schools have courses in evolution but only cover evolution in terms of human genetic variation, drug resistance and virulence of pathogens, and adaptation by natural selection (Nesse and Schiffman 2003; Downie 2004; Childs et al. 2005; Harris and Malyango 2005). However, efforts to bring the science of evolution to greater prominence in both undergraduate and medical school training are underway (e.g., Nesse et al. 2010; Antolin et al. 2012). The science of evolution is basic to biology, and the synthesis of evolution and medicine can influence medical practice by providing improved diagnosis and therapies. Reaching back to the curriculum at Edinburgh in the 1700s and onward, evolutionary perspectives in medicine were at one time provided under the subjects of comparative anatomy, geographic medicine, and natural history (Burnet and White 1972; Anderson 2004). Erasmus Darwin was keenly aware of these connections. In modern times, we know that applying evolutionary thinking to individual patients is important, as each patient has a different evolutionary history and therefore a different genetic makeup, different reactions to drugs, and oftentimes different disease symptoms (Meyer 1999; Omenn 2010). In managing health care, such differences can result in life, death, or long-term morbidity. The synthesis of evolution and medicine provides a framework for connecting numerous seemingly unrelated observations by linking proximate effects of disease to the context of their ultimate origins (Williams and Nesse 1991; Purssell 2005; Nesse and Stearns 2008; Naugler 2008). Evolution has many faces that can be seen in genetics and adaptations of both humans and pathogens, and understanding disease depends on understanding the evolutionary history that binds them.

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