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Introduction

The history of science is important for understanding the development of ideas. This is certainly true in evolutionary studies. Four nineteenth-century naturalists framed a thesis and an antithesis that still concern us now, two centuries later.

1.1 Thesis and Antithesis

Jean-Baptiste Lamarck in France proposed a radical thesis involving "transformation" of species to explain the diversity of life on Earth and changes seen in the fossil record. Charles Lyell in England, citing Carl Linnaeus of Sweden, countered Lamarck with a reactionary antithesis consistent with his own uniformitarian view of earth history: creation imbues species with characteristics that never vary. Charles Darwin in England, influenced by the other three, had the last word. All made lasting contributions to our understanding of evolution. The full history is complicated, but, simplifying, we shall focus on Lamarck, Lyell, and Darwin.

1.1.1 Jean-Baptiste Lamarck

> *À mesure que les individus d'une de nos espèces changent de situation, de climat, de manière d'être ou d'habitude, ils en reçoivent des influences qui changent peu à peu la consistance et les proportions de leurs parties, leur forme, leurs facultés, leur organization même . . . à la suite de beaucoup de générations qui se sont succédées les unes aux autres . . . se trouvent à la fin transformés en une espèce nouvelle, distincte de l'autre.* [As the individuals of one of our species change their situation, climate, manner of being or habit, they receive influences that gradually change the consistency and proportions of their parts, their form, their faculties, and their organization itself . . . after

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many generations, these individuals are at length transformed into a new species, distinct from the first.]

Jean-Baptiste Lamarck, 1809, Philosophie Zoologique, Tome Premier, *pp. 62–63*

Jean-Baptiste Lamarck was born in 1744, in Picardy in northern France. He was born with the title *chevalier* or knight. Lamarck's career included military service, which ended with an injury at the age of 22. Medical studies followed, and then a ten-year career as a botanist. Lamarck published a three-volume *Flore Française* in 1778. When the *Museum National d'Histoire Naturelle* in Paris was founded in 1793, Lamarck was appointed *enseigner*, not of botany, his field of specialization, but of invertebrate paleontology. Lamarck embraced the new position and published *Système des Animaux sans Vertèbres* in 1801, and then his two-volume *Philosophie Zoologique* in 1809. Lamarck died in Paris in 1829 at the age of 85.

Lamarck is famous for two ideas. The first is our focus here, the idea of transformation little by little, "*peu à peu*," of one species into another in the course of "*beaucoup de générations*." Thus Lamarck (1809, pp. 77–78) inquired, rhetorically, is it not possible for species known only as fossils to have changed and become the species we see alive today? Transformation is expressed too in his assertion that "it is not the form, either of the body or its parts, that gives rise to the habits and manner of living of animals; but, on the contrary, the habits, manner of living, and all other influential circumstances that have, in time, given rise to the form of the body and its parts in animals. With new forms, new facilities have been acquired, and little by little nature has succeeded in forming animals as we now see them." (Lamarck, 1809, p. 268).

Lamarck's second idea is thoroughly discredited and often used to denigrate all of his writings. This is the idea, expressed in two "laws," of the inheritance of acquired characteristics. The first law attributed the physiological development of an organ in an individual to its use. The second law was a conjecture that developments resulting from use and disuse were heritable, somehow, and passed from individuals to their descendants (1809, p. 235). In one of his examples, Lamarck proposed that continual striving to browse in treetops, sustained for a long time by all giraffes, was sufficient to explain their long legs and necks (1809, pp. 256–257). Remember that little was known of heredity in 1809 beyond the close resemblance of parents and offspring.

1.1.2 Charles Lyell

We must suppose, that when the Author of Nature creates an animal or plant, all the possible circumstances in which its descendants are destined to live are foreseen, and that an organization is conferred upon it

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which will enable the species to perpetuate itself and survive under all the varying circumstances to which it must be inevitably exposed.

Charles Lyell 1832, Principles of Geology, Volume II*, pp. 23–24*

Charles Lyell was born in 1797 in Forfarshire, in the east central lowland of Scotland. Lyell was educated in classics and started his career as a lawyer at the age of 23, but within a few years he gave up this profession in favor of travel and geological studies. Lyell is best known for *Principles of Geology*, published in three volumes in 1830, 1832, and 1833. The full title of all three volumes is *Principles of Geology, Being an Attempt to Explain the Former Changes of the Earth's Surface by Reference to Causes Now in Operation*. Lyell was an empiricist who traveled widely and spent his life promoting the "uniformitarian" view expressed in the subtitle of *Principles*. Lyell revised *Principles* regularly, and the twelfth edition was published posthumously. Lyell died in London in 1875 at the age of 77.

Here we are concerned with the first edition of Lyell's *Principles*, specifically the first edition of the second volume, which was published in January of 1832. Volume I was a review of changes in the physical or inanimate world. Volume II provided a parallel review of progress in what Lyell called "animate creation." On the title page of volume II, Lyell quoted Playfair (1802, §412, pp. 469–470): "A change in the animal kingdom seems to be part of the order of nature, and is visible in instances to which human power cannot have extended." Did Lyell really believe change in the animal kingdom is part of the order of nature?

Lyell answered this question on the very first page of the volume II text, where he proposed to inquire "whether species have a real and permanent existence in nature; or whether they are capable, as some naturalists pretend, of being indefinitely modified in the course of a long series of generations?" Lyell never repeated or explained the Playfair quotation but avidly pursued the French "pretenders" Jean-Baptiste Lamarck and his younger colleague Étienne Geoffroy Saint-Hilaire. In Lyell's favor, Gavin de Beer (1960) and the *Oxford English Dictionary* credit him with the first use of the word "evolution" in the English language in the sense in which it is now widely employed in biology. Lyell's use of evolution is found in a passage in chapter 1 of *Principles of Geology*, *Volume II* (1832, p. 11) where he questioned Lamarck's fanciful belief in "gradual evolution" from sea to land.

Étienne Geoffroy Saint-Hilaire published a *Mémoire* in 1828 exploring the possibility that "antediluvian" beings gave rise to animals living in modern times (Geoffroy Saint-Hilaire 1828). In volume II of *Principles*, Lyell translated Geoffroy Saint-Hilaire as saying that "there has been an uninterrupted succession in the animal kingdom effected by means of generation, from the earliest ages of the world up to the present day" and "ancient animals whose remains have been

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preserved in the strata, however different, may nevertheless have been the ancestors of those now in being" (Lyell, 1832, p. 2). Lyell dismissed Geoffroy Saint-Hilaire's ideas by noting that they were not generally accepted, and then focused his refutation on Jean-Baptiste Lamarck and on Lamarck's *Philosophie Zoologique* (Lamarck, 1809).

Lyell criticized Lamarck's concept of species, writing that "the majority of naturalists agree with Linnaeus in supposing that all the individuals propagated from one stock have certain distinguishing characters in common which will never vary, and which have remained the same since the creation of each species" (Lyell 1832, p. 3). Lamarck had argued that individuals change, little by little, and after many successive generations are transformed into a new and distinct species (paraphrasing Lyell, 1832, p. 5, and the full quotation cited above). "*Peu à peu*," little by little, is a phrase that appears often in *Philosophie Zoologique*, but Lyell's 1832 uniformitarianism seemingly excluded such changes to life on Earth.

Lamarck's novel thesis of species changing and transforming little by little in response to the environment was contradicted by Lyell's reactionary antithesis, citing Linnaeus, of species created by an "Author of Nature" with their organization conferred upon them. If we relax Lyell's "creation" of species and "organization conferred upon them" to represent only distinct origins and characteristic essences, we see that the conflicting views of Lamarck and Lyell, developed in the eighteenth and nineteenth centuries, survive and divide us still.

1.1.3 Charles Darwin and the Origin of Species

> I do believe that natural selection will always act very slowly, often only at long intervals of time, and generally on only a very few of the inhabitants of the same region at the same time. I further believe, that this very slow, intermittent action of natural selection accords perfectly well with what geology tells us of the rate and manner at which the inhabitants of this world have changed.
>
> *Charles Darwin 1859,* Origin of Species*, pp. 108–109*

Charles Darwin was born in 1809 in Shrewsbury, Shropshire, in the West Midlands of England. He started medical school at the age of 16 but neglected medical studies in favor of natural history. Darwin's professional career began in 1831 when, at age 22, he embarked as "naturalist" on the survey ship *H. M. S. Beagle* for a nearly five-year round-the-world voyage. The ship left Plymouth Sound in England on December 27, 1831, and returned to Falmouth Harbour on October 2, 1836. The *Journal of Researches* resulting from the voyage was published in 1839, and soon republished as the now-classic *Voyage of the Beagle*. Darwin is best known for the *Origin of Species* or, to give the book its full title: *On the Origin*

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of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life. This was published in 1859 when Darwin was 50 years old. Darwin died at Down House, Kent, in 1882 at the age of 73.

Darwin took the then newly published first volume of Charles Lyell's *Principles of Geology* with him on the *Beagle*, and we know that he read much of it before the ship's first stop in the Cape Verde Islands off the west coast of Africa. Darwin received the second volume of Lyell's *Principles* some ten months later when the ship was docked in Montevideo in South America (Darwin's own copy survives, inscribed "Montevideo, November 1832"). This is important because Lyell's second volume deals extensively with the transmutation of species and what we today call 'evolution.' As outlined above, the second volume of *Principles* opens with a critique of evolutionary ideas expressed by the French zoologists Jean-Baptiste Lamarck and Étienne Geoffroy Saint-Hilaire.

A naturalist at sea has little to do but read and think. This explains how Darwin was able to read much of the first volume of Lyell's *Principles* before reaching the Cape Verde Islands. It also means he had ample time to read and reread the second volume of *Principles* before reaching the Galápagos Islands in the Pacific some three years later. It is the second volume in which Lyell presented Lamarck's thesis of species changing and transforming little by little in response to the environment, and his own antithetical objections to such transformation. Lyell's writing is so clear and forceful that both alternatives are impressed on any reader, and both were surely clear to Darwin.

The *Beagle* reached the Galápagos Islands on September 15, 1835 and departed on October 20, 1835. In the Galápagos, Darwin visited the islands of Chatham (now San Cristobal), Charles (Santa María), Albemarle (Isabela), and James (Santiago). He was initially more interested in mockingbirds than finches, and was able to collect mockingbirds from all four islands. Later, while organizing his collections, Darwin recognized that the islands of Charles and James had similar mockingbirds that differed from those on both Chatham and Albemarle, where each had its own characteristic form. Darwin combined these observations with reported differences in the tortoises of different Galápagos Islands, and reported differences in the foxes of the eastern and western Falkland Islands that he had visited in 1834. In the "Ornithological Notes" that Darwin wrote in 1836 while still at sea, he reasoned that "archipelagos will be well worth examining; for such facts [differences found on neighboring islands] would undermine the stability of species."

Darwin started a "Red Notebook" in 1836 while he was still at sea. This was initially a catalogue of places visited by the *Beagle* during the last year of the voyage. Then in 1837 he added various geological ideas to the Red Notebook, and in March of that year some notes on "transmutation" or speciation. On page 130 of

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the Red Notebook he wrote: “The same kind of relation that common ostrich bears to the Petisse [common rhea to lesser rhea]; extinct Guanaco to recent [extinct llama to recent llama]: in former case [geographic] position, in latter time (or changes consequent on lapse) being the relation.— As in first cases distinct species inosculate, so must we believe ancient ones: ∴ not gradual change or degeneration. From circumstances: if one species does change into another it must be per saltum — or species may perish . . . Inosculation alone shows not gradation.” The transcription here is from Sandra Herbert in Barrett et al. (1987). Darwin’s notes seem conflicted because “inosculate” would imply gradation. However, Darwin’s “if one species does change into another it must be per saltum” is perfectly clear. He had not yet made the metaphorical examination of archipelagos that would undermine the perceived stability of species.

Darwin started the first of the notebooks he devoted to transmutation of species, his “Notebook B” later that year, during the summer of 1837. The early pages were seemingly inspired, to some extent, by his grandfather Erasmus Darwin’s *Zoonomia* (Darwin, 1794–1796). Darwin wrote on page 3 of Notebook B: “Seeds of plants sown in rich soil, many kinds, are produced, though new individuals produced by buds are constant, hence we see generation [sexual reproduction] here seems a means to vary, or adaptation.” Then on page 7: “Animals, on separate islands, ought to become different if kept long enough apart, with slightly different circumstances. — Now Galápagos Tortoises, Mocking birds; Falkland Fox . . .” Darwin’s branching diagrams first appear on pages 26 and 36. On the latter he wrote: “Case must be that one generation then should be as many living as now. To do this and to have many species in same genus (as is) requires extinction.” Then on page 37 he wrote: “With respect to extinction we can easily see that variety of ostrich, Petise [lesser rhea] may not be well adapted, and thus perish out.” The transcription here is from David Kohn in Barrett et al. (1987). The notes are telegraphic but give us, already in the summer of 1837, an outline of a theory for the origin and evolution of species. This involved: (1) the production of variation, (2) geographic separation or isolation, and (3) differential survival based on adaptation.

With this outline, why did it take a prolific author like Darwin 22 years to flesh out his theory of natural selection in the *Origin of Species*? First, much of the evidence was subtle and beyond the experience of potential readers, so it required careful presentation; and second, the evidence supported and extended the thesis of Lamarck and contradicted the reactionary antithesis of Lyell, who was by then Darwin’s friend and patron. Interestingly, and for whatever reason, Darwin did not use the word “evolution” in any form in the *Origin* until the closing sentence, where he wrote that “endless forms most beautiful . . . have been, and are being, evolved.”

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1.2 Evolutionary Synthesis of the 1930s and 1940s

Much happened in the years following publication of the *Origin of Species*. New discoveries in paleontology and systematic biology continued, but the greatest progress was made in our understanding of inheritance.

1.2.1 Progress in Understanding Inheritance

One of the most interesting and transformative discoveries in genetics came in the 1860s, shortly after publication of the *Origin of Species*. The Moravian biologist and friar Gregor Mendel determined that each phenotypic trait in his fertilized experimental peas was represented by two and only two underlying genetic factors (or gene alleles). These factors segregate, assort independently, and dominate or subordinate, leading to characteristic combinations of phenotypes in subsequent generations. Mendel's study (Mendel, 1866) was published in a Moravian journal that must not have been widely seen because the study had no impact until the year 1900.

In another development, August Weismann (1883) recognized that inheritance in multicellular organisms depends on germ cells or gametes that are separated and effectively insulated from the somatic cells comprising the rest of the body. Thus Weismann eliminated the possibility of any direct Lamarckian inheritance of characteristics acquired through use or disuse.

Hugo de Vries was the first of later geneticists to discover Mendel's 1866 publication, which he reported in a footnote to a similar study of his own. A botanist, de Vries went on to develop a "theory of mutations" to explain discontinuous phenotypic variation. He considered genetic mutations leading to new phenotypes sufficient to explain the origin of species (de Vries, 1901).

The focus on Mendelian inheritance soon led to cytological identification of chromosomes as carriers of genetic material and determiners of sex. Genes and gene alleles are more cryptic and were necessarily recognized by what they do functionally. Modern genetics emerged as breeding experiments began to be carried out using a variety of organisms: *Oenothera lamarckiana*, *Zea mays*, *Drosophila melanogaster*, *Mus musculus*, *Cavia porcellus*, and others.

1.2.2 Microevolution and Macroevolution

Theodosius Dobzhansky (1937) initiated the Modern Synthesis of evolution when he published *Genetics and the Origin of Species*. This made new developments in genetics, expressed in the technical writings of R. A. Fisher, J. B. S. Haldane, T. H. Morgan, Sewall Wright, and others, accessible to a broad range of evolutionary biologists.

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Dobzhansky regarded evolution as any change in the genetic composition of populations, recognizing that this might have small or large consequences depending in part on the time involved. This led him to distinguish "microevolution" and "macroevolution," borrowing the terms from Philiptschenko (1927). Dobzhansky wrote (1937, p. 12): "There is no way toward an understanding of the mechanisms of macro-evolutionary changes, which require time on a geological scale, other than through a full comprehension of the micro-evolutionary processes observable within the span of a human lifetime."

Dobzhansky's single sentence highlights three important contrasts in evolution: (1) minor change versus major change, (2) short timescale versus long timescale, and (3) process versus pattern. The problem in each instance is to understand how one side of each contrast is related to the other, that is: how minor changes are related to major changes; how short timescales are related to long timescales; and how processes are related to patterns.

Three years after Dobzhansky's book appeared, Richard Goldschmidt published *The Material Basis of Evolution* (Goldschmidt, 1940). Here, he contradicted Dobzhansky and argued that "the facts of microevolution do not suffice for an understanding of macroevolution" (Goldschmidt 1940, p. 8). Goldschmidt proposed the word "macromutation" (p. 182) for systemic mutations leading to what he had previously labeled "hopeful monsters." He went on to claim that a "monstrosity [hopeful monster] appearing in a single genetic step might permit the occupation of a new environmental niche and thus produce a new type [new species] in one step" (Goldschmidt, 1940, p. 390). Finally, he concluded: "species and the higher categories originate in single macroevolutionary steps as completely new genetic systems" (Goldschmidt, 1940, p. 396).

1.2.3 "Modern Synthesis" of the Twentieth Century

Advances in the study of inheritance answered some questions about evolution and evolutionary change, but others remained. In the 1930s and 1940s scholars interested in evolution made a conscious effort to broaden their communication and comprehension. We have already mentioned Theodosius Dobzhansky and his *Genetics and the Origin of Species*. The Modern Synthesis took its name from a book by Julian Huxley (1942) titled *Evolution: The Modern Synthesis*. Another book on *Systematics and the Origin of Species* by Ernst Mayr (1942) brought systematics, phenotypic variation, and biogeography into the emerging synthesis.

The fourth book commonly included in the Modern Synthesis is *Tempo and Mode in Evolution* by paleontologist George Gaylord Simpson (1944). While exemplary in many ways, Simpson's book shows that the "Modern Synthesis" was a partial synthesis at best. Simpson proposed the term "quantum evolution" for

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"the relatively rapid shift of a biotic population in disequilibrium to an equilibrium distinctly unlike [its] ancestral condition . . . [Quantum evolution] may be involved in either speciation or phyletic evolution . . . It is . . . believed to be the dominant and most essential process in the origin of taxonomic units . . . such as families, orders, and classes. It is believed to . . . explain the mystery that hovers over the origins of such major groups" (Simpson, 1944, p. 206).

Thus, at the end of the Modern Synthesis we are still left to wonder at the relationship of microevolution and macroevolution, to wonder at the relationship of micromutation and macromutation, and to wonder at an origin of species and higher taxa that is said to involve a mysterious "quantum" origin followed by a new equilibrium.

1.3 Quantification of Rates

Charles Darwin recognized that rates are important but he seemingly made no attempt to quantify what he meant by fast and slow. Dobzhansky's (1937) only explicit consideration of rate was his characterization of some groups of organisms as having an unlimited store of variation and evolving rapidly, while he characterized others, such as the "living fossil" brachiopod *Lingula*, as being conservative and showing no change through epochs of geological time.

Huxley (1942, p. 56) discussed evolutionary rates briefly, observing that "no rate of hereditary change hitherto observed in nature would have any evolutionary effect in the teeth of even the slightest degree of adverse selection." Mayr (1942, p. 297) wrote of different rates of evolution in different groups or in different periods within the same group, noting that "an animal group that is searching for a new 'adaptive peak' may undergo rapid evolution, but as soon as this peak has been reached evolution may begin to stagnate."

George Gaylord Simpson was the only Modern Synthesis author to attempt a real quantification of rates, approaching the problem from a paleontological point of view. J. B. S. Haldane followed up on this, taking both a paleontological perspective and a more general biological view.

1.3.1 George Gaylord Simpson (1944)

Simpson's (1944) *Tempo and Mode* was explicitly about rates of evolution. How fast, he asked, do animals evolve in nature? "It is the first question that the geneticist asks the paleontologist" (Simpson, 1944, p. 3). Geneticists envisioned evolution as change in the genetic composition of populations, and Simpson considered that it might be desirable to define evolutionary rates in terms of genetic change per year, per century, or through some other unit of absolute time.

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However, he recognized that genetic change was unknowable in extinct populations. Simpson assumed, as a compromise, that morphological change should be proportional to genetic change, and rates based on morphology should be similar to rates of any underlying genetic modification.

Change can be studied in individual morphological characteristics, yielding what Simpson called "unit-character" rates. Change can be studied in a number of related morphological characteristics, yielding what he called "character-complex" rates. Finally, change can be studied in morphological characteristics representing whole animals, yielding what he called "organism" rates. Unit characters can be studied in relation to each other, yielding what Simpson called "relative" rates, or they can be studied in relation to time, yielding what Simpson called "absolute" rates.

In *Tempo and Mode* Simpson started by comparing rates of change in tooth shape in the evolution of horses. He measured "paracone height" or the crown height of a tooth, measured on an upper molar, and he measured "ectoloph length" or the anteroposterior crown length measured on the same molar. Simpson then defined "hypsodonty" as the ratio of paracone height to ectoloph length. In other words, hypsodont teeth are relatively high crowned. When horses first appeared in the fossil record at the beginning of the Eocene epoch of Cenozoic time they had low-crowned molars: The crowns were only about one half as high as they were long. Later, in the Miocene epoch, acquisition of progressively more high-crowned hypsodont molars enabled horses to chew and digest more abrasive vegetation. Horses today have molars with crowns about three times higher than their anteroposterior length. This is a sixfold increase in terms of proportion.

The first table of data in *Tempo and Mode* listed measurements of paracone height, ectoloph length, and hypsodonty for teeth of five genera and species of Cenozoic-era horses. Simpson combined these in a figure (Simpson's figure 2), assuming first that ectoloph length represented overall body size and then, provocatively, that logarithms of both might increase at a constant rate (that is, both, on a proportional scale, might increase steadily in relation to time). If this "orthogenetic" assumption were true, then the spacing of species should be proportional to the geological time separating species. The geological timescale was poorly constrained in 1944, but Simpson's result was sufficiently different from expectation that he rejected the idea of ectoloph length and body size changing at a constant rate. Comparison of paracone height to ectoloph length showed that if one increased at a constant rate then the other did not. Plotting paracone height and ectoloph length against geological time, as best it was known, suggested that neither increased at a constant rate.

Simpson was seemingly unaware that the Russian paleontologist Alexei Petrovich Pavlov calculated an evolutionary rate for horses some dozen years earlier

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