The Growth of Biological Thought

Diversity, Evolution, and Inheritance

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instantaneous speciation through a drastic mutation is one of the only two conceivable methods of speciation. That such instantaneous speciation can actually occur (through polyploidy) was not proven until the second decade of the twentieth century. The only other possible form of speciation within the essentialistic paradigm is speciation by hybridization, as proposed by Linnaeus (Larson, 1971: 102). After Linnaeus had found three or four natural hybrids and had named them new species, he became possessed by the idea that all species had originated by hybridization.
404 In the course of the 1760s and 1770s his views became increasingly bizarre and in the end he thought that God had created only the orders of plants, and that all taxa of the categories below the order, down to the species, had resulted from "mixing," that is, hybridization.

This conclusion was vigorously opposed by Linnaeus' contemporaries. The plant hybridizer Kölreuter made numerous species hybrids in the 1760s but demonstrated that, contrary to Linnaeus' claims, these hybrids were not stable (Chap. 14). In later hybrid generations, he observed much segregation and a gradual but inevitable breakdown of the supposedly new species. This was a great relief to the essentialists, for it would have been quite unthinkable that one could produce a new *eidos* by mixing or fusing two previously existing ones.

A modern is apt to forget that prior to Darwin virtually everybody was an essentialist. Each species had its own species-specific essence and thus it was impossible that it could change or evolve. This, for example, was the cornerstone of Lyell's thought. All nature, according to him, consists of constant types, each created at a definite time. "There are fixed limits beyond which the descendants from common parents can never deviate from a certain type." And he stated emphatically: "It is idle . . . to dispute about the abstract possibility of the conversion of one species into another, when there are known causes, so much more active in their nature, which must always intervene and prevent the actual accomplishment of such conversions" (1835, II: 162). Yet, one searches Lyell's *Principles* in vain for a citation of such causes. It was simply impossible to adopt evolutionary thinking until the dogma of the constancy of species was destroyed. Lyell as well as his "catastrophist" opponents showed that it is quite conceivable to reconcile the fossil record with an essentially nonevolutionary concept of the history of the earth.

A realization of the dominance of essentialistic thinking helps

to solve another puzzle. Why had all the attempts of the preceding 150 years, from Leibniz to Lamarck and Chambers, to develop a substantial theory of evolution been such failures? These failures are usually attributed to the lack of a reasonable explanatory mechanism. This is in part true, but that this is not the whole truth is indicated by the fact that the majority of the biologists who accepted the theory of evolution after 1859 simultaneously rejected Darwin's proposed explanatory mechanism, natural selection. What had made them evolutionists was not that they now had a mechanism but that Darwin had demonstrated the evolu- 405
tionary potential of species and had thus made possible the theory of common descent, which explained so successfully almost everything about organic diversity that had been previously puzzling. The destruction of the concept of constant species and the posing and solving of the problem of the multiplication of species were the indispensable basis of a sound theory of evolution.

This new way of approaching the problem of evolution Darwin did not owe to Lamarck or any of the other of his so-called forerunners. They were all concerned with vertical evolution, with improving perfection, with evolution in the grand style. Rather, it was Lyell, the antievolutionist, who made the crucial contribution by making the reductionist move of dissecting the evolutionary movement into its elements, the species.[6] Lyell felt that one would never be able to come to firm conclusions concerning the history of organic life as long as one formulated the argument in terms of such generalities as progression and trends toward perfection, as Lamarck had done. Organic life, said Lyell, consists of species. If there is evolution, as claimed by Lamarck, species must be its agents. Thus, the problem of evolution cannot be solved by vague generalities but only through the study of concrete species, their origin, and their extinction. This led him to ask some very specific questions: Are species constant or mutable? If constant, can each species be traced to a single origin in time and space? Since species become extinct, what limits their life span? Can the extinction and the introduction of new species be currently observed and attributed to currently observable environmental factors?

Lyell thus admirably posed the right questions, questions which Darwin and Wallace pondered over in the ensuing decades. Lyell himself, being a dyed-in-the-wool essentialist, consistently came up with the wrong answers to his questions. For him it was types that originated and types that died out. Extinction and origination of species were two sides of the same coin. He never

understood, at least not until Darwin and Wallace pointed it out to him, that the evolution of a new species population is a totally different process from the extinction of the last survivors of a dwindling species.

By the 1820s almost all geologists had come to agree that many species had become extinct over the course of time and that they had been replaced by new species. Several competing theories were proposed to account both for the extinction and for the introduction of new species. Some geologists believed that the extinctions had been catastrophic, in the most extreme case with God repeatedly destroying his entire previous creation, as Agassiz believed. Or did species die out individually either because their life span had run out or because conditions had become unsuitable for them? It was most important for the development of Darwin's theories that Lyell had opted for the last of these alternatives and had thus directed attention to ecology and geography and their contribution to the history of faunas and floras.

Lyell's *Principles of Geology* was Darwin's "bible" as far as the problem of evolution was concerned. There is abundant evidence that throughout most of the *Beagle* voyage Darwin accepted Lyell's conclusions without questioning. Lyell started from the same two observations as Lamarck: species live in a constantly (but slowly) changing world, and species are extremely well-adapted to their station in life. Since Lamarck believed that species could not become extinct, he concluded that they must undergo constant evolutionary change in order to remain adapted to the changes in their environment. Lyell, as an essentialist and theist, believed that species are constant and cannot change, therefore they cannot become adapted to the changes in their environment and must become extinct.

Lyell's explanation of extinction is reasonably plausible. He contributed one important thought, subsequently particularly developed by Darwin: it is not only the physical factors of the environment that can cause extinction but also competition from other better-adapted species. This explanation was of course in agreement with the concept of the struggle for existence, as it was widely held prior to Darwin's reading of Malthus.

Lyell was far less successful in his attempts to explain the replacement of the extinct species. In order to uphold his principle of uniformitarianism, he postulated that new species are introduced at an essentially constant rate, but he failed completely either to provide any evidence for such an introduction of species or to

suggest any mechanism. Thus he laid himself open to the criticism of a German reviewer of the *Principles* (Bronn), who accused Lyell of having abandoned the principle of uniformity with respect to organic life. Lyell (1881) attempted to defend himself in a letter to his friend Herschel by saying that some unknown intermediate causes might be responsible for the introduction of new species. However, the description of the process by which new species are introduced is quite irreconcilable with any conceivable secondary causes: "Species may have been created in succession at such times and at such places as to enable them to multiply and endure for an appointed period and occupy an appointed space on the globe." The repeated choice of the word "appointed" indicates that for Lyell each creation was a carefully planned event (Mayr, 1972b). Such a frank appeal to the supernatural worried even Lyell a little, and he took considerable solace in Herschel's pronouncement: "We are led by all analogy to suppose that [the creator] operates through a series of intermediate causes and that in consequence the origination of new species, could it ever come under our cognizance, would be found to be a natural in contradistinction to a miraculous, process." As a mathematician and astronomer Herschel did not realize that except for evolution (and, as we now know, some chromosomal processes) there are no intermediate causes that could produce constant species at the right time and in the right place. Indeed, what Herschel and Lyell postulated was exactly the kind of miracle which they overtly rejected. Elsewhere, of course, Lyell admitted frankly that he adhered to "the perpetual intervention hypothesis" with respect to the concept of the creation (Lyell, 1970: 89). No wonder Darwin gave so much space in the *Origin* to the rejection of the special-creation hypothesis (Gillespie, 1979).

It is quite impossible to develop an evolutionary theory on the foundation of essentialism. Essences, being nonvariable in space and time, are nondimensional phenomena. Since they lack variation, they cannot evolve or bud off incipient species. Lyell thought he had solved the problem of the introduction of new species by pointing out that they will occupy vacant stations (niches). As an essentialist (and just like Linnaeus), he thought of speciation in terms of the introduction of a single pair that would be the progenitor of the new species. There are reasons to believe that Darwin prior to March 1837 held similar typological ideas. This is indicated by his description of the origin of the second *Rhea* species in South America. Progress in the speciation problem was not

achieved until naturalists discovered that species taxa are dimensional phenomena. Species have an extension in space and time; they are structured and consist of populations which, at least in part (when they are isolated), are independent of each other. Thus, contrary to Lyell's insistence, species vary and each isolated species population is an incipient species and a potential source of the origin of diversity. According to Lyell's thesis, the vacant mockingbird niche on the Galapagos would be filled by the "introduction" (by whatever means) of the mockingbird species on the

Galapagos. However, that each island had its own species was not explicable by Lyell's mechanism. Isolation and gradual evolution would explain it. This is the lesson Darwin learned from the Galapagos avifauna.

Darwin Becomes an Evolutionist

A great deal of research has been conducted in recent years to reconstruct, step by step, Darwin's "conversion." What Darwin himself says on the timing of his becoming an evolutionist is rather misleading. He starts the introduction of the *Origin of Species* with these sentences: "When on board H.M.S. *'Beagle'*, as naturalist, I was much struck with certain facts in the distribution of the inhabitants of South America, and in the geological relations of the present to the past inhabitants of that continent. These facts seemed to me to throw some light on the origin of species—that mystery of mysteries, as it has been called by one of our greatest philosophers." This implies, as does a similar statement in the autobiography, that he had become an evolutionist during the South American phase of the *Beagle* voyage. However, this is not substantiated by his journals. Indeed, when collecting on the Galapagos, he labeled the collections from the different islands simply "Galapagos," quite unaware of the phenomenon of geographic variation.[7] He should have seen the truth when the governor of the Galapagos told him that the tortoise of each island was recognizably different from those of the other islands, but this observation was not enough. Yet, what Darwin had seen in the Galapagos puzzled him sufficiently to pen these prophetic comments on the homeward voyage of the *Beagle* (June? 1836): "When I see these islands in sight of each other and possessed of but a scanty stock of animals, tenanted by these birds but slightly differing in structure and filling the same place in nature, I must suspect they

are varieties . . . If there is the slightest foundation for these remarks, the zoology of the Archipelagos will be well worth examining: for such facts would undermine the stability of species" (Barlow, 1963).

It was not until March 1837, when the celebrated ornithologist John Gould, who was working up Darwin's bird collections, told him of the specific distinctness of the mockingbirds (*Mimus*) collected by Darwin on three different islands in the Galapagos that Darwin finally recognized the process of geographic speciation. Apparently it was not until a good deal later that he learned

that some of the finches also were restricted to certain islands. As a result, as Darwin stated in the *Origin*, "when comparing . . . the birds from the separate islands of the Galapagos archipelago, both with one another, and with those from the American mainland, I was much struck how entirely vague and arbitrary is the distinction between species and varieties" (p. 48). It became clear to Darwin that many populations (as we would now call them) were intermediate between species and variety, and that particularly species on islands, when studied geographically, lacked the constancy and clear-cut delimitation insisted on by creationists and essentialists. Darwin's species concept was thus shaken to its foundations.

The spring of 1837 was one of the busiest in Darwin's life, and it was not until summer that he began to follow up on his conversion to evolutionism. In his journal he wrote: "In July [1837] opened first notebook on 'Transmutation of Species'—Had been greatly struck from about month of previous March on character of South American fossils—and species on Galapagos archipelago. These facts (especially latter) origin of all my views."

His encounter with Gould in March 1837 was the watershed in Darwin's thinking.[8] The destruction of the concept of constant species had a domino effect. Suddenly everything appeared in a new light. What had seemed so puzzling about his observations on the *Beagle* now seemed accessible to explanation: "During the voyage of the *Beagle* I had been deeply impressed by discovering in the Pampean formation great fossil animals covered with armour like that on the existing armadillos; secondly, by the manner in which closely allied animals replace one another in proceeding southward over the continent; and thirdly, by the South American character of most of the production of the Galapagos archipelago, and more especially by the manner in which they differ slightly