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A Matter of Individuality: Hierarchy Theory at the Dawn of Evolutionary Biology

Niles Eldredge and Stefano Dominici

The American Museum of Natural History, New York, and

Museo di Storia Naturale, Firenze, Italy

Seeing species as "individuals," a gambit begun in recent times by Ghiselin (1974), became a mini-industry in evolutionary theory through the 1980s. That species have births, histories and deaths, as have individual organisms, was an appealing concept to many evolutionary biologists with a "taxic" (Eldredge, 1969) orientation. For paleontologists with a "punctuational" perspective, the concept was especially appealing, as stasis if anything accentuated the "reality" of species—with little or no cumulative adaptive, phenotypic change accruing between the "births" of species and their eventual "deaths." Such an approach led directly to full-blown explorations of hierarchy theory (e.g. Eldredge, 1985, 1986).

It turns out that all this literature was reinventing the wheel—albeit a long-forgotten one. The Italian geologist Giambattista Brocchi (1814) had long ago suggested what Pancaldi (1984) has called "Brocchi's analogy"—consisting of two parts: (1) that species have births and deaths analogous to those of individual organisms; and (2) that species have intrinsic longevities. Brocchi had concluded from his work on Tertiary marine invertebrates that extinction is primarily a reflection of species growing old and dying, rather than the result of environmental events.

Nor is this mere historical curiosity. Brocchi's work was reviewed by Horner (1816) in Edinburgh—a hotbed of radical, pro-transmutational thinking—and Brocchi was well-known and respected in the British scientific community. His analogy appears (though without attribution) in the increasingly-notorious Anonymous essay of 1826 in the first volume of Jameson's *Edinburgh New Philosophical Journal.* That essay contains what appears to be the first use of the word "evolution" in the modern sense in the English language; considers what Lamarck's vision of transmission might look like in the empirical fossil record; exhorts the importance of

endemism in evaluating such patterns—and uses Brocchi's analogy as part of the conceptual template for evaluating such patterns.

There is no direct evidence that Darwin—who was a medical student in Edinburgh in 1826—read that paper. But there is a growing consensus that he must have. He is known to have read the Lamarckian Robert Grant's four papers in the same volume—at least one of them using Darwin's own data, without attribution. His early work on Argentinian fossils at Bahia Blanca (Eldredge, 2009) began his close examination of spatiotemporal replacement patterns of species three years before he reached the Galapagos. Both components of Brocchi's analogy are present in Darwin's essay *February 1835*—and is explicit in his *Red Notebook* passages of early 1837. Indeed, Darwin letter to Jenyns in 1844, saying that his initial exploration of the "question of the immutability of species, i.e. whether species are *directly* created, or by intermediate laws, (as with the life and death of individuals)"—constitutes a clear statement on the importance of Brocchi's analogy in Darwin's earliest transmutational work. Though Darwin's theory began to focus on adaptation shortly thereafter, he still mentions the possibility that species have innate longevities in his *Origin* (1859).

The search for "intermediate" ("natural," or "secondary") causes was a hallmark of developing British science in the 1820s and 1830s. Darwin's initial transmutational theory—essentially a geographically-based, saltational model of species origins—was developed directly from seeing species as individuals, and applying the two components of Brocchi's analogy to his own in-the-field empirical data on spatiotemporal species replacement patterns in southern South America. Thus hierarchy theory was foundational to the origin of evolutionary theory as we know it today.