How Systematics Became "Phylogenetic"

Niles Eldredge

Gareth Nelson, my former colleague at the American Museum of Natural History (AMNH), taught me the rudiments of the new-fangled "phylogenetic systematics" on a few paper napkins in a pizza parlor in Washington, D.C., sometime during the summer of 1970. We were in Washington to attend the Smithsonian's "Summer Institute in Systematics." Gary, along with his Ichthyology Departmental Chair, Donn Rosen, had been busy introducing their AMNH colleagues to the ideas of German entomologist Willi Hennig on the protocols of conducting strictly genealogical reconstructions of the relationships among species—and reflecting those results precisely in Linnaean classifications.

I had been putting off grappling with what seemed to most of us at the time as a challenging new set of ideas—promising myself that I would turn to Hennig and his ideas once I had completed my doctoral dissertation. By the summer of 1970, the time had come as Nelson sketched out and explained the first cladograms that I had ever contemplated seriously. By the time I began to publish the results of my dissertation work (Eldredge 1971)—in a paper that was the forerunner to the more famous one naming "punctuated equilibria" (Eldredge and Gould 1972)—I had grasped the power and significance of this new approach to systematics. Accordingly, I included one of the earliest paleontological cladograms in the second of these early papers on punctuated equilibria.

Nelson had been fond of saying that, contrary to prevailing wisdom, fossils are not necessary for phylogenetic reconstruction. As a young paleontologist, I found his

dismissal of fossils overblown; in particular, my take on the modern world of systematics certainly revealed no love of, appreciation for, or, in many cases, even respect for, the fossil record that I had already come to love and respect so highly. Yet Gary did have a real point: there is no doubt that the living biota is united by descent from progressively remote common ancestors—consequently the pattern of evolutionary relationships among strictly living species can in principle be resolved just on the basis of the anatomical (and now molecular) patterns of similarities and differences among the living species alone.

Phylogenetic systematics was for a time also known as "cladistics," a term apparently coined by Ernst Mayr who disparaged this new approach, and so naturally a name rejected, at least in the long run, by the majority of those who adopted the new approach. The older systematists—particularly and most vociferously Mayr and the paleontologist George Gaylord Simpson (both, by the way, former members of the AMNH staff)—pointed out that systematics had long since been based on the evolutionary relationships of species and higher taxa. The largely younger, then-newer crowd of phylogenetic systematists countered that the principles of reconstruction of phylogenetic analysis had always remained vague and uncodified—and that inasmuch as evolution produces genealogically linked skeins of species, the goal should be the development of an explicit methodology for analyzing genealogies—with the further task of reflecting the results of such phylogenetic analyses as rigorously as possible in classifications.

The proof of the pudding was in the eating: when "cladists" started to publish analyses showing that lobe-finned fishes are most closely related to amphibians and the rest of the tetrapod vertebrates (a result in itself not in dispute) and claiming that therefore rhipidistians, lung fish, and coelacanths are not fish in the older sense of traditional

N. Eldredge (✉)
Division of Paleontology,
The American Museum of Natural History,
Central Park West at 79th Street,
New York, NY, USA
e-mail: epunkeek@amnh.org

classifications (meaning that there really is no valid taxon "fish" in an evolutionary sense), the results troubled the traditionalists: everyone knows what a fish is! Likewise, that birds are an advanced group of dinosaurs—a part of the old "Reptilia"—while the extinct mammal-like "reptiles" are most closely related to the true Mammalia—meant that the old familiar term "reptiles" had to go. As did the older classification of higher Primates into the Families Pongidae (great apes) and Hominidae (humans and our closest fossil relatives): because we are most closely related to chimps than the other great apes, it makes no genealogical sense to classify chimps with other apes and us separately.

The furor engendered by the upstart arrival of Hennig's ideas has long since died down—and phylogenetic systematics is now the de facto order of the day. By the 1980s, recognizing that the essence of the analytic approach is the precise mapping of the distribution of characteristics in the attempt to separate relatively derived (advanced) from primitive features (and from "convergent" or "homoplastic" characters as well)—with groups to be defined and recognized solely on shared possession of "derived" features, algorithms that did the job on computers began to replace hand drawn cladograms on paper (whether napkins or otherwise). I leave it to the contributions in this, Dan Brooks' excellent Special Issue on the Teaching of Phylogenetics—with their welcome emphasis on teaching the nature and significance of this entire approach to analyzing the diversity of life—to set forth the basic principles of phylogenetic systematics (readers will also find many important contributions on this subject in previous issues of this journal). Right now, though, I want to explore how it was that systematics became "phylogenetic" in the first place.

At its heart, systematics is the search for natural groups of organisms, and their affinities with other natural groups. Defining those groups, and classifying them, was the original basic problem of systematics—and remains so to this day. At its inception, systematics was explicitly non-evolutionary: Linnaeus—whose *Systema Naturae* (Linnaeus 1858), replete with its hierarchical system of classification, was arguably the starting point of modern systematics—was no transmutationist. Though he may have waffled slightly on the subject of transmutation near the end of his life, basically Linnaeus did his work outside the realm of the as-yet-to-be-widely-accepted notion of transmutation—what we have long since come to call evolution. It is also the case that other pre-nineteenth century naturalists, concerned with understanding, describing, and codifying the diversity of life, did discuss transmutation to some extent—but I think it fair to say that the notion of evolution played no direct role in

systematics—the business of naming and classifying species—in the eighteenth century.

As a second marker point in the history of systematics, consider the use that Darwin (1859) made of the Linnaean hierarchy in his *Origin of Species*. Darwin simply said (with the aid of the only diagram published in his epochal book) that the fact that natural groups of organisms (he was fond of the term "allied forms" ever since he was a kid on the *Beagle* in the 1830s) was exactly what you would expect to find (in the parlance of modern philosophy of science terms, "predict" to find) if descent with modification—evolution—is true. For one of the two grand, most general predictions of evolution—the notion that all organisms on earth are descended from a single common ancestor in the remote geological past—says that, as genealogical lineages diversify, there will be a nested array of species and species–lineages that are progressively inclusive: closely related species are allied in a common genus; genera within families, and so on. Descent with modification—with the division of lineages thrown in, will automatically produce a nested array of genealogical lineages, marked by nested arrays of shared characteristics—the raw data of systematics.

There has been a lot of argument in the past half century over how much the theory of evolution—meant as the set of ideas of *how* the evolutionary process works—has or should influence how systematics is done. Many contemporary phylogenetic systematists—including among them some of the best and the brightest—continue the search for natural groups and their affinities openly ignoring even the basic, elemental fact that the groups are natural, and their "affinities" real, because evolution has happened. But I do agree with them that there is a natural system to be discovered, and the fundamental task of that discovery can and even should be pursued without the added baggage of notions of how life has evolved. Pushed into a corner, cladists (I do still cling to the term—risking pejorative connotations) will admit that life has evolved.

Given that universal admission—that a process of genealogical descent has produced not only the diversity of life on earth, but also the existence of natural groups that are easily seen to be nested à la Linnaeus' hierarchy—the question becomes: When and how did evolution come into the mix of systematics? We have established two points: Linnaeus in 1758 and Darwin in 1859; somewhere, someplace in between, someone recognized the connection between evolution and the existence of natural groups.

I have come to the (rather obvious) conclusion that the recognition of natural groups of "allied forms" was a necessary—if not entirely sufficient—precondition for the task of looking for a natural (i.e., non-miraculous)

explanation for the origin of new species. And it was specifically the question: *What natural (or "secondary") causes were responsible for the advent of the modern fauna,*— the currently extant species of animals, plants, fungi, and micro-organisms (to the extent the latter were known and considered at the beginning of the nineteenth century)? During the first three decades of the 1800s, naturalists became keenly aware that progressively younger and younger fossils approximate more and more closely to the species still alive—with many if not all known modern species showing up in the youngest sediments (historians have long noted this "progressivism," or the "Law of Succession" as Darwin [1839] called it in the first edition of his *Journal of Researches* [aka *The Voyage of the Beagle*], written long after Darwin had privately accepted the truth of transmutation—but have nearly universally failed to grasp its true significance in the writings of the earliest transmutationists). Even Georges Cuvier, never an overt convert to transmutation, pronounced this progressive modernization of the fossil faunas as "perhaps the greatest mystery" of natural history—in his eulogy to his colleague and archrival Jean-Baptiste Lamarck.

In an article elsewhere in this issue (Dominici and Eldredge 2010), the pre-Darwinian history of early transmutational thought is considered in some detail. In this essay, I want to draw a tighter connection between systematics and evolution via the early history of the explicit tracing of lineages of species—up to and including the advent of the modern fauna. The two figures that stand out most clearly as the founders of modern evolutionary biology are the aforementioned Jean-Baptiste Lamarck and the lesser known, but (especially because of his great influence on the young Darwin on his *Beagle* voyage in 1831–1836 and the earliest years thereafter back home in England) equally important Italian Giambattista Brocchi. Both framed theories of transmutation based on the notion of natural groups. And (score one for paleontology!) both based their ideas on their readings of the empirical record of fossil sequences of mollusks. The notion of evolution as a serious scientific idea came from these two great invertebrate paleontologists—whose specific point of departure was the explanation of the origin of the modern molluscan fauna.

The details of their ideas differed drastically. Lamarck (1801) came first, with his *Système des Animaux sans Vertèbres*. In his section "On Fossils," Lamarck argues against the general claim of Cuvier that all fossil species are now extinct—through "revolutions" that we would now call mass extinction events. To the contrary, Lamarck says, some of the species of his Tertiary fossils from the Paris Basin are still very much alive. Yet it is true, Lamarck admits, most of his fossil species are not to be found still living in the modern fauna, though they are usually closely similar to still-living species and belong to the same genera, families, and orders.

Lamarck concluded from his study of the fossil and recent molluscan fauna that the main reason why most of his fossil species no longer are alive was not that they had fallen victims to Cuvierian-style extinction—but rather that they had slowly and inexorably changed through time into something else—up to and including the modern fauna. Many who respected him and who were themselves beginning to adopt transmutational views (such as the Scotsman Robert Jameson in the 1820s) roundly criticized Lamarck—not because of his transmutational views per se, but for what many took to be his unwarranted flights of fancy on the subject: Lamarck (1801, but also 1809) thought that, in effect, species are in constant flux through time, and even geographically—patterns most of his fellow naturalists could not see. What matters in the context of this issue on phylogenetics, though, is that Lamarck had a naturalistic explanation for the origin of the modern fauna that was based on the tracing of lineages of similar species up the stratigraphic column until the advent of the modern fauna.

Giambattista Brocchi (1814) published the second important monograph, *Conchologia Fossile Subapennina*, on Tertiary fossils after Lamarck (again, for details, see Dominici 2010, this issue; Dominici and Eldredge 2010, this issue—the latter including the linking of Brocchi's monograph to the early work and thinking of Charles Darwin; and Eldredge 2009 for more details of Darwin's early work on the *Beagle*). Because the rocks in Italy that Brocchi studied were younger than those that Lamarck studied in the Paris Basin, Brocchi found that he had fossils in his collection belonging to roughly 50% of the known species of the modern Italian marine molluscan fauna. Unlike Lamarck, Brocchi thought species are fundamentally stable entities—which from time to time give birth to descendant species—just as organisms reproduce and give birth to descendant organisms. The process of successive births and deaths of species accounts for the modernization of the fauna—Brocchi's very different (i.e., from Lamarck's) explanation of the ultimate appearance of the modern fauna.

What I find most arresting about Brocchi's (1814) words from the standpoint of linking phylogenetics explicitly to a theory of transmutation are his comments on the importance of lineages. Brocchi (1814; Dominici 2010; Dominici and Eldredge 2010) says, in effect, that it is useless to study lineages of Mesozoic fossils (including invertebrates—ammonoids are wholly extinct, as are most other Mesozoic molluscan taxa) as they lead nowhere: they shed no light on the origin of the modern fauna.

But, Brocchi also says, the study of modern mollusks is fundamentally boring—as long as one is merely cataloging the living species. But such a catalog does have potential meaning and, indeed, a strong interest and value if one uses it comparatively and thinks in terms of lineages. The origin of the modern fauna becomes the target issue and can be studied by tracing lineages of closely similar—related—species up through progressively younger beds.

Thus Brocchi and Lamarck, with their very different interpretations of very similar data, were the first, I believe, to introduce empirically based lineage-thinking to the origin of the modern fauna. In so doing they initiated the modern study of evolutionary processes—by looking for direct links between closely related species through temporal sequences of fossils. They did not invent "phylogenetic systematics"—which, as the contributions in this issue make clear, is a set of formal rules on how to study lineages objectively. But they did extend the early form of systematics, with its all-important recognition of natural groups, into a new domain: the scientific study of the evolutionary process itself. They succeeded in so doing by making systematics phylogenetic.

And, to me, it is icing on the cake that both Lamarck and Brocchi were invertebrate paleontologists!

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