



Phylogenetic Reconstruction Then and Now

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A Review of Henry Gee, ed., *Shaking the Tree: Readings from Nature in the History of Life*, University of Chicago Press, Chicago, 2000, 411 pp., (Pb) ISBN 0-226-28497-2, \$27.50, (Hb) 0-226-28496-4, \$78.00.

Peter J. Bowler, *Life's Splendid Drama: Evolutionary Biology and the Reconstruction of Life's Ancestry, 1860-1940*, University of Chicago Press, Chicago, 1996, 526 pp., (Pb) 0-226-06922-2, \$22.00, (Hb) 0-226-06921-4, \$42.00.

Two phylogenies

It is disconcerting to suddenly become aware of a major trend that has been going on all around you. This happened to me in reading Henry Gee's *Shaking the Tree*. The book is an anthology of articles published in the 1990s in the journal *Nature*, with commentary by the editor. I do a fair amount of reading in contemporary biology, although I read more in the history of biology. I was surprised to realize how strong the scientific interest has become in the study of phylogeny. The interest is not only in the systematics of existing groups, but also in *deep* phylogeny, the tracing of relationships between fossils and extant organisms, and the reconstruction of ancient ancestors of divergent taxa. This new interest is a confluence of several independent developments. One contributing factor is new data from paleontology, and new kinds of data such as molecular sequences. Another is methodological, in the nearly universal acceptance of cladistic (aka "phylogenetic") systematics. Another is technical, in the computerization of systematics, which allows for the assessment of phylogenetic inferences well beyond the range of the unaided scientific mind. A fourth factor is the rapid growth in the 1990s of evolutionary developmental biology, also known as Evo Devo. The Gee volume cannot be absolutely current, of course; the most recent paper is from 1997.

But a broad range of important papers, together with updated bibliographies by the editor, brings the reader up to date on the breadth of this growing interest.

But there's the rub. Is the interest in phylogeny really new? My out-of-date prejudice was that a fascination with phylogeny was typical of the late nineteenth century, but not of twentieth century evolutionary biology. Apparently I was only out of date by one or two decades. The mainstream of evolutionary biology after the Evolutionary Synthesis of the 1930s and 1940s was concerned much more with the mechanism or the process of evolutionary change than with the pattern of phylogeny that could be extracted from paleontology and phylogenetic reconstruction. The real heyday of deep phylogeny had already passed when the Evolutionary Synthesis was formed. Its peak was in the 1880s, when Ernst Haeckel, Carl Gegenbaur and most other practicing evolutionists were constructing evolutionary trees, in part by examining the earliest developmental stages of embryos.

An intriguing parallel exists between these two episodes of phylogenetic frenzy. One of the constituents of the modern florescence of deep phylogeny is Evo Devo, the study of the interrelation between evolution and development. Combined with modern molecular methods, Evo Devo seems to provide exciting new resources for ancestral reconstruction. I personally find Evo Devo intriguing from a methodological point of view. But during most of the twentieth century, developmental biology had been considered even less important than deep phylogeny to evolutionary theory. So the two flowerings of deep phylogeny (the 1880s and the 1990s) are associated with unusually strong interests in the role of developmental in evolution. Are there any other parallels?

It is hazardous to look to the past for lessons for the present, but it would at least be instructive to see the similarities and contrasts between then and now. Fortunately we have an excellent recent source concerning the popularity and the practice of phylogeny in the nineteenth century. It is Peter Bowler's 1996 book *Life's Splendid Drama*. Bowler discusses phylogenetic practices in the period between the publication of Darwin's *Origin* and the formation of the Evolutionary Synthesis. In two earlier books, Bowler brought to academic attention the fact that evolutionary thought during this period was not at all what we would now think of as Darwinian (Bowler 1983, 1988). That is to say, the principle of natural selection was not generally accepted as the central causal mechanism in evolutionary change. There was a great deal of disagreement about the causes of evolution, and selectionists (Darwinians in the post-Evolutionary-Synthesis sense) were but one of many schools.

Life's Splendid Drama examines the central role of phylogeny during that period. Bowler believes that historians have overlooked this tradition because

of their concentration on evolutionary mechanisms. The modern centrality of mechanisms has directed historians' research towards natural selection and its alternatives (Lamarckian inheritance, orthogenesis, and so on). In contrast, Bowler shows that "the first generation of evolutionary biologists" was made up of morphologists and embryologists who were interested in reconstructing the history of life, not in identifying mechanisms. This first generation and their successors are the core of his narrative. He considers the first generation to be irrelevant to modern evolutionary theory, and of interest primarily to historians. "If we wish to tell our story as a triumphant advance towards modern evolutionism, we may be justified in ignoring the role of morphology in the Darwinian revolution. But if we want to understand what evolutionism actually meant to late nineteenth-century biologists . . . we ignore it at our peril (Bowler 1996: 14)."

I believe that *Life's Splendid Drama* has more relevance to modern science than its author suspects. In what follows, I will first describe the contents of *Shaking the Tree*. I will next sketch some of Bowler's findings regarding nineteenth century phylogeny, and finally use them as a perspective from which to view the practice of phylogeny embodied in Gee's anthology. A striking irony emerges from this comparison. In many ways, today's phylogenetic methods are more similar to those of the nineteenth century than to the methods of the 1930s that replaced them. From a twentieth century neoDarwinian perspective, the evolutionary morphologists were an irrelevant historical distraction. From the perspective of the phylogeneticists in Gee's volume, the morphologists seem more or less on the right path, and the neoDarwinian emphasis on adaptation was the distraction. The path of science has strange twists and turns. A "triumphant advance" seen from one historical perspective looks like a mere detour from another.

Phylogeny Today: *Shaking the Tree*

The theme of the book is the history of life on earth. The topics are mostly, but not entirely, phylogenetic studies of particular groups or characters. Two of the five Parts are tangential to phylogeny. Part 1 covers broad and methodological themes. Stephen Jay Gould and Niles Eldredge discuss the present state of the punctuated equilibrium debates, Eörs Szathmáry and John Maynard Smith analyze major transitions of grade (prokaryote/eukaryote, protist/metazoa) in terms of information transmission, and Caro Beth Stewart discusses the use of parsimony in systematics. Part 3, the other non-phylogenetic section, concerns broadly ecological issues, including Proterozoic stratigraphy (Andrew Knoll and Malcolm Walter),

early terrestrial ecosystems (Willa Shear) and the Permo-Triassic extinction (Douglas Erwin).

The other three Parts are phylogenetic. Part 2 deals with evolutionary developmental biology, the phylogeny of ontogeny. Sean Carroll writes on homeotic genes in the evolution of arthropods and chordates, and E. M. de Robertis and Yoshiki Sasai on dorsoventral patterning in Bilateria. Neal Shubin, Cliff Tabin and Sean Carroll discuss the evolution of limbs in various taxa, and Conway Morris describes the fossil record of early metazoa. Parts 4 and 5 are case studies in phylogeny. Part 4 covers the origin of early land plants (Paul Kendrick and Peter Crane), of angiosperms (Peter Crane, Else Marie Friis and Kaj Pedersen), of jawed vertebrates (Peter Forey and Philippe Janvier), of tetrapods (Per Ahlberg and Andrew Milner), of birds (Luis Chiappe), and of mammals (Michael Novacek). Part 5 is distinct only because it deals with taxa that are lower in rank and closer to home. It covers the origin of primates (Robert Martin), Hominoidea (Peter Andrews), and the genus *Homo* (Bernard Wood).

Phylogeny Before the Synthesis: *Life's Splendid Drama*

Bowler's book contains a great deal of information about a number of debates within the older phylogenetic tradition about the origins of various taxa (mammals, tetrapods, etc.) and characters (fins, limbs, etc.). It reports a single overall historical trend during the period. The first generation of evolutionists was heavily influenced by the continental tradition of idealistic morphology, and its use of ideal Types in morphological explanation. As time passed the influence of idealism waned, and phylogenetic studies became more and more consistent with a broadly Darwinian adaptationist viewpoint. The trend was away from idealism and typology, and towards adaptation and environmental causes of change. The trend did not directly bring about the Evolutionary Synthesis. Discoveries in experimental and population genetics were needed for that. Nevertheless, Bowler convincingly argues that the intellectual climate among phylogeneticists was favorable to the Synthesis in the 1930s in a way that it had not been in the 1880s. The increasing interest in adaptation, and the waning interest in morphology and its typological commitments, set the stage for the Synthesis even though the later phylogenetic practitioners had no involvement with genetics or population studies.

Scholars who write about the history of science have taxonomic problems that cannot be helped by cladist methods. To make any interesting claim at all, we must generalize over *kinds* of scientists. But how should these scientist-kinds be constructed? Actual living scientists embraced combinations of

theoretical and methodological beliefs that are not neatly portioned into categories. The case at issue is the tradition of nineteenth century morphology, variously labeled *idealist*, *transcendental*, and *typological* because of its use of ideal Types.

Historians fall into two camps on the defining characteristics of this category. One camp presents idealism/typology as centered on a commitment to metaphysical idealism, according to which real-world species are manifestations of eternal non-material Types. On this view, idealist metaphysics alone prohibits evolutionary change (Coleman 1976: 150). In some accounts idealism is described as a version of natural theology, a variant “idealistic” version of Reverend Paley’s anti-evolutionary Argument from Design. I will call this the *metaphysical concept* of idealism and typology.¹ The other camp presents idealism as one party to a dispute that was orthogonal to the evolution/creation debate, namely the structure/function debate (Russell 1982, Ospovat 1981). Structuralists considered organic form (structure) to provide the deepest insights into organic nature, while functionalists (adaptationists or teleologists) considered adaptation and functional design as primary. The structuralists of the early nineteenth century were idealist typologists, arguing for the importance of Unity of Type. Functionalists, including Cuvier and the British natural theologians, considered commonalities of structure (the structuralists’ types) as mere byproducts of similar functional needs. Evolution was not directly at issue. After the publication of Darwin’s *Origin*, the concept of evolution changed the nature of the structure/function debate. But structuralist idealists were not *by reason of idealism alone* opposed to the new evolutionary viewpoint. As Darwin himself pointed out, the structuralist archetype could be reinterpreted as an ancestor. Many structuralists accepted evolution, and simply reinterpreted the ideal archetypes as ancestor-archetypes. Both before and after the acceptance of evolution, Types were used in structuralist explanations of organic form. I will therefore call this the *explanatory concept* of idealism and typology.²

Bowler holds to the metaphysical concept of idealism. He therefore sees a great deal of tension in the tradition of evolutionary morphology, since idealism is at odds with evolutionism by its very definition. Even though Bowler’s stated purpose is “not to decide which were the ‘right’ and ‘wrong’ theories as judged by modern standards” (Bowler 1996: 6), his narrative makes very clear that the move away from typology and towards adaptation is a move in the direction of truth.³

I prefer the explanatory concepts of idealism and typology. I see no more internal tension in Gegenbaur’s structuralist version of “Darwinism” than in the adaptationist “Darwinism” of the same period. The adaptationist version of Darwinism was heuristically useful in field studies, but until the twentieth

century no one could demonstrate that the facts of heredity were consistent with natural selection as the primary cause of evolutionary change (Gayon 1998). Structuralist morphology had been a pre-evolutionary project, but it was not necessarily an anti-evolutionary project. The project stretched back to Goethe (inventor of the term “morphology”) and the *Naturphilosophs*, and included von Baer, Geoffroy, several Edinburgh opponents of natural theology, and Richard Owen.

The goal of the project was the *explanation of form* (Nyhart 1996). Ideal types within this tradition are best understood as hypothetical entities, of indeterminate ontological nature. After the early excesses of the *Naturphilosophs*, typologists were cautious in their claims about the reality of hypothetical constructs like the Type. Most of them declined to specify any particular ontological status for the Type. One exception was Richard Owen, in his much-cited declaration of Platonic Idealism in 1849. This has now been shown to have occurred under pressure from Owen’s theologically conservative backers (Rupke 1994: 202). Types were at first individuated by the comparative morphology of adults. The recognition of nested sets of (adult) homologies revealed types within Types. Embryology soon provided other criteria for morphological unities, as distinct body parts in different species were seen to develop from common embryological precursors. So both comparative morphology and embryology contributed to the study of form. Comparative studies revealed relations among forms of adults, and embryological studies showed how related adult forms arose from modifications of common embryological processes.

Darwin acknowledged that the morphological and embryological knowledge gathered by this tradition was his best evidence for descent with modification. After publication of the *Origin* most morphologists accepted descent with modification. The goal of *explaining form* was modified but not abandoned. Pre-evolutionary morphologists (unlike natural theologians) had considered the natural system of taxonomy to reflect *real* relations among organisms, even though the ontological nature of the relations was usually unspecified. Descent with modification allowed the morphologist to pin down the reality of those relations. The comparative aspect of the explanation of form (by reference to common types) became a phylogenetic explanation of form; the archetype became an ancestor. Evolutionary morphologists, the first generation of evolutionary biologists, interpreted Darwinism as a new and liberating approach to the explanation of form. (See Di Gregorio 1995: 259 on the extent to which evolutionary morphology can be given a justification in Darwin’s *Origin*.)

This nineteenth century structuralist goal of explaining form is seldom recognized by biologists in the twentieth century. Disinterest in form can

be seen in the various reasons given for practicing phylogeny. Dobzhansky considered the previous century's interest in phylogeny to have been motivated by a desire to prove descent with modification, a proof that was no longer needed (Dobzhansky 1937). Bowler presents the narrative of phylogeny as an end in itself. The history of life has its own fascination, and no further excuse is needed. This is reflected in his title: the history of life is indeed a splendid drama. But neither of these motives reflects the purpose of phylogeny in the nineteenth century. Phylogeny then was a means to an end, the end of explaining form. The biogenetic law (ontogeny recapitulates phylogeny) was not merely a tool with which to dig up phylogenetic relationships. It played a role in the explanation of how phylogenetic history shaped ontogeny, and thereby shaped organic form. It boggles the modern mind to read Haeckel's claim that phylogeny is a "mechanical cause" of ontogeny. A necessary step towards understanding that peculiar pronouncement is recognition of the explanation of form as an explanatory goal. Evo Devo biologist Brian Hall recognizes in the nineteenth century evolutionary morphologists the combined goals of explaining form and of determining phylogeny. "By the late nineteenth century a solution to the generation of organismic form appeared to be at hand in homologous germ layers and conserved stages of embryonic development. This evolutionary embryology [of biologists like Haeckel and Balfour] was applied to relationships among organisms and in a search for the ancestors of the vertebrates (Hall 1999: 69)". I would only add that phylogeny and form-explanation were not distinct, but interrelated endeavors.

Darwin and the evolutionary morphologists differ in their explanatory goals. For Darwin, the embryological and morphological patterns had value only as evidence for descent with modification. The archetype had been transformed into an ancestor, and Darwin had no other use for it. The explanation of form was not Darwin's problem. But for the evolutionary morphologists, the new ancestor/archetype was a theoretical tool to be used in solving the old problem of form. Mere identification of ancestors was not enough. The explanation of form required some principle of transformation to connect ancestral form with the form of contemporary organisms. The phylogenetic explanation had to involve the processes that explain the ontogenetic origin of form, namely embryological development. This was the role of the biogenetic law. Besides identifying or hypothesizing ancestors, the biogenetic law also helped to explain how current form arose out of ancestral form via phylogenetic changes in the ontogenetic processes by which form is generated in each successive generation. *Explanation, not mere narrative, was the goal of phylogeny.*

Even if evolutionary morphology was (as I claim) a coherent program, it was certainly not a persistent one. By the 1890s most of the followers of the evolutionary morphologists had abandoned phylogeny and devoted themselves to experimental studies of embryology and inheritance. Application of the biogenetic law required theorists to distinguish the ancient developmental processes from those that had been interposed as larval adaptations. Embryological knowledge was not equal to this task. *Life's Splendid Drama* documents how this came about. Conflicting recapitulationist reconstructions could not be resolved by embryological or morphological methods. Embryologists drifted away from phylogenetics, and the program of evolutionary morphology gave way to phylogenies based increasingly on paleontology and scenarios of adaptation.

Bowler blames idealism for several regressive tendencies in early phylogenetic studies. Some of these tendencies are not related to explanatory typology/idealism as I conceive it. One example is the tendency to think of a "main line" of evolutionary progress aimed towards human beings. This tendency can be seen in non-typologists as well as typologists, and seems unrelated to the explanatory use of types. But Bowler does identify one "regressive" practice that is very much tied to explanatory typology. Changes in the practice were indeed movements along the road to the Evolutionary Synthesis. Bowler reports that when idealists hypothesized ancestors, they depicted them as idealized abstractions of embryological processes, not as real organisms with real functional needs. His example is the work of Adolf Naef.

Naef proposed a hypothetical developmental pattern which could be modified to produce both annelids and chordates . . . it represented the primitive features of the developmental process stripped of any specialized details that would have had to exist in the ontogeny of a real organism. . . . But since there was no need to think about the starting point as a real organism, there was no incentive to search for the adaptive modifications that might have indicated how the early members of the group had lived, or the kinds of adaptive pressures that might have forced their transformation into the divergent forms we know today. (Bowler 1996: 56)

Even though Naef was writing in the 1920s, Bowler's account of his method is quite consistent with the principles used by earlier typologists to unify groups and hypothesize ancestors. In the 1870s Haeckel proposed the *Gastrea* (a hypothetical gastrula-shaped organism) as an ancestor to all metazoans. The ontogeny of *Gastrea* can be modified into the ontogenies of its descendants (obviously, since they all pass through a gastrula stage in their embryogenesis) and the question of *Gastrea's* special adaptive needs was ignored. A

related pre-evolutionary kind of reasoning lay behind Geoffroy's claims of the 1820s that the body forms of arthropods and vertebrates were homologous but inverted, so that the dorsal nerve cord of vertebrates corresponded with the ventral nerve cord of arthropods. In Geoffroy's typology, the type shared by vertebrates and arthropods was not an ancestor but an abstract (i.e. ideal) ontogeny and body plan that was inversely manifested in the two groups.

The only quibble I have with Bowler's description of Naef's thinking is his honorific use of the term "real." Metaphysical idealism was not the reason for the typologists' concentration on developmental patterns. The reason was their commitment to the explanation of form. This explanation ties ancestral ontogenetic form-generating processes to those of descendants through evolutionary changes in ontogeny. Typologists followed the rule that says "Identify an ancestral ontogeny that can be modified into the ontogenies of the descendent groups." Ontogenies are "real" things, and every real metazoan must have one (on pain of remaining a zygote!). Adaptationist phylogeneticists follow a different rule: "Identify ancestral characters and selective forces such that the forces might cause the characters to diverge into the descendent forms." Let us baptize these two rules the *generative* rule and the *adaptive* rule. Any "real" organism must follow both rules – it must develop ontogenetically and it must fit its environment.

Moreover, any phylogenetic change must *conserve* obedience to both rules – each descendent must maintain both its ontogeny and its fitness. Typologists' concern for form made them attend to the generative rule and ignore the adaptive rule. Adaptationists attended to the adaptive rule and ignored the generative rule. It is no more "realistic" to ignore ontogeny than it is to ignore adaptation.

Even if I am correct that typologists were just as concerned with reality as were adaptationists, they were certainly playing a loosing game in the early twentieth century. Those who clung to the generative rule were increasingly seen as anachronisms. Evolutionary morphology was an old-fashioned program, and virtually all embryologists had become experimentalists. By the time of the Synthesis, when embryologists did discuss evolution it was usually to repudiate the biogenetic law (Churchill 1980). Bowler documents the gradual transition from a typological to an adaptationist phylogenetic practice. Debates about morphological/embryological transformations gave way to more "Darwinian" questions about the selective advantages enjoyed by the earliest members of new groups. What did the first amphibian gain from walking on land? Escape from predators, or perhaps efficiency in locating the rapidly dwindling ponds (Bowler 1996: 253–257). Why did birds evolve wings? Evolutionary morphologists (in this case Thomas Huxley) had proposed that ratites, running birds, were the first to evolve from dinosaurs.

Flight was held to be a later innovation. As phylogeny became more adaptationist, the transformation of an ostrich's wing to a lark's wing made no adaptive sense. Adaptive explanation required that the first birds had evolved in the trees, with ratites as a later modification. Arboreal ancestors would have had a use for wings, and identifying that use became a necessary requirement for constructing the phylogeny (*ibid*: 273–289). “Evolutionists were no longer satisfied with the construction of phylogenetic trees based on morphological relationships. They were now beginning to construct adaptive scenarios to explain particular transformations, exploiting information about changing environments derived from geology (*ibid*: 246)”. “We have seen how the possibility of an environmental trigger was called upon to explain the origin of the vertebrates and each vertebrate class (*ibid*: 433).”

Comparisons

The present discussion of phylogeny will contain a 50 year gap representing the period between the end of Bowler's narrative and the beginning of Gee's anthology. How was phylogeny practiced and shaped during these years? It seems to have been of much less theoretical importance than previously. Selection at the level of populations rather than phylogenetic patterns is the center of attention. The principle that macroevolution is an extrapolation of microevolutionary (populational) processes was stated as a working hypothesis by Dobzhansky in 1937, but it was soon accepted as an established fact. While there was still a splendid drama to narrate, the narrative no longer served a theoretical purpose.

A large part of the story of this era must involve the notoriously virulent three-way debates about phenetic, cladistic, and evolutionary systematics (Hull 1988). Today's cladists might argue that phylogeny was neglected by Synthesis biologists because the evolutionary systematics by which it was practiced was in principle unable to resolve phylogenies.⁴ With no pressing reason to practice it, and no assurance of success, it is no wonder that phylogeny lost its interest to biologists. This question deserves more study. But I will now bracket those years, and examine how the phylogenetic practices of the 1990s as seen in Gee's book relate to those reported by Bowler.

Sometime during the twentieth century the trends that Bowler traced into the 1930s were reversed. Adaptive scenarios are hard to find in the pages of *Shaking the Tree*. Scenario-construction is nowhere endorsed, and specific scenarios are usually introduced only to reject them on the basis of cladistic, paleontological, or ecological evidence.

One of the more detailed discussions of adaptive scenarios is the discussion by Ahlberg and Miller of the influence of a 1981 paper by Donn Rosen

and colleagues about the origin of tetrapods (Gee 2000: 268; Rosen et al. 1981). The paper is described as a “conceptual turning point.” The paper by Rosen et al. used cladistic methods to conclude that lungfish are the closest living relatives of tetrapods, and critiqued the use of adaptive scenarios as unfalsifiable. As a turning point, the paper is very odd: no later author has accepted its conclusion about the lungfish/tetrapod linkage. What makes it a landmark? It rejected adaptive scenarios on methodological grounds, and replaced them with cladistic studies of the sequences of character acquisition. From that point on, all studies on the origins of tetrapods used cladistic methods and shunned adaptive scenarios. Alberg and Miller list three traditional adaptive scenarios about the origins of limbs, and include the two cited above from Bowler: predator avoidance and the search for dwindling ponds. On current cladistic and fossil evidence, limbs were probably first acquired by fully aquatic organisms, not by fish dragging themselves onto the land. The adaptive requirements of walking on land had nothing to do with the origin of tetrapods.

A similarly bleak assessment of the value of adaptive scenarios appears in Chiappe’s chapter on the origins of birds. The arboreal explanation of the evolution of flight (cited above from Bowler) comes in for special criticism. The ancestral mode of life for birds appears to have been terrestrial, based on phylogenetic and paleoenvironmental evidence (e.g. the Solnhofen lagoons were not surrounded by forests but by sparse small plants!) (Gee 2000: 292). Chiappe discusses a controversy surrounding the inclusion of the flightless, stout-forelimbed, turkey-sized *Mononykus* within Aves. Critics oppose its inclusion on grounds that the animal’s forelimbs do not suit it for “birdlike” activities (e.g. they look adapted for digging rather than flying) and do not appear to be derivable from flight-adapted wings. For Chiappe, a cladistic analysis trumps an adaptive scenario every time. “Assumptions about evolutionary processes or adaptational scenarios, such as these, are misleading when identifying historical relationships. Phylogenetic reconstruction should be based exclusively on the hierarchical distribution of homologies among taxa, and a given phylogenetic hypothesis can be rejected only by providing an alternative hypothesis for which supporting evidence outweighs that of the original hypothesis (*ibid.*: 297)”. By “alternative hypothesis” Chiappe clearly means alternative *cladistic* hypothesis. Adaptive scenarios do not even count as alternative hypotheses.

Part 5, on primates and included taxa, contains slightly more discussion of adaptation than Part 4, which discussed higher taxa. Nevertheless, even though Andrews’s chapter is entitled “Evolution and Environment in the Hominoidea”, discussion of the environment is very general (“paleoenvironments that may have been more wooded than has formerly been

thought”). General differences between arboreal and upright skeletal traits are mentioned but not discussed in detail, and the only specific adaptation mentioned is the relation of tooth morphology to diet. Wood’s chapter on *Homo* has some discussion of traits associated with upright posture, such as the close-packed morphology of the human foot. These discussions are the exceptions; a few comments on adaptation in chapters primarily based on non-adaptive criteria of relatedness. One principle is quite clear: adaptive scenarios are discussed *only after* phylogenetic hypotheses are established. Phylogeny is epistemologically prior to adaptive theorizing. A century ago, phylogenies derived from morphology were abandoned in favor of those based on adaptive scenarios. By the 1990s, the process had reversed.

A different but equally dramatic reversal can be seen in Part 2, on evolutionary developmental biology (Evo Devo). Arguments that mainstream evolutionary theory suffered from its inattention to development have been around since the late 1970s. But the real growth spurt in Evo Devo occurred after molecular discoveries in the 1990s of the sharing of regulatory genes among groups that have been reproductively isolated for over 600 million years. The problem with the biogenetic law as a phylogenetic tool had always been that it was impossible in practice to untangle conserved developmental stages from evolutionary innovations. Phylogeny could not be read from ontogeny because evolutionary innovations were interspersed early and late throughout ontogeny, not neatly tacked on at the end. If the phylogenetically oldest mechanisms were clearly marked in ontogeny, such things as larval innovations would not confound reconstruction of ancestors. The new molecular homologies changed all that. They are extremely early in their action, and their structural commonality seems beyond question. When we see them function in similar ways in ontogeny, we simply can’t help but believe that the ontogenies they control today are transformations of ontogenies that they controlled in ancient ancestors.

The similarities between Evo Devo and nineteenth century typology are striking. Some authors acknowledge this fact. In their chapter on the dorsoventral axis, de Robertis and Sasai reproduce Geoffroy’s 1822 illustration of a dissected lobster lying on its back to reveal the axis inversion in comparison to a vertebrate. Recent molecular evidence gives dramatic support to Geoffroy’s conjecture. Genes designating the dorsoventral axis in chordates are homologous to those in arthropods, but with reversed polarity. Homologous genes mark the dorsal side of a chordate and the ventral side of an arthropod. The authors also allude to Haeckel’s *Gastrea* theory. Haeckel does not come out a winner like Geoffroy. *Gastrea* is replaced by *Urbilateria*, the newly hypothesized ancestor of chordates, arthropods, and all other bilaterally symmetrical animals. Other authors discuss the ancestral ontogenies

of less-ancient groups. From Carroll's chapter, "It now seems likely that all insect diversity has evolved from a body plan [archetype?] sculpted by the same set of homeotic genes (*ibid.*: 76)." The chapter by Shubin and Tabin discusses the different developmental roles of homeotic genes in the evolution of vertebrate and arthropod limbs.

The limb has been a mainstay of structuralist study ever since Owen's 1849 attack on the adaptationists of his era (Owen 1849). The evolution of the fin and limb involved the successive cooption of a portion of the sequence of *Hox* genes that specifies the body axis into paired fins, then again into three nested expression domains corresponding to the three "compartments" of the limb (corresponding to the thigh, shin, and foot). Each iteration of expression specifies the anterior-posterior axis of the respective body parts. The authors point out that the developmental sequence recapitulates the sequence of phylogenetic acquisition of these compartments (Gee 2000: 104). The serial repetition, with subsequent specialization, of developmental patterns is a very old theme in structuralist biology.

Bowler's description of Naef's idealist methodology applies perfectly to the chapters in Part 2 of Gee. Reconstructions yield a hypothetical ancestral ontogeny that could be modified to produce descendent ontogenies. *Urbilateria* is such a construction, representing shared features of the developmental process but stripped of any specialized adaptive details. The reconstruction ignores the "adaptive pressures that might have forced their transformation into the divergent forms we know today." These authors follow the generative principle and ignore the adaptive principle, as did Naef and the nineteenth century structuralists both before and after Darwin. Evo Devo reflects the program of explanatory typology, as I sketched it above (and in Amundson 2001).

Some Evo Devo practitioners are leery of typology, a fact that is quite understandable given its anti-scientific reputation during most of the twentieth century (Richardson et al, 1999). Nevertheless, the terms "body plan" and "bauplan" are now used with no apparent embarrassment, and even "archetype" springs up regularly. De Robertis and Sasai showed no embarrassment in pointing out the similarities of their views to Geoffroy and Haeckel. An important theoretical need is being recognized in citing long-dead typologists and adopting their vocabulary. Evo Devo revives the old morphological goal of explaining form. The title of Lynn Nyhart's history of nineteenth century morphology resonates with Rudolf Raff's 1996 Evo Devo manifesto: *Biology Takes Form* and *The Shape of Nature*.

Two major features are shared by the phylogenetic programs of the nineteenth and late twentieth centuries. First, phylogenies are constructed on the basis of shared characters, without hypotheses about adaptive forces that

might have favored the transformations. Second, many ancestral reconstructions involve “idealized” abstractions of developmental processes, specifically formulated so that transformations in the hypothesized ancestral ontogeny will yield the ontogenies observed in the derived groups. These hypotheses, too, ignore questions about adaptive causes of change.

Contrasts and conclusions

There are of course disanalogies in the two cases. The cladistic methods of phylogeny are only superficially similar to traditional morphology. Cladistics has no concern for organic form *per se*, and does not restrict systematic treatment to characters with morphological significance. Cladists disapprove (in principle) of adaptive scenarios only in their use as criteria for constructing or testing phylogenetic hypotheses. Once a hypothesis is constructed on cladistic grounds (i.e. in the absence of adaptive theorizing) it can be used to test alternative adaptive scenarios.

Evo Devo shares the explanatory goal of evolutionary morphology, as I understand it. But Evo Devo cannot play the central role in phylogenetic reconstruction that embryology played in the 1880s. Like adaptive scenarios, scenarios of ontogenetic change now depend on independently verified phylogenies for their legitimacy. Evolutionary morphology had ignored function because it was committed to the study of form. Modern cladistic phylogeny is neutral between form (Evo Devo) and function (adaptationism), and is a necessary contributor to testable hypotheses of either type. One additional problem bars Evo Devo from the mainstream of phylogeny, at least at the present. The molecular study of development is so labor intensive that only a few model organisms are well understood developmentally. It is no wonder that nineteenth century embryology could not bear the weight of phylogenetic reconstruction.

One moral to be taken from this case, as from the history of science generally, is the transience of methodological pronouncements. Scientific hypotheses that appear irresolvable, incoherent, or even “unfalsifiable in principle” at one time can turn out to be perfectly reasonable under new circumstances. Hypotheses about ancestral ontogenies would have been called unfalsifiable by experimentalists around 1900, if that Popperian curse had been available to them at the time. The same epithet was applied by Rosen et al. to adaptation scenarios in 1982. These scenarios are now seen to be falsified by cladistic and paleontological evidence. Surely if one is able to *falsify* an adaptive scenario, one should not have called it *unfalsifiable* in the first place! Nevertheless, scientists and historians work within their own scientific and historical contexts. We cannot know what new kinds of data will be avail-

able in the future, and we must base our methodological pronouncements (overstated as they may turn out to be) on our present understandings. The generative principle *was* a foolish way to conduct phylogeny in the context of the Synthesis, and betting on the availability of new adaptive data was a good gamble. In the 1990s, new adaptive data did not seem all that promising, but vast new sources of molecular and other non-adaptive data was beckoning. Adaptive scenarios are treated as scornfully today as reconstructions based on ontogeny were fifty years ago.

Some historians may be able to abstract themselves from their own era, avoid the sin of whiggish history, and write as if scientific truths (as they understand them) are irrelevant to their narrative of historical events. Neither Bowler nor I are among this saintly brood. Bowler's disapproval of nineteenth century typology reflects his confidence in the adaptationism of modern neoDarwinism. But I am hardly qualified to throw stones. My sympathy for nineteenth century typology reflects my interest in the essentially similar enterprise of modern Evo Devo.⁵

Notes

¹ Besides Coleman, the metaphysical concept of idealism/typology is expressed in Mayr 1964, Ghiselin 1969, Hull 1973, and Ruse 1979. Ruse 1979 and Hull 1983 recognize important differences between idealism and natural theological creationism, but still see idealism as a barrier to evolutionary thinking.

² Besides Russell and Ospovat, the explanatory concept of idealism/typology is expressed in Nyhart 1996, Di Gregorio 1995, Rupke 1994, Lyons 1999, and Amundson 1998.

³ For example, idealists are said not to have rejected evolution completely, but were only able to incorporate "what they could understand of it" into their accounts, and found it "difficult to throw off the legacy of the old typological viewpoint (Bowler 1996: 55; 58)." Historical figures whose work is similar to modern adaptationism are often described as taking a "more realistic" approach (*ibid.*, p. 101; 258).

⁴ I owe this point to Kevin Padian, in personal communication.

⁵ This paper has been greatly improved by the comments of Rasmus Winther.

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