



One Very Long Argument

DOUGLAS H. ERWIN

Department of Paleobiology, MRC-121

National Museum of Natural History

Smithsonian Institution

Washington, DC 20560

USA

E-mail: Erwin.doug@nmnh.si.edu

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The distribution of organisms in morphologic space is clumpy. Cats are like felids, dogs are like canids and snails are (mostly) like gastropods. But cats are not like dogs and snails are not like clams. This clumpy distribution of morphology has long posed one of the greatest challenges to evolutionary biologists. Does it represent the extinction and disappearance of a once-continuous distribution of morphologies, clades perched on the summits of persistent selective peaks *ala* Sewell Wright, or a primary signature of the evolutionary processes? And if the latter, what processes are responsible for generating it? Although often couched in discussions of the origin of higher taxa, such taxa are but proxies for this clumpy distribution, and ultimately the latter is the critical issue for macroevolution and for Stephen Jay Gould's *opus*. Underneath all the controversies over whether species constitute individuals, whether speciation serves to divide intra-specific adaptation driven by natural selection from a set of inter- and supra-specific evolutionary processes, and over the impact of catastrophic mass extinctions on evolutionary trends, the fundamental issue is simply one of clumpiness (or, if you prefer, the inhomogeneous distribution of morphologies).

Iurii Filipchenko, a Russian geneticist and the mentor of Theodosius Dobzhansky, introduced the term macroevolution in 1927 because he believed that the origin of the characters associated with higher taxa (those beyond the species level) required a different process of evolution. Filipchenko believed macroevolution was driven by cytoplasmic inheritance, but his general argument was consistent with other saltationists and macro-mutationists of the time, including the paleontologist Henry Fairfield Osborne and the geneticist Richard Goldschmidt. These evolutionary biologists shared the

view that the appearance of higher taxa necessarily involved novel evolutionary processes, although they differed over their nature. Dobzhansky introduced the term macroevolution to English-speaking evolutionary biologists in (1937) but rejected his mentor's distinction between macro- and micro-evolution. Osborne's orthogenesis had become sufficiently pervasive that Dobzhansky evidently felt compelled, at the dawn of the Modern Synthesis, to reject both orthogenesis and saltational views. Dobzhansky wrote:

. . . there is no way toward an understanding of the mechanisms of macroevolution, which require time on a geological scale, other than through a full comprehension of the microevolutionary processes. For this reason we are compelled at the present level of knowledge reluctantly to put a sign of equality between the mechanisms of macro-and micro-evolution. (Dobzhansky 1937: 12)

Gould's final testament is an argument that our level of understanding of evolution has progressed to the point where Dobzhansky's equality can be rejected in favor of a much-expanded view of evolution. Toward the end of *Structure*, Gould writes:

I am quite content to allow that no fundamental laws of nature, and no entirely novel causes or phenomena, make their first appearance in larger slices of time. But at these broader scales and intervals, the known principles of genetics and the documented mechanisms of selection, may operate by distinct and emergent rules that, as a consequence of time's tiering, cannot be fully predicted from the operation of the same kinds of causes at lower levels. (p. 1327)

Throughout *Structure* Gould rejects calls for new evolutionary processes other than a hierarchical expansion of selection to encompass multiple levels both above and below the canonical individuals of traditional Darwinism, and greater incorporation of the structuralist perspectives on the constraints that limit the range of variability available to selection, at whatever hierarchical level. Gould's views on macroevolution can perhaps best be appreciated by considering the variety of potential means by which macroevolution could be distinct from microevolution (leaving aside the issue of whether they really are distinct, an issue that Gould considers at great length).

New evolutionary laws

Filepchenko and Goldschmidt each represent the view that macroevolution proceeds via distinct and unique evolutionary mechanisms. While not denying the efficacy of natural selection for adaptation within species, and

even for the creation of new species, such views invoke different mechanisms to establish new clades. This position requires the expansion of evolutionary processes beyond mutation, natural selection and random drift, with different processes for intra- and inter-specific evolutionary change. In the first half of *Structure*, which emphasizes the historical development of macroevolutionary ideas, Gould considers the views of Goldschmidt, Osborne and other lesser known evolutionists in great detail. As noted above, Gould himself categorically any argument that macroevolution requires an expansion of process, albeit with a rather interesting discussion of his 1980 *Paleobiology* paper, which has been widely viewed as an argument for a neo-Goldschmitean renaissance. Relatively few recent evolutionary biologists have advanced this particular view of macroevolution (but see Bateman and DiMichele 2002, for an exception).

The principle difficulty with this possibility has always been that the process is almost always inferred from pattern, rather than directly observed. Defenders reasonably argue that since the frequency of such events is likely to be low, patterns that do not appear to be sufficiently explained by known processes must suffice for the recognition of new processes. Yet it is rare that an evolutionary (historical) pattern requires a unique process. Species are not particle detectors, however much some theorists may wish this were true.

Structuralism

As a saltationist, Francis Galton arguably belongs in the preceding section of this taxonomy, but Gould begins his discussion of post-Darwinian saltationists with Galton because Galton makes the link between saltationists and structuralists, and moreover makes it in a way that clearly appeals to Gould's love of iconography. Galton used a polyhedron as a metaphor for the origin of novelty, arguing that a polyhedron is most stable when resting on a long edge. It is reasonably resistant to perturbation, but if forced hard enough it will fall to the next edge, normally a short one. Such short edges are stable, but far less so than long edges, and the polyhedron can be further deflected with little effort, until another long edge is reached. Galton argued the genome operated in a similar fashion: resistant to perturbation, but when disturbed, falling in preferred directions. These sudden shifts represent Galton's saltations, while the movement in directions established by the internal structure of the polyhedron incorporates a structuralist, or formalist perspective. If Galton's metaphor applies to evolution at multiple levels (i.e. if the polyhedron is fractal), it can also be seen as an explanation for the clumpy

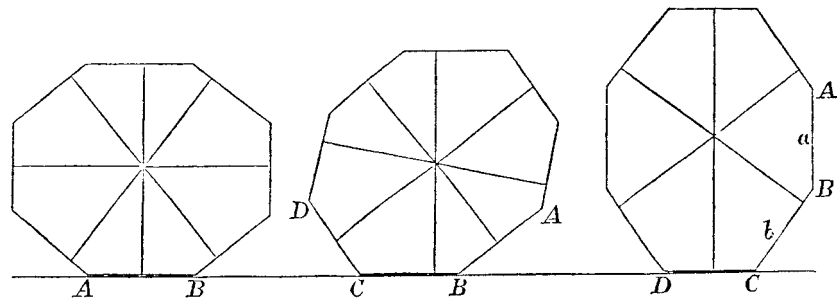


Figure 1. Galton's own illustration of his model of the polyhedron. Note how the themes of saltation, or facet flipping, and constraint in strictly limited pathways available for change arise from a similar geometric basis in this mode of depiction.

distribution of morphologies, with the long edges defining the larger clumps, and the short edges the variations on a theme.

Structuralism appeals to internal forces such as geometric constraints as a source of constraint and directed variability to produce novel designs. This view traces its heritage to D'Arcy Thompson, long a hero of Gould's, but encompasses Osborne's orthogenesis and more recent reincarnations in the work of Stuart Kauffman and Brian Goodwin. From this approach, structural rules, inherent in the biology of organisms, generate the diversity of phenotypes we observe, not functional responses by organisms to their biological and physical environment. Inherent in the structural view is the idea that the properties of organisms "push back" in Gould's words (p. 351) against the effects of selection, limiting, channeling and modifying the influence of the environment.

Both saltationism and structuralism, whether in the positive, creative sense or the negative, constraining sense produce variation that is non-isotropic and thus, in Gould's view, pose significant and related challenges to traditional Darwinism. By constraining the range of biologic variation presented to selection they may significantly impact the course of evolution. Gould readily admits in the discussion in Chapter 5 that Galton represents a fairly unique example of a combination of saltationist and structuralist perspectives, since structuralists normally do not emphasize saltationism, and many of the early saltationists lacked a structuralist perspective.

I share Gould's interest in structuralism, for it provides a fascinatingly different view of the evolutionary process. If variability is truly not isotropic (the essential claim of structuralism, as well as other views on constraint) then the range of opportunities presented to natural selection are far less than at least some Darwinians suppose. Gould argues that a properly expansive view of evolution requires incorporation of both the negative, or inhibitory,

aspects of constraint as well as the positive aspects in the sense of channeling evolutionary responses along preferred paths (preferred by allometric or developmental ease rather than in some vitalistic sense).

Gould's examination of this issue proceeds along two different paths, the first more traditional than the second. In Chapter 10, his discussion of historical constraints considers in turn each element of Dolf Seilacher's now standard ternary diagram of functional/historical/structural constraints. While acknowledging the significance of constraints that limit possibilities, Gould spends more time stressing the potential importance of positive constraints that reflect patterns and directions not built by natural selection. The concept of spandrels of course plays a prominent role as a source of constraint, but Gould develops a veritable menagerie of what he terms the 'exaptive pool'. Spandrels (architectural consequences), we learn, are but one kind of milton (available but currently unused things), a class also encompassing manumissions (miltons arising through current unemployment of a feature) and insinuations (miltons arriving through random drift). Inherent potentials become franklins and in the end all I could think of was Benjamin Franklin and John Milton tilting at windmills.

Although the form may be more Rocco than needed, Gould develops a credible and, at least in some circles, needed argument that the success of species and clade-level selection must in large part reflect the possibilities provided by structural and historical constraints (whether miltons or franklins) captured in his exaptive pool during the formation of species. Since this exaptive pool is constructed of elements essentially unseen by natural selection, their later use in the establishment of evolutionary trends suggests another way in which macroevolutionary pattern is acting if not in opposition to natural selection, at least orthogonal to it. The difficulty, here and throughout *Structure*, is that we must largely rely on Gould's arguments for theoretical plausibility and sufficient relative frequency. Rarely is a mass of data presented to justify and support Gould's conclusions.

The remarkable discovery over the past decade of the pervasive nature of deep homologies among developmental control genes provides one of the rare exceptions to the general dearth of data, and provides the second, and far more compelling, thread comes of Gould's discussion of constraint. The deep homologies among developmental elements of the bilaterian metazoa provide a new view of the Cambrian radiation. Gould plows little new ground here, but provides a rich discussion of the data to support his argument that the preservation of the role and function of the multiple hox genes, *Pax6* in eye development and the many other examples should not be possible if natural selection as pervasive as claimed. The preservation of these elements can only be explained if natural selection operates under a great range of both positive

and negative constraints. Gould observes: “this recognition of internal channeling as the root cause of parallelism – the principal basis for ascribing evolutionary change, and not only limitations, to historical constraint – lies at the heart of evo-devo’s theoretical novelty and importance to the Darwinian worldview” (p. 1157).

The Cambrian radiation thus becomes one of the premier examples of Gould’s theory of macroevolution, as it must, placing developmental constraints in a central role in one of the greatest evolutionary acts in the history of life:

... we may infer that bilaterian diversity unfolded along the channels of developmental patterns held in common from the beginning of the holophyletic clade. Bilaterian diversity, in other words, represents an extensive set of modifications and tinkering upon a basic pattern set by history at the outset, and then adumbrated in one biologically brief episode to establish all fundamental building plans . . . do these historical invariants represent a set of mechanically limited and excellent, perhaps even optimal, designs that natural selection would have established in much the same way at any time . . .? Or do they represent just one possible solution among numerous entirely plausible alternatives . . . each yielding a subsequent history of life entirely different from the outcome actually experienced on earth? (p. 1159)

This is much the same argument that Gould articulated in 1989 in *Wonderful Life*, his chronicle of the incredible soft-bodied fossils of the Burgess Shale and their meaning for understanding the history of life, but with the necessarily novel (since the data simply did not exist in 1989) support from developmental biology. I must add that I can only go part way in agreeing with Gould, for Eric Davidson and I have recently argued that these deep homologies represent a shared developmental toolkit to produce vectoral patterning and other elements rather than the conservation of morphological features (Erwin and Davidson 2002). In contrast to the views of some developmental biologists, our argument suggests the last common bilaterian was a relatively simple organism. I would agree with Gould that all the potential architectural diversity was encapsulated within this urbilaterian over 600 million years ago, but to me the structuralist argument that Gould makes, that these deep homologies channeled the patterns of bilaterian evolution, is far less obvious. The diversity of bilaterian morphologies is remarkable, even humbling. Although I agree with Gould that the morphological variety captured within the Middle Cambrian Burgess Shale is startling, (and surpassed by the Early Cambrian Chengjiang biota from Yunnan Province, China), there have been a few architectural innovations since the Cambrian. Gould’s structuralist argument ultimately remains unconvincing.

If macroevolution is a theory unique and different from microevolution it must contribute something to our view of evolution beyond a new view of speciation and, perhaps, an explanation for trends in the history of life. Macroevolution must also address those critical events in earth history that make that record so much richer than neontologists could ever have imagined. It is only in the final two chapters of the book, here in Chapter 11 addressing developmental evolution and the Cambrian radiation, then with mass extinctions in Chapter 12, that Gould really confronts these issues. In many ways much of the book is far more a ‘bottom-up’ view of macroevolution than one might want (or than we might expect from someone like James Valentine) but this is in keeping with the tenor of Gould’s career.

While the extreme structuralist views do pose quite a challenge to the Richard Dawkins of the world, in reading *Structure* I could not help but feel that Gould was perhaps being too much the Knight of the Woeful Countenance. Most modern evolutionary biologists would, I think, concede that variation is far from isotropic. The evidence from evo-devo establishes that historical and developmental constraints are indeed pervasive. These discoveries have provided a wealth of unanticipated mechanistic detail, but I do not think that even the most ardent Darwinist really expected dugongs to turn into dingos. This is far less than demanded by the structuralists, of course, but Gould also seems to expect more from this than the data can yet support.

Hierarchy

Punctuated equilibrium, the proposal that speciation patterns are divorced from much intra-specific adaptive evolution because of rapid divergence of a sub-population to form a new species, serves as the basis for Gould’s argument, the intellectual guts of the book. The hierarchical expansion of evolutionary theory with selection occurring at a number of discrete levels requires evolutionary individuals at each level. Cell lineages, individual organisms and species all become individuals, with macroevolutionary trends produced by species selection and clade-level sorting. Steve Stanley was the first to recognize the larger implications of Niles Eldredge and Gould’s original punctuated equilibrium work, but this hierarchical view has since been championed by Gould, Niles Eldredge, Elisabeth Vrba and many others. Gould’s longest chapter (at 279 pages!) provides both a detailed examination of the evidence for and against punctuated equilibrium as well as Gould’s personal views of the debate. Indeed, autobiographical elements are woven throughout this volume as Gould describes his own struggles with the issues raised, responds to many critics, and indulges in ‘extending and revising’ his previous remarks (as we say in Washington).

For over two decades much of the controversy over this hierarchical expansion has revolved around the issue of how to construct a theory of higher-level selection in which the focal level truly is not decomposable to natural selection at the individual level. Cell lineages, species or clades must possess a suite of appropriate traits that impart fitness to that level which are not reducible to fitness at another level (particularly to that of individuals within species). Gould canvases the various means to produce such traits and concludes, correctly in my view, that differential proliferation remains the most plausible (plausibility, of course, is not the same as effective). But are such traits results of aggregate properties of individual organisms within a species, or emergent at the focal level? Gould argues cogently for emergent properties, but this divisive issue is unlikely to be resolved by theoretical arguments.

Gould takes a surprisingly catholic view of macroevolution, acknowledging later that species selection may not be the only potential macroevolutionary mode, raising the possibility that biases in the production of new species along a preferential vector may be sufficient to establish trends in the absence of species selection. To be truly macroevolutionary such directional speciation must be based on the same emergent, species-level traits required under the definition of species selection. Gould raises this issue largely as a theoretical possibility, since there is little empirical support for such a process.

The real significance of the hierarchical view comes through in Gould's discussion of constraints in Chapter 11, where he argues that the upward cascading effects from spandrels (and miltons) provide species a suite of emergent, exaptive effects. This evolutionary flexibility is, in Gould's view, among the most important generators of evolutionary novelty. This discussion culminates in my nomination for the most truly Gouldian phrase in the volume:

The species, in this view, acts as a shelter or arbor, that holds itself fast by active utilization of the properties that build its well-defined individuality. By fostering internal change, and thereby gaining a large supply of upwardly cascading exaptive effects, species use the features of all contained lower-level individuals through the manifestation of their effects on the shelter itself. The species, through its own distinctive features of individuality, and requiring neither indulgence nor apologia from human understanding, will continue to operate as a powerful agent in Darwin's world, whether or not we parochial organisms, limited by our visceral feelings and traditions of language, choose to expand our view and recognize the sources of evolutionary potency at distant scales of nature's hierarchy. (p. 1293)

That mass extinctions often serve to remove clades without respect to their prior adaptive status seems incontrovertible. How else to explain the virtual disappearance of articulate brachiopods in the end-Permian event, the boom and bust pattern of ammonites through the Mesozoic, or the disappearance of rudist bivalves in the late Cretaceous? This forms the third tier of Gould's hierarchical view of evolution, albeit without the involvement of another level of selection. Instead there is an evolutionary singularity imposed by the mass extinction that renders, at least temporarily, irrelevant trends and patterns established before the mass extinction.

I have little qualm with Gould's analysis of the evolutionary significance of mass extinctions, but the ecological poverty of his analysis is particularly evident in this discussion. Gould has long had a particular aversion to the inclusion of G. Evelyn Hutchinson's ecological play within his evolutionary theater. Yet all macroevolutionary events, mass extinctions chief among them, play themselves out through macroecological processes. Changing biogeographic patterns, competition between species or clades, and the acquisition of resources and space matter for macroevolution as much as microevolution, albeit at a different spatial and temporal scale (hence macroecology). Without inclusion of these processes we have little likelihood of understanding either mass extinctions or the biotic rebounds that follow them, and their exclusion ultimately renders *Structure* fascinating but incomplete as a new theory of macroevolution.

Evolutionary uniformitarianism

New laws, constraints and multiple levels of selection have been the most widely discussed elements of a macroevolutionary theory broad enough to encompass the patterns documented from the fossil record. There is, however, an additional possibility. I found perhaps the most intriguing aspect of *Structure* lay in the virtual absence of any discussion of this fourth explanation for the clumpy distribution of morphologies: that evolutionary processes are not time-invariant, but have themselves evolved over time. There are two distinct possibilities here. Were macroevolutionary events more common early in the history of clades (one possible explanation for the clumpy distribution of morphologies)? If so, then there may have been a higher likelihood that large morphologic transitions could occur in deep time, or that such innovations were successful if they occur. These two options are very different. The first suggests, in effect, that macroevolution was driven by a time-inhomogeneous mutation pressure; the second option is that such macroevolutionary changes are homogeneous (and equally probable today) but that such changes are

simply less likely to survive and found new clades. Either would produce a non-uniformitarian pattern of macroevolution.

This has always been the least discussed of any of the four alternatives, and Gould only touches on the issue of evolutionary uniformitarianism in passing, failing to recognize it as a distinct option. (I am not suggesting the Tome should have been even longer, only that somewhere in 1343 pages he could have found a place to mention the possibility). I could find only a few sections that could be interpreted as addressing the issue, and only two direct acknowledgements of the issue. In the first, Gould writes of punctuated equilibrium:

... punctuated equilibrium treats time homogeneously, and species as independent agents; the theory therefore includes no inherent, or logically enjoined, predictions about the nature of temporal clumping in the ecological interactions among species. (p. 916)

Leo Buss's suggestion that multicellular individuals arose as a means of mediating conflicts between individual-level selection and selection among cell lineages is the second area of evolutionary uniformitarianism addressed by Gould. Gould acknowledges that selection at the level of cell lineages now appears to be effectively suppressed, at least within the best understood multicellular lineages, but argues that this does not mean that selection at this hierarchical level was not significant at an earlier point in earth history. Neither Buss nor Gould address the broader implications of the cell lineage argument for macroevolution. I can only conclude that he viewed this evolutionary suppression of a hierarchical level as a unique event, and not a signature of how evolution operates.

Several lines of evidence suggest that reconsideration of evolutionary uniformitarianism is probably warranted. Lateral (or horizontal) gene transfer turns out to be a ubiquitous element of evolution, particularly among bacteria and archaea (Gogarten et al. 2002; Ochman et al. 2000). Genetic homogenization has been so extensive that scientists attempting to reconstruct the early history of life are actively debating whether the basal part of the tree can even be recovered (e.g. Woese 2000). Although lateral gene transfer continues today, some interpretations of the data suggest it was more extensive early in earth history, and perhaps had more far-reaching impact. How has the rate of successful primary symbiosis changed over time? Do organisms preserve other examples of such frozen historical changes? The early origin of metazoan architectures (both morphological and developmental) and a similar pattern among both algae and vascular plants at least suggest a non-uniformitarian macroevolutionary pattern.

I think the reason Gould and most other evolutionary theorists fail to confront this possibility is not the lack of evidence, but in part because it is

politically the least tractable solution. Many biologists have been incensed by the punctuated equilibrium model and other aspects of macroevolution simply because it suggests that the realm of evolutionary processes is larger than can be readily examined in the narrow slice of time we have for experimental manipulation. Imagine then the rumpus that would erupt from the suggestion that that realm is not only larger, but changes over time. In fairness to Gould I must also record that his view of structural constraints and their influence on evolutionary trends is only coherent within a uniformitarian system.

This criticism of Gould is not to suggest that he does not consider history, for contingency and historical constraint form critical elements of his view of evolution. But these historical events influence the course of evolution with a clade and do not represent a temporal vector to the operation of evolutionary change.

In the end Gould concludes that historical constraints must be the primary driver for clumped occupation of morphospace:

I argued that the markedly inhomogeneous occupation of morphospace – surely one of the cardinal, most theoretically important and most viscerally fascinating aspects of life’s history on earth – must be explained largely by the limits and channels of historical constraint, and not by the traditional mapping of organisms upon the clumped and nonrandom distribution of adaptive peaks in our current ecological landscapes. In other words, the inhomogeneous occupation of morphospace largely records the influence of structural rules and regularities emerging “from the inside” of inherited genetic and developmental systems . . . and does not only . . . reflect the action of functional principles realized by the mechanism of natural selection. (p. 1174)

The Structure of Evolutionary Theory was intended by Gould as the foundational document for a new and expanded view of evolution, much as Ernst Mayr’s 1963 volume *Animal Species and Evolution* served as the consensus view of the Modern Synthesis for several decades. In a sense Gould wrote this as a combination of Mayr 1963 and Mayr’s later, and equally magisterial *The Growth of Biological Thought* (1982) (brevity evidently being in short supply in Cambridge). Gould’s own magisterial overview of evolutionary thought in the first half of *Structure* is indeed a seminal contribution. He brought deep reading and great insight to writing this volume and they shine through on the historical sections, much as they did in his 1977 *Ontogeny and Phylogeny*. But as in that volume, the later sections of *Structure* must, I think, be counted as less successful. Gould is a forceful advocate for the importance of a hierarchical view of evolution, but I remain unconvinced that this expansion of evolutionary thought, however useful and necessary, finally resolves the issue of the clumpy distribution of morphologies. If, as

many evolutionary biologists seem increasingly to believe, there is a new and expanded evolutionary theory waiting to appear it may require an even broader canvas than employed by Gould.

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