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C. R. Palevol 2 (2003) 335–352

COMPTES RENDUS PALEVOL

Evolution

Evolution's past and future: an introduction and partial précis to Stephen Jay Gould's *The Structure of Evolutionary Theory*

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Received 26 June 2003; accepted 23 September 2003

Written on invitation of the Editorial Board

Abstract

In *The Structure of Evolutionary Theory*, his last and largest book on evolution, Stephen Jay Gould conceives of the structure of evolutionary theory since Darwin as comprising three major propositions. First, natural selection is the most important direction-giving force in evolution. Second, it operates at the level of the individual organism. Third, selection can be extrapolated smoothly from its actions on individuals in living species throughout geologic time, to produce the gradual divergence of species and adaptations that characterizes the history of life. Challenges to each of these major propositions, according to Gould, can be of three kinds of severity. The most severe challenges, if true, would nullify one of the major propositions entirely, thus destroying the integration of the theory (and perhaps the logic and support of its other propositions). Other, less severe challenges would revise, modify, and expand the content and scope of one or another of the propositions, but not destroy any of them or the theory *in toto*. Still other, even less severe challenges add to what is known and extend the scope and possibilities of the theory, but do not call for a revision in its fundamental structure. Gould acknowledges that the theory has withstood all presumptive challenges that would destroy it, and has accommodated those that simply extend and add to it. His principal concern is with those challenges that would revise the theory substantially: for example, if processes other than natural selection were of great importance in evolution; if selection acted in important ways at the level of species and clades, and (or) at the level of the genes, alleles, and chromosomes; and if the extrapolation of what is known from living populations could not by itself explain many patterns of large-scale evolution seen in the fossil record. He thinks that, both through the history of evolution since Darwin and in the present day, challenges that substantially revise these basic propositions are valid, and that the theory needs to integrate them in order to retain the explanatory power that it has had for many decades. ***To cite this article: K. Padian, C. R. Palevol 2 (2003).***

Résumé

Passé et futur de l'évolution: une introduction en manière de résumé à l'ouvrage de Stephen Jay Gould. *The structure of Evolutionary Theory*. Dans son dernier et plus grand ouvrage *The Structure of Evolutionary Theory*, Stephen Jay

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doi:10.1016/j.crpv.2003.09.024

Gould conçoit la structure de la théorie évolutionniste depuis Darwin comme comprenant trois propositions majeures. D'abord, la sélection naturelle est la force la plus importante conférant une direction à l'évolution. Ensuite, elle opère au niveau des organismes individuels. Enfin, la sélection peut être extrapolée progressivement, depuis son action sur les individus au sein des espèces vivantes, au travers des temps géologiques, jusqu'à produire la divergence graduelle entre espèces et les adaptations qui caractérisent l'histoire de la vie. Les défis vis-à-vis de ces trois propositions peuvent être, selon Gould, de trois ordres de sévérité. Les défis les plus sévères, s'ils étaient vérifiés, pourraient anéantir complètement l'une des trois propositions majeures, détruisant ainsi l'intégration de la théorie (et peut-être aussi la logique et l'assise de ses autres propositions). D'autres défis, moins sévères, pourraient conduire à réviser, modifier ou étendre le contenu et la portée de l'une ou l'autre des propositions majeures, mais sans en détruire, ni aucune, ni la théorie dans sa totalité. Enfin, d'autres défis, encore moins sévères, pourraient ajouter à ce qui est connu et étendre la portée, la pertinence et les possibilités de la théorie, mais n'appellent pas de révision de sa structure fondamentale. Gould reconnaît que la théorie a surmonté tous les défis présomptifs qui auraient pu la détruire et s'est accommodée de tous ceux qui n'ont fait que l'amplifier et l'enrichir. Son intérêt se porte principalement sur certains défis, qui pourraient entraîner une révision substantielle de la théorie : par exemple, si d'autres processus que la sélection naturelle avaient une grande importance dans l'évolution, si la sélection agissait de façon importante au niveau des espèces et des clades, et (ou) si elle était active au niveau des gènes, des allèles ou des chromosomes, ou encore si l'extrapolation de ce que l'on connaît au niveau des populations vivantes ne pouvait expliquer de nombreux patrons évolutifs observés dans l'évolution à grande échelle et révélés par la documentation paléontologique. Il pense qu'au travers de l'histoire de l'évolutionnisme depuis Darwin, tout comme dans la recherche d'aujourd'hui, se révèlent des défis valides, qui contraignent à réviser substantiellement les trois propositions majeures, et que la théorie se doit de les intégrer, de façon à conserver la puissance explicative qu'elle a eu pendant de nombreuses décennies. ***Pour citer cet article: K. Padian, C. R. Palevol 2 (2003).***

Keywords: constraints; Darwinism; epistemology; evolutionary theory; Gould; heterochronies; hierarchy; History of Sciences; synthetic theory

Mots clés : contraintes ; darwinisme ; épistémologie ; Gould ; hétérochronies ; hiérarchies ; Histoire des sciences ; théorie évolutive ; théorie synthétique

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Version française abrégée

Stephen Jay Gould est mort en avril 2002 juste au moment où son livre testament était à l'impression. Il n'a pas vécu assez pour voir l'accueil fait à l'ouvrage, sinon les tout premiers comptes rendus, ni discuter et défendre son abondant contenu avec ses collègues. C'est bien dommage car il avait travaillé par intermitence à ce livre pendant près des trente dernières années. Bien qu'il n'ait pas été envisagé comme devant être son dernier ouvrage, ce livre était destiné à offrir un argumentaire intégré, un état complet des copieuses considérations et analyses de Gould concernant l'histoire et la structure des concepts majeurs de la théorie évolutive.

Le destin d'un livre orphelin est de moins attirer l'attention que quand l'auteur peut donner des interviews ou des conférences à son sujet. Sans doute tous ses lecteurs auraient-ils souhaité pouvoir entendre Gould répondre aux questions, idées et critiques soulevées par ses collègues comme par les journalistes. Grâce à la longue popularité de Gould auprès de son public, on peut penser que le livre se vendra bien, mais sera-t-il lu? Du fait de sa taille imposante, cet ouvrage pourrait bénéficier d'une sorte de résumé ou de précis, ne serait-ce qu'à titre de main secourable tendue au lecteur potentiel. De plus, comme il ne sera pas traduit en d'autres langues ni assimilé par le public non anglophone avant un certain temps, ce lectorat pourrait bénéficier d'une brève introduction.

Il est impossible de résumer en quelques pages un ouvrage qui en compte plus de 1400 – en fait plusieurs livres en un seul volume. Je ne prétends pas le faire ici. Tout résumé reflète nécessairement aussi les points de vue et centres d'intérêts subjectifs de son auteur et doit être apprécié en conséquence. Ce « prends garde lecteur ! » étant entendu, je souhaiterais offrir ici ce que j'espère être un résumé des thèmes majeurs du livre (ou de certains d'entre eux!) accompagné de commentaires choisis. Stephen Gould a présenté son propre résumé de l'ouvrage sous la forme du premier chapitre, mais il met lui même en garde sur le fait que cela ne peut contenir tout l'ensemble. Aussi conclut-il par une exhortation à lire le livre – une tâche intimidante mais qui en vaut la peine.

The Structure of Evolutionary Theory [10] est divisé en trois grandes sections. La première (environ 90 pages) est un résumé de l'ouvrage entier. (Pour les gens pressés ou ceux dont l'intérêt n'est que superficiel, c'est la partie à lire ; il est alors facile de se plonger ensuite dans diverses parties du livre couvrant en détail tel ou tel sujet particulier). La seconde partie "Histoire de la logique et du débat Darwinien" (à peu près 500 pages) reprend de la première partie la structure de base de la théorie évolutive et en développe les aspects les plus centraux depuis les prédécesseurs de Darwin jusqu'à pratiquement la fin du XX^{e} siècle. La troisième partie, « Vers une théorie évolutive révisée et étendue » (à peu près 750 pages), utilise ce qui a déjà été présenté au lecteur pour suggérer une façon nouvelle et synthétique d'appréhender la théorie évolutive dans sa totalité. Gould sauve de l'oubli et renouvelle certaines idées anciennes traditionellement négligées, révise et étend quelques idées centrales de l'évolutionnisme et consigne l'intégration nouvelle au champ évolutionniste de domaines qui en avaient été longtemps séparés, ou qui ne s'étaient pas développés en phase avec lui. Cela ne surprendra aucun de ceux déjà familiers de ses conceptions fondamentales sur la théorie de l'évolution, de dire qu'il met l'accent sur la théorie Darwinienne conventionnelle (telle qu'elle fut historiquement formulée jusque dans les années 1970). De plus, qu'il perçoit principalement l'évolution comme un processus hiérarchique, avec à la fois une intégration et une indépendance considérable entre les différents niveaux. Ensuite qu'il y a beaucoup plus à tirer de la documentation paléontologique que ne l'ont attendu bien des biologistes évolutionnistes travaillant au niveau des populations et des gènes. Enfin que ceux qui ne consultent pas les sources primaires sont condamnés à rester des ignorants et à redécouvrir ce que l'on savait déjà.

Concrètement, Gould conçoit la structure de la théorie de l'évolution depuis Darwin comme comprenant trois propositions fondamentales. La première est que la sélection naturelle est la force la plus importante donnant une direction dans l'évolution. La seconde est qu'elle opère au niveau de l'organisme individuel. La troisième est que la sélection peut être extrapolée sans hiatus depuis son action sur les individus dans les espèces actuelles, au travers des temps géologiques, jusqu'à produire la divergence graduelle entre espèces et les adaptations qui caractérisent l'histoire de la vie.

Les défis à ces trois propositions majeures peuvent être, selon Gould, de trois niveaux de sévérité. Les défis les plus sévères, s'ils se vérifiaient, annuleraient complètement l'une des propositions fondamentales, détruisant ainsi le pouvoir d'intégration de la théorie (et peut être aussi la logique et le support de ses autres propositions). D'autres défis, moins sévères, pourraient réviser, modifier, voire étendre le contenu et la portée de l'une ou l'autre des propositions fondamentales, mais sans en détruire aucune ou la théorie dans sa totalité. D'autres défis, enfin, encore moins sévères, ajoutent à ce qui est connu et étendent la portée et les possibilités de la théorie, mais ne nécessitent pas de révision de sa structure fondamentale.

Gould reconnaît que la théorie a résisté à tous les défis présomptifs qui auraient pu la détruire et s'est accommodée de tous ceux qui ont simplement permis son expansion en y ajoutant. Son intérêt principal concerne ces défis qui pourraient entraîner une révision substantielle de la théorie: ainsi par exemple, si des mécanismes autres que la sélection naturelle étaient d'une grande importance dans l'évolution, ou si la sélection agissait de façon importante au niveau des espèces ou des clades, et (ou) aussi au niveau des gènes, des allèles et des chromosomes. Ou encore si l'extrapolation de ce qui est connu au niveau des populations ne pouvait pas expliquer des canevas d'évolution à grande échelle observés dans la documentation paléontologique. Il pense que, aussi bien du point de vue de l'histoire de la théorie depuis Darwin, que de l'état actuel des connaissances, divers défis qui imposent une révision substantielle de la théorie sont valides, et que la théorie doit donc en intégrer les conséquences, de manière à conserver la puissance explicative qu'elle a eue pendant de nombreuses décennies.

1. Introduction

Stephen Jay Gould died in April 2002, just as his valedictory tome, *The Structure of Evolutionary Theory*, was being printed [10]. He did not live to know of any but its earliest reviews, nor to discuss and defend its vast contents. This is a great shame, because he worked on the book intermittently for the better part of three decades. Though it was not intended to be his last work, it was meant to be an integrated statement, a full account of his copious considerations and analyses of the history and structure of the major concepts of evolutionary theory.

An authorless book, unfortunately, is bound to receive less attention than one whose author can give interviews and lectures. Probably anyone who reads it will wish that he could hear Steve Gould respond to questions, ideas, and criticisms from colleagues and journalists. Steve's long-standing popularity with his public will ensure that many copies of the book will be bought. But will they be read? Its sheer size calls for some kind of précis, if for no other reason than to give the potential reader a handhold. And, because it will not be translated into other languages for some time, non-Anglophonic readers may benefit from a brief introduction.

It is impossible to summarize 1400 pages – in fact, several books in a single volume – in only a few pages. I make no pretense to do so here. And any précis will necessarily reflect a reviewer's subjective background and interests, and must be read accordingly. With this *caveat lector*, I would like to provide what I hope is a summary of (only some of!) the major points of the book, along with some selected commentary. Steve's own summary is presented in his first chapter; but as he cautions, this cannot encapsulate the full contents; he concludes with the exhortation to "read the book!" – a daunting task, but worth the effort.

The Structure of Evolutionary Theory is divided into three major sections. The first (about 90 pages) is a summary of the entire work. (For those with only a casual interest, this is the part to read; it is easy to dip into more extensive treatments of particular topics later in the book.) The second section, "The history of Darwinian logic and debate" (about 500 pages), takes the basic structure of evolutionary theory from the first section, and develops the most central parts of the theory, from Darwin's antecedents to nearly the end of the 20th Century. It follows both historical and some recent challenges to the overall theory and its parts. The third section, "Towards a revised and expanded evolutionary theory" (about 750 pages), uses what the reader has already been presented to suggest a new and synthetic way of thinking about the whole of evolutionary theory. Gould rescues and renovates some old ideas that have been traditionally overlooked, revises and expands some central ideas of evolution, and reports new integrations of fields that have long been separated or out of synchronization. It will surprise no one familiar with his basic views on evolutionary theory to say that his emphasis is on conventional Darwinian theory (as it was historically formulated through about 1970); that he views evolution as predominantly a hierarchical process, with considerable integration as well as independence among levels; that there is far more to learn from the fossil record than most evolutionary biologists who work on populations and genes have expected; and that those who do not read primary sources are doomed to remain ignorant and rediscover what has been long known.

2. *La mise en scène*

Gould begins with an exchange between Charles Darwin and Hugh Falconer. Falconer (1808-1865), a botanist and vertebrate paleontologist, was well known and well liked by everyone, including Darwin. Like most savants of his time, Falconer was a creationist. His studies of the teeth and skulls of fossil elephants and other animals convinced him that fossil species showed immutability and permanence in their forms. Because species did not vary importantly through time, they must have been created. But after considering Darwin's arguments in *The Origin of Species*, Falconer changed his mind. Gould quotes Falconer in his great work on American fossil elephants [6], celebrating Darwin for having given evolution, then the most "backward and obscure branch" of biology, a philosophical impetus, and says that "he has laid the foundations of a great edifice;" but Falconer concludes that Darwin "need not be surprised if, in the progress of erection, the superstructure is altered by his successors, like the Duomo of Milan, from the roman to a different style of architecture." Darwin shot back in a letter: "... far from being surprised, I look at it as absolutely certain that very much in the *Origin* will be proved rubbish; but I expect and hope that the framework will stand."

Gould seizes on this contrast between what Falconer viewed as the *foundation* that Darwin laid, versus the *framework* (*charpente*) that Darwin insisted would persist, to set up the first important question of his book (Fig. 1). What is evolutionary theory? What,

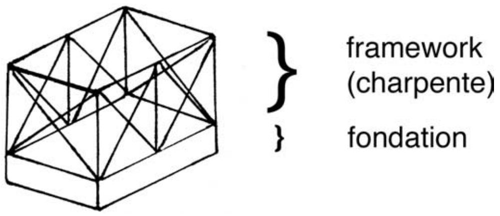

Fig. 1. A diagram that contrasts metaphorically the "foundation" of evolutionary theory that Falconer attributed to Darwin, versus the "framework" (*charpente*) of theory that Darwin believed he had established and that would last, and that Falconer suspected would be substantially changed by later workers.
Fig. 1. Un schéma qui distingue métaphoriquement les fondations de la théorie de l'évolution que Falconer attribuait à Darwin, de la charpente de la théorie que Darwin pensait avoir lui même établie pour durer, et dont Falconer soupçonnait qu'elle subirait dans l'avenir des changements substantiels.

in sum, is Darwinism? One can trace the genealogy of an idea, Gould says, and one can see its original substance. But intellectual heritage is a strange animal. It is false, he thinks, to proclaim oneself an intellectual heir if the original concepts have been too greatly altered. Falconer thought the framework (that is, the concepts) of Darwin's evolutionary theory would be greatly altered in the future; Darwin thought most of it would stand. Gould asks, then, what are the central concepts, and what sorts of challenges and changes can be sustained without making something completely different of Darwin's original formulation? Was Falconer right?

3. The central structure of evolutionary theory

Gould's answer is to visualize the basic formulation of evolutionary theory since Darwin as a kind of tripod (Fig. 2). The mechanism of natural selection is more than just a single leg of the tripod; it is the essence of the tripod itself. The three supporting legs are as follows. First is the proposition that natural selection acts on the *individual level*, not on lower or higher levels of organization. (Gould calls this "agency"). Second is *natural selection*, as the most important (though in Darwin's formulation not the only) force in shaping evolution. Selection "creates" the fit as well as eliminates the unfit. This "creativity" is at the heart of Darwin's view of the role of natural selection, as Gould sees it (Gould calls this central shaping force "efficacy"). Third is the presumption that the processes

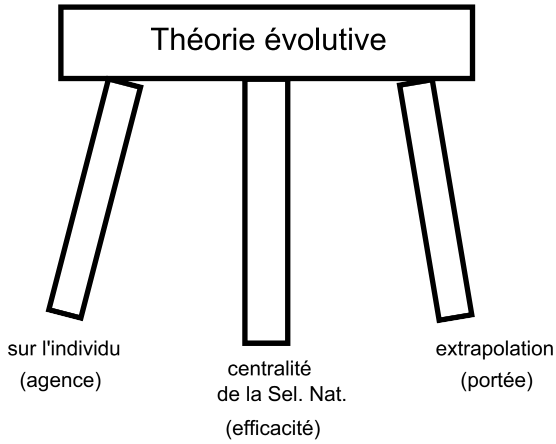

Fig. 2. A depiction of what Gould regards as the tripod of the structure of evolutionary theory. The three legs of the tripod represent the *efficacy* of evolution (natural selection), its *agency* (the fact that selection primarily works on the individual level), and its *scope* (the ability to extrapolate the effects of natural selection seen in populations to the sweep of evolutionary change through time).
Fig. 2. Portrait de ce que Gould voit comme le trépied structurant la théorie évolutionniste. Les trois jambes du trépied représentent respectivement a/ la cause efficiente (*efficacy*) de l'évolution, c'est-à-dire la sélection naturelle, b/ sa cible (*agency*), le fait que la sélection agisse principalement au niveau de l'individu et enfin c / sa portée (*scope*) c'est-à-dire la possibilité d'extrapoler les effets de la sélection naturelle observés au sein des populations jusqu'à rendre compte du changement évolutif général à travers le temps long.

seen in organisms and environments of today, particularly natural selection, can be *extrapolated* to describe and account for the patterns seen throughout the (necessarily incomplete) fossil record, the great sweep of life through time. (Gould calls this "scope").

Seldom content with a single metaphor when more will serve, Gould inverts the tripod and superimposes it on a lovely drawing of an unusual fossil coral by Scilla in 1670 [23] (Fig. 3). Conveniently for Gould's metaphor, this particular coral has three major branches, but more importantly, it has a jointed skeleton. This autotomy allows part of the coral to be broken or shed without destroying it, provided the break is not too deep. Always thinking hierarchically, Gould adapts Scilla's drawing to represent several different levels of challenges to evolutionary theory. He calls these "cuts" and divides them into three kinds, of decreasing severity. First are the "K-cuts" or "killing cuts" (*coupes tueuses*). If one of these is delivered to a main branch, the coral will die, and so respectively will evolutionary theory collapse if its major propositions fail. So, for

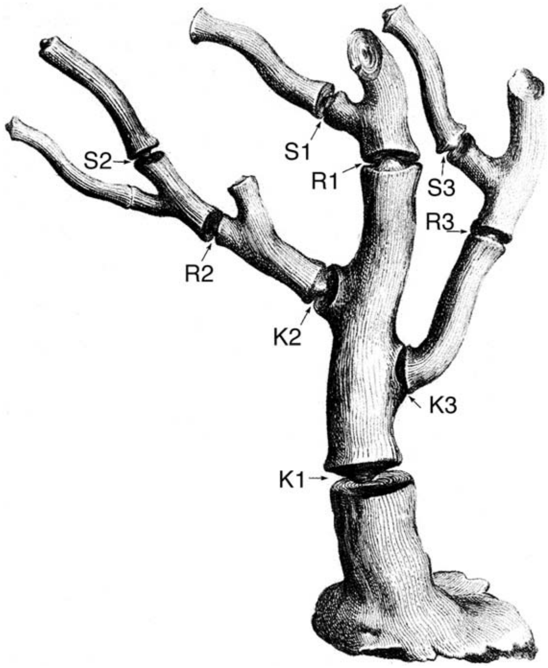

Fig. 3. The same set of concepts, but inverted to correspond to this drawing of an autotomous coral by Scilla in 1670 [23] (after Gould [10]). Gould extends the metaphor of the preceding figure to show how, just as certain kinds of cuts can produce effects of greater or lesser severity in the coral, various kinds of challenges to the three major tenets of evolutionary theory can threaten to destroy it, revise it substantially, or simply extend and augment it.

Fig. 3. Le même groupe de concepts, mais retournés pour s'ajuster au dessin d'un corail capable d'autotomie figuré par Scilla en 1670 [23] (d'après Gould [10]). Gould amplifie la métaphore de la figure précédente pour montrer comment, à la manière des amputations pouvant produire des effets plus ou moins drastiques sur le corail, divers types de défis aux trois propositions fondamentales de la théorie évolutive peuvent menacer de la détruire, de la réviser substantiellement ou simplement de la nuancer en l'amplifiant.

example, a K-cut on the first branch (K1) would be to establish that natural selection does not exist as a major force in evolution. (This destroys the proposal of "efficacy"). Natural selection, as the central mechanism of Darwin's evolutionary theory, also becomes the central trunk of the coral that represents Gould's view of the theory. A K2 cut might allow that natural selection exists, but that it is not "creative" in favoring and disposing of individuals, or that the source and scope of variation somehow limit what natural selection can control; therefore the mechanism would be of no real importance. (This destroys its "agency"). A K3 cut would admit that natural selection may be important in populations and can be creative, but that it is impossible to extrapolate its effects through time, because other processes assume greater importance on that larger scale. (This destroys the "scope" of this evolutionary theory).

Of less severity, but still serious, are "R-cuts" (*coupes de révision*). These revisions rework and modify central concepts, but are not fatal; they are conceptual expansions and integrations that accompany new knowledge without destroying the original theory. These are the most complex and interesting cuts, and Gould spends most of that portion of the book that is dedicated to evolutionary patterns and processes in explaining them. Here I briefly describe some examples.

Gould's proposed R1 cut challenges the idea that selection can only work at the level of the individual. Although he disagrees vehemently with Richard Dawkins's idea that selection works primarily at the genetic level (*The Selfish Gene*) [4], he acknowledges that modern molecular genetics has shown us many mechanisms that influence the production of variation, including gene duplication, meiotic drive, neutral evolution, and the favoring of the production of some amino acids over others (i.e, C + G over A + T). In the same way, Gould forcefully proposes *species selection* (see below) to show that evolution also works at levels above the individual (moreover, he shows, Darwin recognized this).

An R2 cut would severely modify the insistence on the creative efficacy of natural selection by showing how other processes supplement it and sometimes overwhelm or limit its effects. This is one of Gould's favorite topics, and it is a vast one. It encompasses, first of all, the ageless dialectic between *form* and *function* that has been played out as a theme on one historical stage after another, ever since Aristotle [21]. A *formalist* perspective tends to find unity in morphological patterns, and to look for causes of that unity. A *functionalist* perspective sees environmental change as the primary motor of behavioral and morphological change. The latter marvels at the extent to which shape is changed by the necessities of life and survival; the former looks beneath the modifications to the persistent patterns of shape. (One may indeed hear some echoes of the famous debates between Cuvier and Geoffroy, which of course were not about evolution but about morphology).

For Darwinian theory, an R2 cut would be the modification of the omnipotence of natural selection (the *Allmacht* of Weismann, echoed by ultra-adaptationists of the Modern Synthesis who regard natural selection as a process that optimizes adaptation) by inherent constraints. These constraints are essentially habits that result from inherited patterns; their causes are primarily what we would call today genetic, ontogenetic, and phylogenetic processes. For example, land vertebrates have a body plan that features a single multipartite backbone and four (not six or three) limbs. This historical contingency results from the fact that the first animals to invade the land had four limbs, and so did their aquatic ancestors, who used those limbs in quite different ways than animals do on land. The tetrapod skeletal pattern persists for historical reasons related to ancestry. Gould, like other developmental evolutionary biologists, sees such constraints as both "positive" and "negative": these habits of form sometimes channel organisms into exploiting new opportunities by virtue of their functional and physiological possibilities, whereas sometimes the same ancestral factors limit organisms from taking advantage of potential opportunities.

Although Gould began his career as a very strong adaptationist, he changed his point of view in the late 1970s, and one of the first results of his change of heart was the famous article with Richard Lewontin [12] entitled "The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme." Gould and Lewontin argued that not all structures of organisms are optimally or even usefully designed, nor did they come into being for adaptive reasons, despite any such adaptive uses they may have since evolved. Gould and Lewontin used the example of spandrels, architectural necessities that fill the spaces between columns in cathedrals. Their painted surfaces frequently tell important stories, but that is not the reason for their existence, nor the source of their origin. To think otherwise is to confuse cause and effect.

These ideas are rooted in the scheme of *Konstruktionsmorphologie* (constructional morphology) developed by Adolf Seilacher of the University of Tübingen in the early 1970s. Gould reproduces Seilacher's conceptual triangle (Fig. 4), complete with identification of its corners, though curiously (and uncharacteristically) with only slight attribution to Seilacher in his discussion. Seilacher's ([24] *et passim*) scheme was that morphology had three major determinants, which could be identified to greater or lesser extent in any structure (much like the geologist's compositional triangle of the relative contribution of clay, calcium, and silica to sedimentary rocks). The *historical* corner of Seilacher's triangle described the effects of phylogeny, genetics, and ontogeny in providing a genealogical influence on form. The *functional-ecological* corner described the influence of the environment, and the organism's corresponding adaptation to it. The *constructional* corner described the influence of the composition of the structure, its material basis, and its

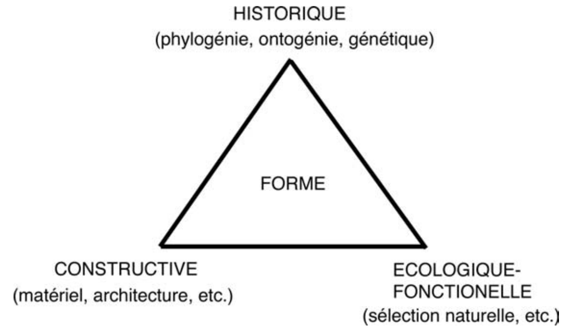

Fig. 4. Seilacher's triangle of constructional morphology, the factors that principally determine the morphology of organisms. At one corner is the effect of *history*, in the form of genetic, ontogenetic, and phylogenetic factors that are inherited (with modification). At a second corner are the *functional-ecologic* factors that select among possible morphological expressions to adapt organisms to their environments. At the third corner are the factors related to the construction of organisms, including their *material properties* and their architecture. Of course, these latter factors are themselves in large part subject to historical constraints because they are inherited patterns. As such, the first and third corners tend to be more *formalistic* (and internalist) in their structure, whereas the second corner is more *functionalist* (and externalist).

Fig. 4. Le "triangle de Seilacher" de la "morphologie constructiviste" explicitant les principaux facteurs de causalité qui déterminent la morphologie des organismes. A l'un des sommets, on trouve les effets de *l'histoire*, sous forme des facteurs génétiques, ontogénétiques et phylogénétiques hérités (avec modification). Au second sommet se situent les facteurs *fonctionnels et écologiques* qui effectuent la sélection au sein des expressions morphologiques possibles en adaptant les divers organismes à leurs environnements. Enfin au troisième sommet se situent les facteurs liés à la construction concrète des organismes, incluant leurs *matériaux constitutifs* et leur architecture. Bien entendu ces derniers facteurs sont eux-mêmes largement soumis aux contraintes historiques dans la mesure ou ce sont des patrons hérités. En ce sens les sommets 1 et 3 tendent à être plus "structuraux" ou "formels"(et internalistes) tandis que le sommet 2 est plus "fonctionnel" (et externaliste).

architecture. All three corners provide “constraints” in the sense of possibilities and limits (“positive” and “negative” constraints, in Gould’s sense). The functional-ecological corner, of course, is where one would expect to see the effects of natural selection; but the other two corners are less functionalist than formalist, because they describe the effects of phylogenetic habit (even the composition of biological structures is basically a question of what is inherited; it cannot simply be changed because of environmental influence).

Gould uses these historical, formalist influences on form, and the genetic and developmental processes that shape form, to substantiate his proposed R2 cut. Natural selection is not all-powerful because it cannot control the factors of genealogical history and constructional composition; some aspects of the self-assembly and the possibilities of change that are inherent in organisms cannot be modified by selection. Nevertheless, once the range of possible form is presented to the environment, natural selection can act; and so the R2 cut is not a denial of natural selection, but a constraint on its reach. Even with constraints, the variation presented to selection is largely “random” with respect to the direction of selection; some biologists regard this as the “creative” potential of natural selection, if not its totipotence. Darwin, unlike Wallace, did not insist on the *Allmacht* (August Weismann’s later term) of natural selection. More importantly, however, selection can still act on parallel variations generated by genetically similar organisms; as a result, parallelism at several evolutionary levels will be common.

R3 cuts challenge the presumed scope, or extent, of evolutionary theory that is based on the extrapolation of gradual rates of natural selection on individuals to the whole of the history of life. If other processes intervene at these higher levels to countermand the effectiveness of natural selection; if the pace of change is not gradual, as Darwinian (or at least neo-Darwinian) theory would predict; then the theory needs substantial revision. In this respect, for example, if punctuated equilibrium (see below) is much more common than gradualism as a description of the patterns of morphology within fossil species (as Eldredge and Gould argued [5,11]), then selection is not constantly fine-tuning morphology to adapt to environmental change, except in the most trivial sense; and it is not gradually shifting morphology to a new form, but maintaining a rather constant form until a new form emerges in a relatively short time. Therefore, the short-term patterns of slight change within populations cannot be extrapolated wholesale to explain evolutionary change on the scale of geologic time.

Another R3 cut assumes major importance if, for example, mass extinctions, whether caused by earth-bound climatic factors (think of Cuvier’s *Révolutions du globe*) or extra-terrestrial factors such as asteroid impacts, complement or even contradict the effectiveness of natural selection in the short term. Without nullifying the effects of selection in the long term of geologic time, such large-scale mechanisms present conditions to which organisms cannot be adapted in advance (though they experience variable success when faced with such catastrophes). In fact, such mechanisms completely overwhelm the quotidian effects of natural selection, at least for a brief interval of geologic time. In David Raup’s words, these mechanisms “reset the evolutionary clock” in the sense that by eliminating many kinds of organisms, they often open the way for the exploitation of environments by new groups. Such discoveries force substantial revision to a smooth, extrapolationist view of evolutionary change to the scale of Deep Time.

There are many kinds of S-cuts (subsidiary cuts or *coupes subsidiaires*), which primarily extend, detail, or augment evolutionary theory, in the normal course of new scientific discovery and integration; they do not need to be discussed here. They elaborate the framework without changing it in any fundamental way.

4. How Darwin reformulated evolutionary theory

A great part of Gould’s book is historical; indeed, there is history on every page, because it was impossible for him to separate ideas from their origins and modifications through time. In the explicitly historical part of his book, Gould recounts the struggles of some of Darwin’s intellectual predecessors (including his grandfather Erasmus Darwin) to establish the reality of evolution and to understand its mechanisms. Darwin, of course, needed to separate himself from the irresponsible speculation of the anonymous author (Robert Chambers) of the *Vestiges of the Natural History of Creation* [1]. The public reaction to this book had made Darwin even more cautious about advancing any

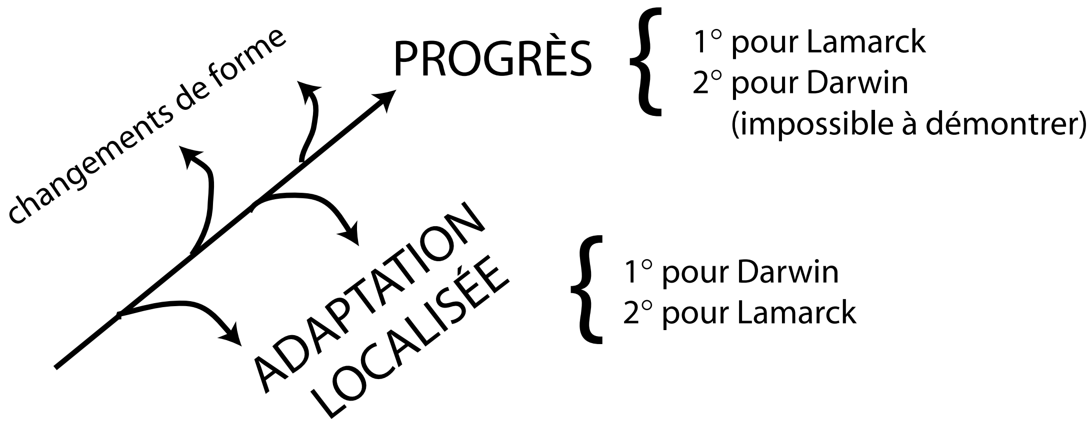

Fig. 5. Differences between Lamarck and Darwin in visualizing the relative importances of progress and adaptation in evolution.
Fig. 5. Les différences entre Lamarck et Darwin dans leurs visions respectives de l'importance relative du progrès et de l'adaptation dans l'évolution.

kind of evolutionary theory. But he had to deal more seriously with the ideas of Lamarck.

Gould and other scholars (such as Frederick Burckhardt, David Hull, and Michael Ghiselin) have shown that Lamarck is almost completely misinterpreted in Anglophonic countries today. Most of what Lamarck really said – notably his grand system of fluid-based influences on natural phenomena, elaborated in his *Hydrogéologie* – was hardly taken seriously by anyone, even his contemporaries in the Jardin des Plantes. Many of the ideas attributed to him, such as the inheritance of acquired characteristics and the use and disuse of parts, were not original to him and were accepted in some form by most savants of the time (including Darwin). On the other hand, Lamarck was not a mystic who believed that organisms "willed" their own evolutionary changes in response to "felt needs" as they moved along some vitalistic, orthogenetic escalator of progress. Lamarck was a materialist who sought material causes, and the term "progress" had neutral connotations that described actual change through time, without any notion of improvement. The *besoins* (often misleadingly translated into English as "felt needs") were not vitalistic, but rather the normal responses to environmental stimuli that all organisms express. For Lamarck [17], use and disuse of parts was explained by the migration of body fluids to and from parts of organisms that were used to greater or lesser degrees as the organisms adjusted to environmental changes. He had no notion of genetics, and neither did Darwin; they simply saw heritability differently.

As Gould presents it, Lamarck understood the two major features of evolution that Darwin later had to explain; but the two men viewed them in very different terms (Fig. 5). To Lamarck, *progress* was the primary force, the most important feature; it embodied the change in organismal forms that successfully adapted to environmental change to become more complex (even as new simple forms were constantly being generated spontaneously). The evolution of *adaptation*, to Lamarck, was a side process, leading to branches that were locally successful but could not really progress further. Darwin's formulation was quite different. Progress was most important to Lamarck, but to Darwin it could not be seen or measured (probably because Darwin saw evolution as primarily a branching process). Conversely, Darwin accepted adaptation (which was of only secondary importance to Lamarck) as of prime importance, and he provided natural selection as its mechanism. Perhaps because Darwin thought in terms of evolutionary trees far more than Lamarck did, he regarded adaptation as the process that produced the variety of living and extinct forms. But adaptation was not enough to produce *divergence* of forms (we might call divergence 'diversification' or 'radiation' in the sense of separation of species [more or less adaptive]). Lamarck saw adaptation as a divergent process, but for him it was divergent from true progress. Darwin did not accept this idea of progress, so he needed a different mechanism to explain how the number of forms could multiply.

Darwin's principle of divergence took its cue in large measure from the patterns of geographical distributions of plants and animals, which were best explained by migration, local adaptation, and eventual divergence. The underpinning of the ability to adapt was variation. The success of placental mammals introduced to Australia (Gould cites Darwin's example), is not because they are competitively superior to marsupials, but because they have greater variability. Lamarck had no concept of population-level variation; he did not think at the level of individuals, but at the level of types of organisms, so he saw adaptation solely in what we might call "macroevolutionary" terms, rather than at the level of individuals within species.

Yet, in one of the most important and original features of the book, Gould shows that Darwin understood and accepted the concept of adaptation and selection *at the level of species*, not just of individuals. The focus on selection at the individual level was so strong for Darwin, Gould says, that even though he realized the necessity of a concept of species selection, "in his distress he hesitated to embrace it." This conclusion will surely upset many evolutionists and historians of science, but in retrospect it is (like many things Gould pointed out in his long career) amazing that it was never noticed before.

Darwin's single illustration in the *Origin of Species*, as everyone knows, is a chart showing how organisms might change through time. In this illustration (Fig. 6), as in others that eventually were published (edited by R.C. Stauffer) in 1975 [27] as *Charles Darwin's Natural Selection* (of which the *Origin* was merely an abstract), Darwin clearly and repeatedly depicts a divergence of several species from a single point, only one of which persists to give rise to other species. This is not simply divergence but radiation, so there is no question of it proceeding simply as gradual, anagenetic change within a lineage. In this figure, Darwin shows that evolutionary trends do not have to be simply the result of unidirectional change within a lineage, but rather the remains of a production of a variety of species that are eventually sorted out by the processes of adaptation and extinction. In this way, evolutionary trends can be produced by selection *at the level of the species*, even though (at the same time) these processes

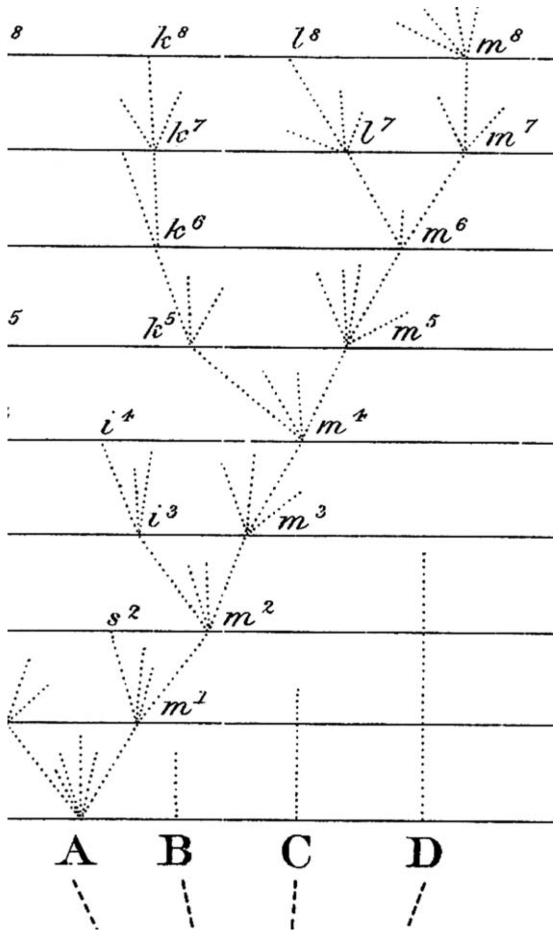

Fig. 6. Part of Darwin's single figure in the *Origin of Species* [3], to show the pattern that indicates that he recognized that selection occurs not just among individuals, but among species.

Fig. 6. Une partie de la figure unique contenue dans « *L'origine des espèces* » de Darwin [3] pour montrer le patron indiquant qu'il avait reconnu que la sélection naturelle n'agit pas seulement entre les individus mais aussi entre les espèces.

are carried out at the level of selection of each individual of each species. Darwin knew that, in effect, it was differential extinction in clades that produced these patterns. (He also realized that the long-term effect of differential extinction would be to separate existing groups so much that it would be difficult to reconstruct their genealogical relationships, which should be the basis of classification [22]). Gould also recognizes this point. For him, this is a principal place where the 'creative' power of natural selection can be observed.

Gould's discovery of this important point – that Darwin himself recognized species selection as a necessary force in the generation of diversity through time – forces an important revision (R-cut) to the tripod of standard evolutionary theory (Fig. 2). The first leg is unchanged; natural selection is still very much in operation. But the proposition of the second leg, instead of exclusively devoted to action at the level of the individual, now must be expanded to accept an important role for species selection, which explains patterns at the macroevolutionary level that cannot solely be explained by selection on individuals (which of course still plays a role). The implications for the third leg may also be important, because it would call into question the ability to extrapolate smoothly from processes seen at the populational level to those at the macroevolutionary level; this would depend on just how separate the processes might be. Gould devotes an extensive discussion to properties of species and clades that cannot be reduced to the individual level. For example, individuals cannot speciate, and therefore cannot have speciation and extinction rates. But clades can and do; and if some rates are higher or lower than others, then there will be a net effect on the relative success of some clades over others, in terms of species diversity.

5. The structure of evolutionary theory after Darwin

The Origin of Species provided the needed mechanism for change to occur through time, even though Darwin provided surprisingly little experimental evidence in his long, inductive argument. He found strong adherents in England, America, Germany, and other countries, although relatively few in France. Darwin had failed to explain the *origin of variation*, a defect upon which the young American paleontologist E.D. Cope built his prize-winning essay that later became *The Origin of the Fittest* [2]. But there were many other challenges, as Gould describes in intricate detail: the ultimate regression to the mean that would result from the blending of different variations; the assertion that variations were not continuous, so evolutionary change was more likely to lurch forward in discrete increments than to proceed gradually (Francis Galton's metaphor of the polyhedron, which Gould uses to great effect); the insistence that typical variations were too small for natural selection to be of any effect; and so on. The perceived insufficiency, the disappointment, and the disaffectation with Darwinism in the later 1800s centered on the erosion of acceptance that natural selection is the principal guiding force in evolution. It was also at the turn of the century that Mendel's work was discovered, and that William Bateson named the new science of genetics. Gould shows how some early geneticists, notably de Vries on the heritability and effects of large mutations, and Bateson himself on abnormalities in development (teratologies and "monstrosities"), tried to get at the range and source of variation, and influenced ideas about the size and character of natural variation. This is one of the most effective and unusual sections of the book, because it is so infrequently treated in texts, and even less frequently integrated with historical theory before and after. Bateson emerges from Gould's account as a pioneer uncelebrated in his own time and largely misunderstood or forgotten by the Modern Synthesis. Yet his decision to focus his research on the study of teratologies, in an attempt to understand how mutations cause substantial morphological change, was in retrospect prescient of much current work in evolutionary developmental biology. In the early decades of the 1900s, experimental geneticists once again began to stress the importance of small variations, even as paleontologists such as Henry Fairfield Osborn insisted on the irrelevance of such variations, and invented mysterious processes such as *aristogenesis* to account for the "creative" and iterative trends seen in related fossil lineages. Evolutionary theory was in disarray.

6. The 'Modern Synthesis' and how it changed Darwinism

Gould's ideas on the history of the "Modern Synthesis of Evolution," its advances and pitfalls, are well known from a number of his previous works reaching back to the early 1980s. But in this book he has the space to expand them and integrate them with what happened in evolutionary biology before and since. The Synthesis, as is well known, was a self-styled "fusion" of the findings of genetics, population biology, and paleontology that began in the early 1930s and still dominates evolutionary thinking today. It reaffirmed the essential postulates of Darwinism while it integrated new discoveries from these fields and abandoned ideas about evolution that had little empirical support. Probably its single most important advance was the development of an entirely new field, theoretical population genetics, that began with accepted generalizations about the action of mutation and selection in natural populations, and quantified these factors to produce a variety of models that showed how and at what rates evolutionary change would be expected to proceed. This advance actually preceded the development of the Synthesis, and in some respects can be regarded as the "foundation" that allowed the "framework" of the Synthesis to develop.

Although it was at first pluralistic, admitting a variety of mechanisms, processes, and patterns of evolution, the Synthesis began to crystallize by the mid-1940s, as the views of its founders changed and became more narrowly insistent on the all-sufficiency of natural selection in evolution. For Gould, this process occurred in two major stages. Historian of science Will Provine calls the first stage, which occurred in the 1930s at the beginning of the Synthesis, *restriction*. In this stage, the ideas of some geneticists about sudden morphological leaps or "saltations," what were then often called "macro-mutations," were rejected as of any importance in evolution. Instead, there was an insistence that the genetic principles first brought forward by Mendel were the basis of change in all organisms. This stage of formation of the Synthesis also rejected ideas of vitalism and teleology, which still tainted some paleontological and general evolutionary theory. There was an affirmation that selective forces, acting upon small mutations, directed all evolutionary changes.

The second phase of the Synthesis, which Gould himself has called the *hardening*, was due primarily to biologist Ernst Mayr (who remained until Gould's death one of his closest and most respected colleagues, despite many differences of viewpoint), followed by the geneticist Theodosius Dobzhansky and the paleontologist George Gaylord Simpson. Strongly influenced by the models of the population geneticists, natural selection became the all-powerful cause of evolution, and all variations that persisted in populations had to be adaptive in some way. Gould cites many examples that show how the founders of the Synthesis, in their own words, admitted evolutionary pluralism early in their careers and denied it in their later writings. These demonstrations are really quite striking, as he also shows how certain biologists (e.g., the developmental biologist and geneticist C.H. Waddington, the population geneticist Sewall Wright, and the paleontologist E.C. Olson), who were very much interested in evolution but not willing to accept all the tenets of the hardened form of the Synthesis, became systematically excluded from its inner circles.

In its mature form, then, the Synthesis stressed this monolithic formula: (1) variations were small and continuous; (2) natural selection, acting on these variations, directed all important evolutionary change; (3) the patterns of change seen at the populational level could be extrapolated smoothly to explain all changes at the levels of higher taxa through geological time. No other processes were seen as important; and if, for example, patterns seen in the fossil record suggested otherwise, it was because the fossil record was too incomplete to assess real evolutionary change. Under this pressure, Gould says, even Simpson was brought into line: in *Tempo and Mode in Evolution* [25] he had discussed the concept of *quantum evolution*, which described the very rapid changes seen in some fossil lineages; but in *The Major Features of Evolution* [26], a revision and expansion of his previous book, quantum evolution was no longer a mode different in *kind* from other evolutionary processes, but only more rapid in *rate*. As Gould points out, Simpson also reduced his view of the importance of genetic drift and of non-adaptive change, and stressed that "selection within phyletic lineages must represent the only important cause of substantial change." In these ways, the three legs of the tripod that Gould describes achieved their firm support of modern evolutionary theory.

7. Evolution Post-Synthesis: Expansion, Revision, Rejection?

In some ways, the discovery of neutral ("non-Darwinian") evolution in the late 1960s and early 1970s, empirically by King and Jukes (see Jukes [15]) and theoretically by Kimura [16], was the first real challenge to the Modern Synthesis. It established that much variation passes unperceived by natural selection, simply because many differences in genetic codon triplets make no difference in their effects at the phenotypic level. Even before this, the discovery in the 1960s that typical organisms harbor far more mutations in their genes than anyone ever suspected (e.g., Wallace [30]), without detrimental effects to the phenotype, destroyed the "classical" idea in genetics that most mutations were harmful in their effects, and that therefore it would be impossible for organisms to carry any substantial mutational load. So much for the restrictive views of the selective importance of adaptive variation at the genetic level! The idea that speciation was a fundamentally adaptive process began to crumble with the discoveries of almost instantaneous and aleatory speciation by chromosomal rearrangement, ecological shifts in timing of mating processes, sexual selection, and other factors. These studies showed that sibling species could be produced rapidly and without adaptive divergence.

But it was perhaps Eldredge and Gould's own theory of *punctuated equilibria* [5] that caused the greatest challenge to the precepts of the modern synthesis. Perhaps the strength of its challenge explains why it was so misunderstood and reviled for so long in some circles. In retrospect, it was no different than any other proposed mechanism of evolution in hypothesizing a general pattern from some specific instances, and in urging a reconsideration of data that had been taken for granted for a very long time.

Simply stated, punctuated equilibria is the generalized observation that in reasonably abundant sequences of fossils, morphology shows little or no directional change throughout the extent of a species. When change comes, it occurs within a relatively brief interval, compared to the interval in which the morphology of the species has remained more or less the same (static). Here, the important thing is not how fast the change occurs (Simpson, among paleontologists, and many theoretical population geneticists had shown in fact and in models just how fast the change could be). Rather, it was that *stasis* in morphology, not more or less constant gradual change, was the rule. This pattern had been more or less ignored in fossil sequences because evolutionists expected to see change; without change, nothing informative was going on. So, the recognition of punctuated equilibria was the recognition, as Eldredge and Gould said, that *stasis is data*, not just noise in the system.

It is important to note that Eldredge and Gould did not simply say that they were describing morphological change. They insisted that they were describing the behavior of species through time. The difficulty with this explanation was that there was no independent way to establish the identity of the species, because the species concept in paleontology is based exclusively on morphology. And there are very few sequences in which a 'parent' and a 'daughter' species co-occur so that a real speciation (splitting) event can be established.

Eldredge and Gould couched their explanation in terms of what was then the most up-to-date formulation of the speciation process: the process of peripatric speciation advocated by Ernst Mayr. In this case, evolution does not occur mainly by the eventual split of one great population into two (by means of some environmental barrier that so often seems to be needed in traditional scenarios of speciation). Rather, speciation occurs when a small, isolated population on the periphery of a species's range undergoes local adaptation and rapid change. (Gould, in the present book, notes that more recent formulations of population modelers have shown that change can happen virtually as fast in large populations; but that is beside the point to the history of the concept itself.)

Why was the reaction to punctuated equilibria so virulent, especially among the population biologists? At first, some took it to be a false pattern because the fossil record was so incomplete. But Gould recounts the testimony of many paleontologists who not only went out to the fossil record and found new instances of this pattern, but others who said that they had suspected it all along but were reluctant to report it! Theoretical modelers, of course, were not prepared for this idea, because after all, evolution is change; why would the absence of change be interesting to model in evolutionary terms? However, there was one populational mechanism, known as *stabilizing selection*, that was soon invoked to account for punctuated equilibria. Stabilizing selection occurs when selection works against both the upper and lower regions of expression of a typical bell-shaped curve of variation in a population. Thus, variation is constrained and phenotypic expression seems to be much more constant and canalized. However, this concept is completely implausible when extrapolated to fossil sequences that last tens of thousands of years, in environments that must be presumed to maintain a completely constant selection pressure on the phenotype. Both assumptions are without support, and there is no independent evidence for stabilizing selection in any given paleontological case. Neither stabilizing selection nor any other kind of selection can be accepted as a default assumption – though as Gould shows, with the hardening of the Synthesis, that is exactly what happened: selection was assumed and very seldom needed to be demonstrated or measured.

In proposing punctuated equilibria, Eldredge and Gould did not at all deny the *efficacy* of natural selection (so the first leg of the tripod remains intact), but rather challenged the pattern that would be expected from a smooth extrapolation of ordinary, minute, fine-tuned selection on small variations to form a pattern of slow, gradual change at the level of the fossil record. This is explicitly an R3 cut to Scilla's coral, because it challenges the scope of evolutionary theory as it was proposed by Darwin and affirmed by the Modern Synthesis.

It would be expected that Gould would give prominent place in his book to what he might well regard as his single most important theoretical contribution to evolutionary theory. What is particularly interesting is how he uses it in his restructuring of the theory. By recasting trends as the results of species selection, for example, he makes punctuated equilibria necessary for a unified theory of evolution that reaches the macroevolutionary level. In the Modern Synthesis, paleontology had no such theoretical role; in fact it had no theoretical role at all.

The central observation of morphological stasis as the predominant pattern in fossil sequences also has a critical role in Gould's reworking of evolutionary theory. The rapidity of speciation and replacement – the "punctuation" part of punctuated equilibria – is logically and empirically separate from the stasis observed through the normal duration of a lineage in the fossil record, if the "equilibrium" part of punctuated equilibria holds true. Eldredge and Gould – particularly Gould – flirted with the idea that long-term morphological stasis could be explained by a kind of *homeostasis* mediated by developmental processes – much as I.M. Lerner had suggested in 1954 [18]. This would be consistent with observations that the developmental system tended to channel, or canalize, morphological expression and to suppress or insulate the developing organism against most insults to the phenotype that were provided by the environment. In other words, organisms tend to develop normally regardless of environmental vicissitudes, though they may be individually affected by extremes suffered during their lifetimes. This would explain why most morphology is fairly constant in fossil sequences (the salient exceptions, which Gould and Eldredge have always been careful to acknowledge, are best seen in marine microorganisms, which frequently show gradual, anagenetic change; however, their morphological features, notably size, are sensitive to changes in temperature, salinity, and other environmental factors).

In recent years, however, Gould has backed away from these developmental explanations (for which, in most cases, there is still little independent evidence despite promising preliminary results). Instead, he has leaned toward the effects of local geographic adaptation to differentiate populations under diverging selective regimes, following the models of Futuyma (e.g., [7]).

On the other hand, Gould has continued to advocate the importance of ontogenetic mechanisms in evolution. His previous *magnum opus, Ontogeny and Phylogeny* [9], stressed the potential of developmental biology to bring us new knowledge of mechanisms of evolutionary change. In his book, Gould concentrated largely on shifts of timing in expression of genes that regulate morphology (i.e., *heterochrony*); but he suspected what was to come. In the present book he is vindicated, and with great delight he devotes dozens of pages to new advances in the molecular genetics of development. The discoveries of *Hox, Pax, homeobox*, and many other gene families have provided the mechanisms to help explain what controls gene expression, timing, regulation, and novelty. Such discoveries are highly relevant to understanding the underpinning of the same two corners of Seilacher's *Konstruktionsmorphologie* discussed above. Gould sees these advances as the most exciting, promising, and revealing for the future of evolutionary biology, and it is difficult to disagree. They are bound to provide new information on how the parts of living organisms assemble themselves, the origins of new ontogenetic mechanisms, and the expression of new morphology. It is to Gould's great credit that he was one of a few evolutionary scientists who saw this coming three decades ago. Not only that; in his fields of evolutionary morphology, paleontology, and history of science, he led the way.

Here again, Gould does not simply point to new discoveries of signaling pathways, or of genes that regulate development and timing of morphological structures. He recurs again to the idea that the same developmental genes in closely related species can create parallel structures (another example of positive constraints). This production can set the stage for higher-level selection. But beyond this, the fact that organisms as different as fruit flies and humans can share similar genes that, when transplanted, perform normal functions in the new organisms, suggests a commonality of body plan that gives a new meaning to "constraints." It suggests a deep homology of some of the principal instructions for assembling animals, despite the role that selection has played in shaping the tree of life.

8. Conclusion: *Quo vadis* the tripod and the coral?

I have tried to summarize perhaps only a tenth of this remarkably complex and integrated work, which is many books in one – including a summary of the structure of evolutionary theory, perhaps the most comprehensive history ever of how it was assembled in all its aspects, a bold analysis of the challenges and revisions that continue to modify the theory as we know it, and the intellectual autobiography of perhaps the most influential (at least as far as public consciousness is concerned) evolutionary biologist of the century.

In the end, Gould is confident that Darwin's theory has survived very well. It has been extended and enriched by many new discoveries that were unanticipated in Darwin's time (S-cuts); it has met the challenges of new discoveries in paleontology, developmental biology, molecular biology, and other fields that have caused what he sees as important and laudable revisions in the theory (R-cuts); and it has not yet been seriously threatened by any K-cuts.

There have been a number of reviews of Gould's book by prominent evolutionists (e.g., [8,13,19,28,29]). These have been variable in their assessments of this work, corresponding in great measure to the scope and understanding of the individual reviewers. Rather than rehash these, I would like to offer several considerations that have not been raised in other reviews. In my view, this is quite possibly the most important book on evolution since *The Origin of Species*, at least for professional scientists. I say this because it is the most comprehensive, and in a much different way than any other book on the subject, because it integrates the history of the field (actually now several fields) with a great deal of empirical analysis; moreover, unlike most accounts of evolutionary biology, it does not restrict itself to population-level phenomena or even concentrate on them – rather, it asks whether these phenomena stand up to the scrutiny of whether they can be shown to have valid effects in the long run of the history of life. Despite its uniqueness, the book is not, in many respects, a great success, and many reviewers have commented on its prolixity, repetitiveness, and self-indulgent length. But then again, *War and Peace* could have been shorter, the Duomo in Milan scarcely needed the wedding-cake decorations on its roof (as Gould himself points out), and Puccini could have benefited from an orchestral arranger who didn't insist on doubling the vocal solos with flutes and horns.

1. Gould's insistence that natural selection must be a "creative" process may trouble or confuse some readers. This is a very old debate and he reviews it well; but in my view, he comes out on the wrong side. Yes, there must be innovation in order for evolution to come up with new forms; but this innovation does not *come from* natural selection, which has most often and most effectively been compared to an editor. An editor, strictly speaking, can only publish what is good and pencil out what is not, and this is basically what selection does. Of course, a good editor can suggest changes, can stimulate authors to do better work, and even go farther. But it remains to be demonstrated that selection in natural populations does this.

   It could be maintained that selection is creative because it can select for combinations of features that are more advantageous to an organism than single features alone would be. This is true, but selection does not place those combinations in organisms, it only selects them once they are there. So it is important to separate the question of where variations come from and the question of what happens to them in populations once they appear.
2. Because Gould is convinced of the creative power of natural selection, he conflates (in my view) the *source* of variation with its *fate*. Where does variation come from? Not from natural selection

itself. Gould has set up his tripod such that he is forced to manifest the "creative" part of evolution in selection itself. What he needs is a fourth leg to the tripod – a leg that represents the source of evolutionary variation. Of course, historically this would not be accurate, because this has not been a major preoccupation of evolutionists. Taking their cue from Darwin, they have taken as given the presence of variation in populations. Darwin had to do so; he understood heredity, but knew nothing of genetics. The source of variation had to be taken for granted. Ernst Mayr's [20] compendium on population-level evolutionary mechanics, *Animal Species and Evolution*, was over 800 pages long; yet only one page was devoted to the role of development in evolution, and that was pretty much to say that development must be important in evolution, but we don't know much about it. Thanks to new advances in molecular genetics and evolutionary developmental biology, this is increasingly no longer the case. So for *historical* reasons Gould's tripod stands; but for *structural* reasons it should rightly become a four-legged stool. Gould devotes dozens of pages in this book to the importance of new advances in developmental evolutionary biology; but he does not see it as a separate field of study, and so he is forced to incorporate it into the other legs of his tripod.

3. Gould completely ignores the great advances that *phylogenetic systematics* has brought to evolutionary biology in the past three decades. This is perhaps not surprising, because he concentrates on processes of evolution, whereas cladistics is a study of patterns. Nevertheless, the use of phylogenies in guiding and testing hypotheses about evolutionary process has become so important that it is surprising, and disappointing, that it is not more extensively integrated into his book. Without phylogenies, for example, one cannot examine the validity of hypotheses about species selection, because there is no independent test of the monophyly and genealogical configuration of the groups in question. Also, with regard to the third leg of the triangle, patterns of diversity through time take on quite different forms when taxa are forced to be monophyletic.
4. Gould says very little about the *origin of adaptations*, surely the central problem in evolution, especially when one concentrates on process. (Of course, he gives substantial attention to speciation, the other of Darwin's major features of evolution, through punctuated equilibrium and other mechanisms). His lack of attention is seen both at the populational level and the macroevolutionary level, and there are substantial literatures that deal with both levels. This is particularly strange because Gould has always been so much more interested in evolutionary processes (such as this one) than in evolutionary patterns (such as questions about the diversity of organisms through time, which also has a vast literature that is given scant attention in his book). Although he spends almost no time on the origin of adaptations, he does spend considerable time on its complementary process, the influence of extinctions – particularly extra-terrestrial mechanisms of mass extinctions on evolutionary theory.

It is possible, beyond personal tendencies and interests, that Gould's lack of attention to the preceding two issues at least partly stems from his training as an invertebrate paleontologist. The invertebrate fossil record is blessed with copious specimens, compared to the plant and vertebrate fossil records. On the other hand, in typical shells there are far fewer characters to mine than can be found in typical vertebrate skeletons, which comprise up to 200 bones with many different features. Perhaps the ease of constructing data matrices of characters and taxa is one reason why phylogenetic systematics, with its search for synapomorphies, took root earlier among vertebrate paleontologists than among their colleagues in other disciplines. (There are many sociological reasons too: see Hull [14]). But there is more: the relatively copious invertebrate fossil record made it much easier to identify related species in adjacent rock sequences, and so to plot a general scheme of relationships that traditionally were not rigorously tested by phylogenetic methods (this began to change in the mid-1980s, but phylogenetics has generally been slower to catch on here than among vertebrate workers). As for the origin of major adaptations, there are no doubt better examples of transitional features and functions among vertebrates than among invertebrates.

5. In his discussions of macroevolutionary patterns and the scope of natural selection, Gould often seems to conflate *extrapolation* and *uniformitarianism* (of which, as he knew better than anyone, there are several different varieties). The two concepts are not the same. Uniformitarianism, in its most relevant form to us today, was basically a denial of magic: an affirmation that the *laws* of the universe are constant, now and in the past – but the *rates or processes* of natural phenomena are not necessarily constant. On the other hand, extrapolation is a question of deriving large-scale patterns from smaller samples, those visible in our own experience of time and space. It is to presume that what we see in the present has more or less always been the case, and that the full scope of change is merely what we know today writ large. The difference between extrapolation and uniformitarianism can be usefully illustrated by the asteroid theory of extinction: it contradicts extrapolation, because we don't observe such mechanisms today and do not project ideas of large impacts from known smaller ones; but it does not contradict uniformitarianism, because it does not suspend the laws of the universe.
6. Gould paid little or no attention to advances in population biology, including quantitative genetics, genetic transilience, and populational sources of adaptive evolution. He missed the shift in focus during the 1980s by Alan Templeton and others that worried less about the geography of speciation and more about its genetics. But these levels of evolution were never particularly important to him. He acknowledged them, much as Ernst Mayr in his books acknowledged developmental biology and paleontology, but then ignored them. Gould's synthesis is no more a synthesis than any other, but the field of evolutionary biology is so factionalized by disparate training – populational biologists generally know little of paleobiology or macroevolution, and vice versa – that it is difficult to know who could craft a synthesis at this point, and whether colleagues in other areas of the field could even appreciate it.

These are only a few issues and questions that Gould's book raises for discussion; others could be found on nearly every page. Perhaps the most unfortunate aspect of these questions is that we will not have Steve Gould to discuss them with. His intellect, the scope and breadth of his scholarship, his incredible memory and facility with knowledge, and his great interest in and support for his colleagues were in the best tradition, not only of science, but of human relations.

Acknowledgements

I am grateful to Professors Armand de Ricqlès and Philippe Taquet for the invitation to contribute this piece, especially on short notice, and to Professor Clark Howell and the members of my graduate seminar that studied *The Structure of Evolutionary Theory* in great detail, for all their insights and reactions. I thank Professor Howell, Dr. Ken Angielczyk, Brian Kraatz, Alan Shabel, Professor David Wake, and Matt Wedel for comments on the manuscript, without implying their concordance with all the views expressed here. A Visiting Professorship from the National Museum of Natural History, Paris provided the funds and study time to make this work possible. This is UCMP contribution No. 1833.

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