

Before hierarchy: the rise and fall of Stephen Jay Gould's first macroevolutionary synthesis

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Received: 3 March 2016 / Accepted: 18 March 2017 / Published online: 29 March 2017
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Abstract Few of Stephen Jay Gould's accomplishments in evolutionary biology have received more attention than his hierarchical theory of evolution, which postulates a causal discontinuity between micro- and macroevolutionary events. But Gould's hierarchical theory was his *second* attempt to supply a theoretical framework for macroevolutionary studies—and one he did not inaugurate until the mid-1970s. In this paper, I examine Gould's *first* attempt: a proposed fusion of theoretical morphology, multivariate biometry and the experimental study of adaptation in fossils. This early “macroevolutionary synthesis” was predicated on the notion that parallelism and convergence dominate the history of higher taxa, and moreover, that they can be explained in terms of adaptation leading to mechanical improvement. In this paper, I explore the origins and contents of Gould's first macroevolutionary synthesis, as well as the reasons for its downfall. In addition, I consider how various developments during the mid-1970s led Gould to identify *hierarchy* and *constraint* as the leading themes of macroevolutionary studies—and adaptation as a macroevolutionary red herring.

Keywords Stephen Jay Gould · Paleontology · Macroevolution · Adaptation · Progress

1 Introduction: two macroevolutionary syntheses

Of Stephen Jay Gould's many accomplishments in evolutionary biology, none was dearer to him than his macroevolutionary theory: the product of several decades of intense labor. Hotly debated since the 1970s, it was based on the idea that Darwinian

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processes operate at a variety of hierarchical levels, including, most notably, the level of species (Stanley 1975; Gould and Eldredge 1977). Ernst Mayr, representing orthodox Darwinism, had earlier argued that macroevolution “is nothing but an extrapolation and magnification of the events that take place within populations [most notably, mutation and natural selection]” (Mayr 1963, p. 586). However, as Gould and Eldredge (1977) realized, the theory of punctuated equilibria represents a challenge to the view that “mutation and natural selection within populations...[are] fully sufficient to render macroevolution” (Gould and Eldredge 1977, p. 140). For if species “originate in geological instants and then do not alter in major ways, then evolutionary trends *cannot* represent a simple extrapolation of allelic substitution within a population” (Gould 1980a, p. 125, emphasis added). Instead, trends must represent the differential survival and reproduction of *species*, perhaps in virtue of irreducible species-level properties (Stanley 1975; Gould and Eldredge 1977). Darwinism, Gould proclaimed, was in need of a major hierarchical expansion (Gould 1982a)—and paleontology would be the primary locus of its construction (Gould 1980b).

Following the early statements of his hierarchy theory (e.g., Gould 1980a, 1982a; Gould and Eldredge 1977), Gould spent the final twenty years of his life refining and extending it, and exploring its philosophical implications (e.g., Gould 1985, 1994; Lloyd and Gould 1993; Vrba and Gould 1986). Especially important was a 1985 paper, “The paradox of the first tier,” in which Gould offered a hierarchical explanation of “our failure to find any clear vector of...[evolutionary] progress,” despite the expectation that natural selection should yield such a vector when extrapolated to geological timescales (p. 4). While Gould admitted that progressive trends could be detected on ecological timescales, such progress was inevitable stymied by contingent events at other “tiers” (e.g., bolide impacts at the “third tier” of geological time). These and similar observations led him to undertake his celebrated reinterpretation of life’s history (refracted through the Burgess Shale fauna), and to highlight, in striking terms, the importance of *contingency* for evolutionary biology (Gould 1989). In the words of Warren Allmon:

[Contingency] became for him the epitome of the general effect of history on evolution. Around it he was eventually to integrate his critiques of progress, adaptationism, gradualism, predictability, and biological determinism, as well as his interests in evo-devo, hierarchy, constraints, unpredictability, and the dashing of the fondest of conventional human hopes. (Allmon 2009, p. 53)

For many of us, this is the only Gould we have ever known: sage enemy of biological progress and incorrigible champion of historical contingency.¹ Yet Gould’s integration of these identities belongs to the *second* major period of his career, and constitutes his “second macroevolutionary synthesis” (the hierarchical expansion of evolutionary theory). Lesser known, and virtually unstudied by historians and philosophers, is his *first macroevolutionary synthesis*: an outgrowth

¹ Recent publications in which this image is foregrounded include Allmon et al. (2009), Prindle (2009), York and Clark (2011), Danieli et al. (2013).

of his “science of form” (Gould 1970a). Short-lived and essentially opportunistic, it was rooted in what Sylvester-Bradley (1959) called “the most distinctive contribution that paleontology has made to modern evolutionary [theory]”—the recognition that parallelism and convergence are ubiquitous features of transspecific evolution (Gould 1971a, p. 257).² Gould’s insight was that paleontologists could cement their status as independent contributors to evolutionary theory if they could explain, in mechanistic terms, *why* parallelism and convergence dominate the evolution of higher taxa. As he wrote in an early publication:

[Just] as increase in size, of itself, subjects organisms to a different realm of forces and requires change in morphology, so also might extension in time bring emphasis to evolutionary events and processes that do not dominate at the species level. In particular, the great parallelism that occurs in independent lineages of most vertebrate classes and orders stands in contrast to the theme of splitting and diversification that predominates at lower levels. (Gould 1968, p. 97)

What forces did Gould believe to “dominate” transspecific evolution that did not dominate “at the species level”? Two were especially important: “forced” mechanical adaptation (i.e., change exacted by the physics of size and shape) and “general biological improvement” (mechanical improvement occurring in a constant physical environment) (Gould 1968, p. 97). Fortunately, such processes (being essentially biomechanical) leave their marks in the skeletons of animals, enabling adaptive hypotheses to be formulated and tested using paleontological materials (Gould 1971a, pp. 256–257). Such testing, Gould hoped, would provoke an important reorientation of “our current perspective [on macroevolution],” thus reinstating paleontology “as a source of new themes for evolutionary theory” (Gould 1970a, pp. 108, 112):

On [our standard picture of evolution], convergence is at best a curiosity worthy of some awe and a few text-book pages and at worst the arch-confounder of phylogeny. But when the theme changes from branching diversity to mechanical optima and limited solutions expressed in an engineer’s language, then parallelism and convergence are among the normal results of adaptation and provide, moreover, a criterion for judging history: for short of being an all-knowing engineer, we must infer biological progress from the observation that, again and again, independent lineages develop the same design to perform a given function. And if parallelism and convergence are more common than we usually think, then the idea of biological improvement must be resurrected ... but in a Darwinian framework. (Gould 1970a, p. 109)

To date, few studies have examined the early period of Gould’s career, and none have recognized the importance (or even the existence) of his first

² Parallelism and convergence are processes resulting in the evolution of similar traits or character states in independent lineages. In the case of parallel evolution, the lineages under consideration must possess a recent common ancestor—for instance, they may be species in a genus, or (according to an older conception) genera within a family. By contrast, convergent evolution occurs when the lineages in question do not share a recent common ancestor.

macroevolutionary synthesis. Richard Bambach, for instance, observes that Gould (1969, p. 497) speaks of “trends toward increased mechanical efficiency” (a statement he regards as “a bit peculiar for Steve”) (Bambach 2009, p. 75). Yet Bambach interprets this statement as an expression of Gould’s “career-long advocacy of a hierarchical nature to evolutionary theory” (ibid, pp. 75–76). This is correct only if Bambach means that, throughout his career, Gould remained committed to the existence of a *causal distinction* between microevolution and macroevolution (it is incorrect if he regards Gould’s early macroevolutionary writings as members of a phyletic sequence culminating in his second macroevolutionary synthesis). In a similar vein, Chris Haufe argues that Gould was a career-long “nomothetic scientist”—that is, a scientist interested in discovering spatiotemporally invariant laws of nature (Haufe 2015, p. 2). But while Gould’s science of form *did* provide a platform for nomothetic researches (i.e., for the inductive discovery of general principles), its primary function was to buttress a research program based on the quantitative study of biological improvement (cf. ibid, pp. 11–12). By overlooking Gould’s first macroevolutionary synthesis, Haufe misses what is most important about his science of form: its promise to provide “functional explanations” of directional changes in higher taxa (Gould 1970a, p. 110). Gould’s first macroevolutionary synthesis, I will show, was the tail wagging the dog of his science of form.

The remainder of this paper is organized as follows. In section two (“Background to a macroevolutionary synthesis”) I explore Gould’s early research program, and situate it within the context of mid-20th century invertebrate paleontology. Section three (“The mechanics of adaptation”) builds on this analysis, and shows how Gould parlayed his “science of form” into a framework for macroevolutionary studies centered on the “principle of limited solutions” (the notion that only a small number of solutions exist to the functional problems faced by animals) (Gould 1971a, p. 257). Section four (“The gradal scheme”) explores Gould’s interest in gradal systems of classification, which furnished him with a model of phylogeny uniquely suited to his explanatory ends. Then, in section five (“The collapse of Gould’s first macroevolutionary synthesis”), I explore the reasons for Gould’s intellectual somersault during the mid-1970s, culminating in the downfall of his first macroevolutionary synthesis. I conclude by considering how the present inquiry enriches our understanding of Gould’s intellectual development, and nurtures new lines of research into the origins and consolidation of his second macroevolutionary synthesis.

2 Background to a macroevolutionary synthesis

2.1 Vindicating D’Arcy Thompson

Stephen Jay Gould was born in 1941 in Bayside, Queens, and completed his Bachelor’s degree at Antioch College in 1963. His earliest intellectual hero was the Scottish polymath D’Arcy Thompson—a celebrated morphologist whose *On Growth and Form* became the guiding light of his early career (Gould 1995,

p. 3). As an undergraduate, Gould admired Thompson beyond measure, and made of him the subject of his senior thesis, published as “Form in Biology” in the *Antioch Scholastic Journal* (1963). Probably it was Thompson’s study of equiangular spirals that launched Gould on the course that would culminate in his Ph.D. dissertation (advised by Norman Newell)—an extensive study of the Bermudan land snail *Poecilozonites*.³ As Niles Eldredge recalls:

Steve had discovered...an unwrapped, unstudied collection of Bermudan Pleistocene land snails in the basement of the Geology Department at Antioch...[S]mitten with the geometric growth of these well-preserved snails...[he] vowed to one day make them the subject of his doctoral dissertation. (Eldredge 2013, p. 6)

Gould was as good as his word, and after “the usual scaling down of initial plans,” produced a dissertation on the species *P. cupula* and *P. bermudensis* in 1967 (Gould 1969, p. 409). A monograph soon followed, at which time Gould had left Columbia University for the Museum of Comparative Zoology at Harvard. Through the vicissitudes of growing celebrity, he continued to publish morphological studies, mostly on the land snail *Cerion*, whose “riotous diversity” stirred one of his most effusive essays (Gould 1983). In addition, he authored a classic review paper on “Allometry and size in ontogeny and phylogeny” (Gould 1966a), made forays into paleoecology and biomechanics (Gould 1970c, 1971b), published a number of historical studies (e.g., Gould 1970b, 1971a), and penned a manifesto baptizing a “science of form” within evolutionary paleontology (Gould 1970a). Not yet thirty, Gould’s scientific star was burning bright; yet it was not until “Punctuated equilibria” (Eldredge and Gould 1972) that he became a known commodity outside of paleontology.

As David Sepkoski observes in *Rereading the Fossil Record*, Gould was among the first generation of paleontologists “adept at quantitative analysis, [and] prepared to employ general theoretical models to explain how evolution worked” (Sepkoski 2012, p. 3). Yet for all his sophistication, Gould’s interests hardly distinguished him as a radical (Sepkoski 2009a). Although he did not express himself thus, his fondest hope was to provide a Darwinian rationalization of D’Arcy Thompson’s morphology—a means of judging “the adaptive reasons for specific pathways in the phylogeny of form” (Gould 1970a, p. 85). This was to be achieved by “a mild mechanistic reductionism” that fused the elegance of Thompson’s biometrical approach with the power of modern computational methods. “A science of form is now being forged within evolutionary theory,” Gould declared in an early paper, “Evolutionary paleontology and the science of form.” “It studies adaptation by quantitative methods, using the organism-machine analogy as a guide; [and] it seeks to reduce complex form to fewer generating factors and causal influences” (Gould

³ Norman Newell was a celebrated invertebrate paleontologist and pioneer of the quantitative study of mass extinctions, who spent the majority of his career at Columbia University and the affiliated American Museum of Natural History (see Sepkoski 2012, Ch. 2). Along with John Imbrie (also an invertebrate paleontologist at the AMNH), Newell was an important influence on Gould’s early career, in particular, his decision to apply quantitative methods to problems in invertebrate paleontology (see Princehouse 2009; Eldredge 2013).

1970a, p. 77). Most importantly, it utilized multivariate statistics, which—although clearly useful to morphologists—had long been neglected because of the immense labor involved in their use (Gould 1967, p. 385). It was for this reason, Gould believed, that Thompson’s promising start had foundered:

Unfortunately, D’Arcy Thompson was about one half-century too early. His approach to form was multivariate in conception; hence it suffered the misfortune of much prophesy—it could not be used in its own time. (Gould 1971a, pp. 253–254)

With the advent of high-speed computing, however, Thompson’s vindication was at hand (Gould 1971a, p. 254). “I am convinced that the computer can be to the science of form what the microscope, telescope and electron accelerator were to their respective fields,” Gould wrote in “Evolutionary paleontology” (p. 102). His confidence stemmed from the fact that much of morphology is ‘inherently multivariate,’ and likewise systematics and evolutionary biology (Gould 1967, p. 385). Bivariate methods had achieved great popularity in virtue of their tractability (which was nonetheless decisive in an era of manual calculation). But this constraint had now been lifted, and enterprising biologists could look forward to a period in which important problems, hitherto intractable, could finally be addressed in a rigorous way. For instance, utilizing an analog computer, David Raup was able to generate a three-dimensional “block” that contained “most of the theoretically possible [forms]” of coiled shells (Raup and Michelson 1965, Raup 1966). From here, Raup proceeded to offer a number of intriguing observations regarding the occupation of morphospace:

When the geometries of naturally occurring species are plotted in [morphospace], it becomes evident that it is not evenly filled. Evolution has favored some regions while leaving others essentially empty. In the empty regions we are presumably dealing with forms which are geometrically possible but biologically impossible or functionally inefficient...It is often easier to explain the absence of forms than their presence. (Raup and Michelson 1965, p. 1294)

Gould saw Raup’s studies as touching a fundamental issue in the science of form, and one that resonated with his own empirical work.⁴ The issue was the cause of form, or what came to the same thing, “the explanation of form in terms of adaptation” (Gould 1967, p. 385).⁵ Gould was determined to put an end to “vague, trivial and untestable” adaptive hypotheses in paleontology, which did little more than formalize the intuitions of individual workers (Gould 1971a, p. 256). What was

⁴ Gould also published a single study in theoretical morphology, a simulation of the spiral morphology of a group of Ordovician organisms known as receptaculids (Gould and Katz 1975).

⁵ To use the terminology of Gould (1971b), Raup’s studies of coiled shell morphology are primarily concerned with the “how” of form: that is, with reducing complex morphologies to a small set of factors that can generate them during growth. However, as Gould (1970a, p. 92) observes, “Raup has extended [his] methods far beyond the simple insight that a complicated form can be produced by a few simple instructions,” and is actively investigating the “why” of form as well (see especially Raup 1967, pp. 54–65). And it is the latter issue, “the explanation of form in terms of adaptation,” which constitutes “the fundamental problem of evolutionary paleontology” (Gould 1967, p. 385).

needed was a means of testing adaptive hypotheses in situ; in other words, a “paleontology of the present,” capable of leveraging the unique precision of the experimental approach. Raup’s theoretical morphology could not do this, but it *could* offer something complementary—a formal model demonstrating what Thompson had long ago suspected: that the space of viable designs is strongly limited by physical laws. Only some organic designs are geometrically possible (able to be instantiated in physical media), and of these only a few satisfy the principles of good design (thus enabling them to exist in an environment). What’s more, these designs “can be determined a priori, and used to predict the forms of undiscovered organisms performing specified functions.” What had once seemed mysterious—for instance, the prevalence of parallelism and convergence in the evolution of higher taxa—can now be “explained and even predicted” (Gould 1971a, p. 257).

If there is a coordinating theme of Gould’s early work, it is the application of multivariate statistics to biological problems, in particular, the problems of form (adaptation).⁶ Indeed, multivariate analysis represented, to Gould, something more than a set of techniques—it was a systematic approach to the problems of life.⁷ As Gould wrote of computerized multivariate analysis (with co-author R.F. Johnson): “[We] must emphasize the influence that this new technology, or any new technology for that matter, must have upon our approach to a problem. A new method is not simply a neutral tool for the resolution of issues in well-established ways (the microscope did not simply let us see things *ad majorem Dei gloriam* on a smaller scale)...[instead,] it imposes its capabilities upon the questions we ask and even upon the theories that support these questions” (Gould and Johnson 1972, p. 488). Yet while the increased application of multivariate methods would doubtless change “the questions [paleontologists] ask, and even...the theories that support these questions,” it would not change the fact that “our ultimate goal in the study of a phyletic lineage is the explanation of each morphological change in terms of its selective advantage, its purpose or final cause expressed materially” (Gould 1966a, p. 621). Gould’s science of form, being a branch of evolutionary paleontology, was first and foremost a science of adaptation.

2.2 Invertebrate paleontology and the science of form

It is noteworthy that the four leading protagonists of Gould’s adaptationist manifesto, “Evolutionary paleontology and the science of form” (1970) were invertebrate paleontologists—Gould, David Raup, Martin Rudwick and Adolph

⁶ See, for instance, Gould (1966b), (1967), (1968), (1969), (1970c), (1972), (1973a), (1973b), (1974), (1975), Gould and Garwood (1969), Gould and Johnson (1972), Pilbeam and Gould (1974). Several of these projects are discussed in Roger D.K. Thomas’s essay: “Gould’s odyssey” (2009), which also considers Gould’s morphological researches after 1975.

⁷ As I mentioned above, it was John Imbrie who is most responsible for Gould’s pursuit of multivariate analyses of form and geographical variation during his early career (Eldredge 2013, p. 8). Recruited to the AMNH by Newell, Imbrie was the foremost paleontological expert on multivariate statistics during Gould’s graduate years, and a keen advocate of factor analysis. For an excellent account of Imbrie’s “statistical paleontology,” see Sepkoski (2012) (pp. 83–91).

Seilacher.⁸ Of course, this was no coincidence. Gould had constructed his science of form to leverage the unique features of the invertebrate fossil record, not the least of which was the sheer wealth of specimens available for analysis. But this effort would be wasted if he could not establish that invertebrate groups display *clear marks of improvement over time*—a prerequisite for their inclusion as objects of macroevolutionary study (Gould 1970a, pp. 108–109). To this end, Gould enlisted one of his favorite argumentative strategies: displaying the constraining effects of some received bit of wisdom. “Rarely do we realize how little our current perspective provides invertebrate life with a history of form—defining history as directional change through time,” Gould lamented (1970a, p. 108). “A history of diversity it surely has, for the pulse of mass extinction established the larger divisions of history’s time and still inspires paleontologists to intense debate.” “So too, in one sense, do we have *change* of form, but it is often placed in a strange static framework that recalls the steady-state of Lyell’s world—change without history” (ibid, p. 109, emphasis added).⁹ But what reason do we have for accepting this “static framework” as the sole appropriate representation of invertebrate phylogeny?

I will argue that our standard picture of evolution prevents us from seeing certain key phenomena in a light that would provide invertebrate life with a history. That picture is the tree of life, a model of diversity with ever diverging branches. The phenomena are parallelism and convergence on the one hand and an aspect of ‘adaptive radiation’ on the other. (Gould 1970a, p. 109)

Why did Gould feel it necessary to establish that invertebrate groups display clear marks of improvement over time? In a word: because if the history of invertebrates is a history of change unaccompanied by mechanical improvement, then the *real* paleontological action lies elsewhere—in the vertebrate fossil record.¹⁰ Invertebrate paleontologists can describe and classify; they can date rocks by examining fossil assemblages and practice functional morphology on particular

⁸ These individuals commanded the most space in the text, and earned the greatest number of citations. Equal in citation number to Seilacher, but featured less prominently in the text, are the vertebrate paleontologists George Simpson and Björn Kurtén.

⁹ Since Gould (1970a) defines “history” as “directional change through time” (p. 108), and since (on the very next page) he equates “history” with “biological progress” (p. 109), “change without history” means something like “directionless change,” or change unaccompanied by mechanical improvement.

¹⁰ George Simpson made this very claim in a 1961 review paper, stating: “The study of fossil *vertebrates* elucidates the general principles of evolutionary biology” (p. 1679, emphasis added). This statement seems innocent enough, until one considers the state of invertebrate paleontology during the first half of the twentieth century (see Rainger 2001). “[It] is almost as if invertebrate paleontology [is] in bondage to geology,” the gastropod specialist J. Brookes Knight complained in a presidential address to The Paleontological Society (Knight 1947, p. 282). The average invertebrate paleontologist is “not a paleontologist at all...He is...a stratigraphical or ‘soft rock’ geologist,” and therefore ill-equipped to investigate evolutionary problems. Edwin Colbert, a vertebrate paleontologist, carried this criticism even further: “[It] is not only a question of lack of interest in the subject, for it is a fact that most of our contemporary geologists are not even competent to take more than a superficial interest in evolutionary problems” (Colbert 1947, p. 289). To be sure, the situation had improved somewhat by 1963, when Gould entered graduate school. But it was far from rectified, even in the elite centers of paleontological training (see Sepkoski 2012, pp. 55ff; Eldredge 2013, p. 6).

groups of organisms. Yet of the outstanding problems of paleontology (the problems of large-scale evolution), they can say but little. In the words of Bobb Schaeffer: “The most convincing evidence for biological improvement through time can be found in the vertebrates, which have numerous skeletal elements associated with both feeding and locomotion” (1965, p. 319).¹¹ Invertebrates, by contrast, are morphologically depauperate, and therefore ill suited to “the mechanical analysis of organic design.” To Gould, such defeatism was flatly unacceptable. According to Gould, the ubiquity of parallelism and convergence vindicates both “the idea of biological improvement” and “the notion of an invertebrate history” (i.e., the notion that the history of invertebrate groups is a history of directional change) (Gould 1970a, p. 109).¹² The reason is that parallelism and convergence become intelligible only when biological improvement is admitted; but once it is admitted, there is no justification for acknowledging it only in vertebrate lineages. It was Gould’s hope that invertebrate paleontologists would recognize this, and dedicate themselves to providing rigorous functional explanations of “evident history.” “That we may do so in the future,” Gould remarked, “is the greatest promise of [the science of form]” (ibid, p. 110).

To conclude, Gould’s early morphological researches were not a manifestation of his later interest in structuralist themes (like *constraint*, which provides a positive alternative to natural selection as an explanation of morphological trajectories in evolution). Rather, they were an attempt to provide a platform from which “evident history” (patterns of directional change) could be explained in terms of mechanical adaptation. Especially important were the phenomena of parallelism, convergence and biological improvement, the third of which Gould believed to explain the other two (at least in certain circumstances). In the next section, I will explore this relationship in greater detail, focusing on the important role of “experimental stud[ies] of adaptation in fossils” (Gould 1970a, p. 80).

3 The mechanics of adaptation

3.1 The science of form as an engineering science

“A science of form is now being forged within evolutionary theory,” Gould announced, in a subtle but calculated turn of phrase (Gould 1970a, p. 77). His message could hardly have been missed by his colleagues, especially those accustomed to respecting disciplinary boundaries. Not paleontology, but *evolutionary theory* was to be the crucible of the science of form, whose purpose it was to “provide new insights into paleontology’s unique domain...transspecific evolution and major patterns in the history of life” (ibid, p. 80). But how was this program to

¹¹ Bobb Schaeffer was a longtime curator of fossil fishes at the American Museum of Natural History, and Gould’s teacher at Columbia.

¹² By “biological improvement,” Gould means mechanical improvement of the engineering type that occurs in a constant physical environment.

be carried out? In other words, how was the science of form to “reinstall paleontology as a source of new themes for evolutionary theory” (ibid, p. 112)?

The answer, in a word, was *by turning the study of adaptation into an engineering science*—one capable of providing mechanical analyses of organic design, and of judging “adaptive reasons for specific pathways in the phylogeny of form” (Gould 1970a, p. 85). On the face of it, this does not seem too different from the various adaptationist research programs already underway in the 1960s. But Gould’s criterion of adaptation was not that of neo-Darwinian icons like Ernst Mayr and George Gaylord Simpson, who regarded adaptations as ‘properties of organisms that add to their expected reproductive success in an environment’ (see, e.g., Mayr 2001, p. 283). (Under this criterion, physiological and behavioral traits are on a par with morphological ones, as concerns their status as adaptations.) Rather, Gould’s criterion of adaptation was that of D’Arcy Thompson, who wrote that “adaptation in the strictest sense” is none but “mechanical fitness for the exercise of some particular function or action that has become inseparable from the life and well-being of the organism” (Thompson 1942, p. 958). Thompson continues:

Of a very different order from all such [non-mechanical adaptations] are those very perfect adaptations of form which, for instance, fit a fish for swimming or a bird for flight. Here we are far above the region of mere hypothesis, for we have to deal with questions of mechanical efficiency where statistical and dynamical considerations can be applied and established in detail. The naval architect learns a great part of his lesson from the streamlining of a fish; the yachtsman learns that his sails are nothing more than a great bird’s wing, causing the slender hull to *fly* along; and the mathematical study of the streamlines of a bird, and of the principles underlying the areas and curvatures of its wings and tail, has helped to lay the very foundations of the modern science of aeronautics. (Thompson 1942, p. 960)

Gould had a problem, however. If the science of form was to succeed in providing “new insights into...transspecific evolution and major patterns in [life’s history],” it is not enough that it should reveal organisms to be adapted to their surroundings—for “who doubts that animals tend to be well-designed?” (Gould 1980b, p. 101). In addition, it must show that the major patterns of evolution are generated by epistemically accessible processes, in particular, processes leading to the increased efficiency of organic structures. Not all adaptations are created equal, after all (this was Thompson’s point), nor are all modifications the stuff of transspecific evolution. Rather, certain modifications are distinguished from the common run of evolutionary changes by “the expanded potential for further progress...conferred upon organisms bearing them” (Gould 1966a, p. 591). It is *these* adaptations that are most likely to be implicated in major evolutionary events—in particular, the origin of new and higher taxa, the chief focus of macroevolutionary studies during the 1960s. Accordingly, if the science of form was to shed light on the workings of transspecific evolution, it needed a way of rigorously analyzing episodes of biological improvement. For this, Gould turned to Rudwick’s *paradigm method*, a technique of formalized analogical reasoning based on a rigorously mechanical notion of adaptation.

3.2 The mechanics of transspecific evolution

Recall that Gould's science of form was a three-pronged venture consisting of statistical, computational and experimental approaches. These addressed a pair of broad problems in evolutionary paleontology: first, how is biological form produced (what morphogenetic rules are implicated in the production of complex structures) and second, what is the adaptive significance of observed changes in form (their "purpose or final cause expressed materially"). In Gould's view (ca. 1970), satisfactory explanations of phyletic history require investigators to address each of these problems—to resolve apparent complexity into a small number of developmental causes, and to specify adaptive reasons for each morphological change. The first problem can be addressed in one of two ways: by multivariate statistical analysis (which describes variability among observed correlated variables) or by mathematical simulations of form (e.g., Raup 1966). In contrast, the second problem needed to be attacked *experimentally*, either by direct manipulation of organic structures or by the analysis of "natural experiments."¹³

But how can a scientist manipulate *extinct* organisms in order to ascertain the significance of particular morphological changes? Here Gould took a pointer from Martin Rudwick, a prominent invertebrate paleontologist and student of mechanical adaptation. According to Rudwick, "The detection of any adaptation in a fossil organism must be based on a perception of the machine-like character of its parts and on an appreciation of their mechanical fitness to perform some function in the presumed interest of the organism" (Rudwick 1964, pp. 34–35). To facilitate this process, he developed his "paradigm method": a test of relative mechanical fitness that pits fossil structures against an ideal of operational efficiency (or "paradigm") specified in engineering terms. The reasoning behind the method can be described in four steps (following Carter 1967, see also Niklas 2009):

1. *Functional specification* A function is proposed for a particular biological structure (the "focal structure"). Ideally, investigators will be able to specify a *range* of possible functions compatible with what is known about the organism's conditions of life.
2. *Identification of the paradigm* The function is transcribed into engineer's terms, allowing the researcher to identify "the structure that would be capable of fulfilling the function with the maximal efficiency available under the limitation imposed by the nature of the materials" (Rudwick 1964, p. 36). (A "paradigm,"

¹³ As Gould observes in "Evolutionary paleontology," natural experiments afford an opportunity to study adaptation *in situ* without limiting ourselves to "modern manipulation" (Gould 1970a, p. 89). (Natural experiments are empirical studies in which the experimental and control conditions are determined by nature, not by human intervention.) Here he cites the work of Adolph Seilacher, who examined patterns of boring on fossilized belemnite shells, which he assumed to be "adjusted to the normal, head-on movement of the belemnite" (Seilacher 1968, p. 279). This led Seilacher to conclude that "the streamlining of the rostrum is related only to occasional backward escapes ([an] 'emergency adaptation')." Gould's 1970 study of parallel evolution in Bermudian microgastropods also utilized a natural experiment, which leveraged historical fluctuations in the availability of calcium carbonate (an important mineral in gastropod shell construction) to test a number of adaptive hypotheses relating to shell morphology (Gould 1970c).

- Rudwick stresses, is just a structural prediction.) If more than one function is being considered, multiple models should be constructed, each embodying a separate paradigm.
3. *Test of predictions* The resulting paradigm is quantitatively compared to the focal structure with regards to its ability to perform the specified function (see Rudwick 1961; Paul 1968). If the researcher has transformed rival functional proposals into paradigms, he or she should then compare the focal structure's 'closeness of fit' to *each* paradigm.
 4. *Assessment of confidence* Finally, the "degree of approximation between [a] paradigm and an observed focal structure is [interpreted as] a measure of the degree of efficiency with which the structure would have been physically *capable* of fulfilling the function" (Rudwick 1964, p. 36). If multiple paradigms were proposed, comparison may reveal which of the paradigms the focal structure most resembles (i.e., which function the observed structure best performs). Of course, the paleontologist cannot know with certainty whether the extinct organism *actually* performed the postulated function. The paradigm method nonetheless furnishes an estimate of functional efficiency that can be compared to that of similar structures, and used to formulate functional explanations of phyletic history (see Gould 1970a, p. 110).

Why did Gould rate Rudwick's "criterion for judging the relative efficiency of structures by...mechanical analysis" as the "central idea" of the science of form (Gould 1971b, p. 61)? The answer has two components. In the first place, Gould believed that "[throughout] the history of paleontology, the greatest deterrent to a science of adaptation has been the lack of quantitative criteria for assessing the relative efficiency of similar structures" (Gould 1970a, p. 85). The "paradigm method" removed this deterrent, and enabled paleontologists to draw a range of inferences regarding the ability of extinct organisms to perform certain (hypothesized) functions. For instance, "[from] our knowledge of natural and artificial aerofoils, and of the structural requirements of their successful operation, we [may] conclude that pterodactyl forelimbs would have been physically *capable* of functioning as an aerofoil," Rudwick claimed in 1964:

All we need, ideally, is a knowledge of the operational principles involved in all actual or conceivable flight mechanisms possible in this universe. Consequently, the range of our functional inferences about fossils is limited not by the range of adaptations that happen to be possessed by organism at present alive, but by the range of our understanding of the problems of engineering. (Rudwick 1964, p. 33)

But Gould was not just looking for a precise way of studying mechanical adaptation in fossils. In addition, he was looking for a precise way of studying the "history of form—defining history as directional change through time" (Gould 1970a, p. 108). Thankfully, the two problems are related, at least so far as "the evolution of most major groups is...a history of mechanical improvement [i.e., improvements of the engineering type that take place in constant physical environments]" (ibid, p. 111). To explain "history," Gould believed, was to provide

functional analyses of directional morphological changes taking place within higher taxa. But to say that mechanical improvement was *actually occurring in a particular taxon* required some standard against which early and late members of a taxon could be compared. Rudwick's paradigms provided such a standard. Should the later members of a taxon more closely approximate a particular paradigm than the earlier members (thus exhibiting greater mechanical efficiency with respect to a hypothesized function), the investigator may conclude that mechanical improvement has taken place in this taxon. Christopher Paul (1968), for example, had "demonstrated that the independent transition from discrete to confluent dichopores in all lines of Ordovician glyptocystids produced an improvement in circulation that can be defined in quantitative and mechanical terms" (Gould 1970a, p. 110). If the science of form was to "reinststate paleontology as a source of new themes for evolutionary theory," more explanations of this type were needed.

3.3 Parallelism, convergence and the principle of limited solutions

Gould was ambitious, and recognized the value of identifying phenomena that, while downplayed by conventional evolutionary theory, nonetheless fell within the scope of his science of form. Especially intriguing were the bugbears of classical taxonomy: parallelism and convergence (Gould 1970a, pp. 109–112). Following a lead from D'Arcy Thompson, Gould suggested that *if* it could be shown that functional problems admit of a limited number of solutions, or *if* physical processes induce structures by mechanical necessity, then the science of form will have made a distinctive contribution to evolutionary theory (1970a, p. 112). Specifically, it will have shown that a "fundamental difference in explanation [exists] for similar events at micro- and macrolevels"—the former can be explained without recourse to mechanical improvement, the latter cannot. Since parallelism and convergence are "dominant features" of the "macrolevel" (Gould 1970a, p. 78), it may even be the case that entirely new pictures of phylogeny are required in order to capture the dynamics of the transspecific evolution (Gould 1968, p. 97, 1971c, p. 416). Extrapolating species divergence over vast times "does not give sufficient emphasis to the massive parallelism and trends towards increased mechanical efficiency that proceed in relatively constant physical environments," Gould urged in a 1969 monograph (Gould 1969, p. 497). "These are the major determinants of patterns in transspecific evolution, but have little relevance to phenomena of intraspecific variation."

What explanations did Gould offer for the phenomena that, in his view, dominate the evolution of higher taxa? As he speculated in a 1968 article, "Ontogeny and the explanation of form," "Three adaptive explanations" will account for most instances of parallelism and convergence:

1. The adaptation is only one among a number of possible solutions; independent development of a large number of features is possible because the genetic change is a small one even though its effects are large—e.g., pedomorphosis.
2. The adaptation arises many times because it is the only possible solution to a given problem: for example, differential thickening of weight-supporting bones and secondary quadrupedalism among dinosaurs to compensate for increasing

- size and streamlining in three orders of secondarily aquatic mammals in response to new environments.
3. The adaptation is a general biological improvement...Parallelism in biological improvement is an aspect of the principle of limited solutions but is separated from the preceding category because the mechanical inevitability that necessitates adaptation is not involved here. The holostean feeding mechanism is viable [although it is mechanically inferior to that of teleosts, which therefore constitutes a biological improvement], but a *Brontosaurus* with two spindly legs would collapse (Gould 1968, p. 97).

These three explanations “separate into two opposing tendencies,” the first of which emphasizes “ease of genetic change” (explanation 1), the second “the principle of limited solutions” (explanations 2 and 3). According to Gould, ease of genetic change is a *microlevel* property, which pertains mostly to evolution within species (“micro-evolution”). It therefore has limited relevance for students of *macrolevel* events, who must instead seek their explanations in the D’Arcy Thompsonian “principle of limited solutions.” But what is the principle of limited solutions, exactly? Gould nowhere explicitly says; yet a careful reading discloses that it contains two claims: one factual, the other epistemic. In drawing this section to a close, it will be useful to express these claims precisely, for they together form the pivot of Gould’s first macroevolutionary synthesis.

I have already described the *factual content* of the principle of limited solutions, which says, in brief, that the laws of mechanics “specify a limited number of good designs for the solution to common problems faced by animals” (Gould 1971a, p. 257). It is this claim that underwrites Gould’s mechanical explanations of parallelism and convergence (explanations 2 and 3, above), and secures paleontology’s essential contribution to any complete theory of evolution (Gould 1969, p. 497). Equally important, however, is the *epistemic content* of the principle, which says that these “good designs” can be determined *a priori*, and used to attribute functions to extinct organisms (Gould 1971a, p. 257). It is this claim that supports the use of paradigm analysis to study biological improvement, and rescues the science of form from the clutches of “vague, trivial and untestable [hypotheses]” (*ibid.*, p. 256). Added together, the two halves of the principle of limited solutions provide a sturdy platform from which paleontologists can attack problems of transspecific evolution. Yet this platform is not the whole of Gould’s first macroevolutionary synthesis. In addition, Gould wished to provide evolutionists with an appropriate iconography of transspecific evolution; and for this he turned to his other intellectual guru (besides D’Arcy Thompson)—Julian Huxley.

4 The gradal scheme

4.1 Huxley and Gould

While Gould’s early writings are permeated with Thompson’s mechanical view of adaptation, another theme is equally prominent—the relationship between size and

shape (which Gould assumed to be adaptive). In *Growth and Form*, Thompson had much to say about this relationship, especially in his famous chapter, “On Magnitude” (Thompson 1942, pp. 22–77). But the subject received its definitive treatment in Julian Huxley’s groundbreaking work, *The Problems of Relative Growth*, published in 1932.¹⁴ *Relative Growth* was primarily a treatise on bivariate allometry, and sought to “penetrate the veil of static morphology” by “circumventing time” (Gould 1997, p. 7). Specifically, Huxley’s strategy was to plot the size of one part of an organism X against the size of the whole organism (or another of its parts) Y , thus enabling the bivariate relationship between X and Y to be expressed in simple mathematical terms. By circumventing time, Huxley discovered a powerful tool for representing allometric trends (changes in shape that systematically accompany changes in size). In addition, he was able to state an influential formalism, the so-called “law of heterogonic growth” (now the “allometric equation”), which supplied the topic for Gould’s first paper, “Interpretation of the coefficient in the allometric equation” (White and Gould 1965).

Few individuals influenced the young Gould more than Julian Huxley, from either an intellectual or a professional standpoint. “I was just awestruck by Huxley,” Gould recalled in a 1998 interview, “so I wrote him a long letter saying how much his work had meant to me” (Princehouse 2009, p. 156). Clearly, Gould impressed Huxley as well, for Huxley responded to his letter by commissioning an article on “Allometry and size in ontogeny and phylogeny” in *Biological Reviews*—Gould’s first landmark publication (Gould 1966a). Several years later, Gould took up another of Huxley’s ideas, the so-called *gradal scheme* of classification, which attempted to provide “fresh insight into the nature of [evolutionary] processes” by circumventing phylogenetic time (Gould 1997, p. 45). The gradal scheme was the final piece of Gould’s first macroevolutionary synthesis, and helped to integrate his various interests in biological improvement, macroevolutionary patterns and the principle of limited solutions (Gould 1968, p. 97, 1970a, p. 112, 1971c, p. 416). Although not a part of the science of form (being instead a part of *systematics*), the gradal scheme provided a view of life’s history that fit the needs of Gould’s macroevolutionary synthesis perfectly. The remainder of this section explores the principles of gradal classification, and its role in scaffolding Gould’s vision of transspecific evolution. I close with a brief recapitulation of the key concepts and aims of Gould’s first macroevolutionary synthesis.

4.2 Gradal classification and transspecific evolution

Julian Huxley was neither a paleontologist nor a taxonomist, yet he made significant contributions to paleontology by proposing refinements to the theory of animal taxonomy. Probably the most influential of these was his distinction between “clades” and “grades” (Huxley 1957, 1958), which was quickly adopted by leading taxonomists like George Simpson (1961) and Ernst Mayr (1963). According to

¹⁴ *Problems of Relative Growth* is dedicated to D’Arcy Thompson, with whom Huxley maintained an active correspondence. Interestingly, the long epigram that follows Huxley’s dedication—a Thompsonian meditation on the correlation of parts—is quoted at length in Gould’s most influential paper, “Punctuated equilibria: an alternative to phyletic gradualism.” .

Huxley, there are two ways of classifying the results of evolution—either by propinquity of descent (monophyly) or by the possession of the similar anatomical, physiological and behavioral properties. The former strategy seems to leave something out—and something of major evolutionary importance (biological improvement). In order to take better account of the progressive aspects of evolution, Huxley counseled, “the customary terminology purporting to define [monophyletic] units” should be supplemented with a secondary terminology “aimed at delimiting steps of anagenetic advance [biological improvement]” (Huxley 1958, p. 27). “The best general term for such anagenetic units would seem to be *grade*,” he wrote (hence, “grades” denote stages of biological progress). “I further suggest the term *clade*, to distinguish monophyletic units of whatever magnitude.” In the future, taxonomy “will have to envisage a two-way system of classification, which will do justice to the facts of biological improvement and persistence of types as well as to those of phylogenetic divergence...This will presumably involve some new terminology, though not necessarily subject to the international rules of nomenclature” (Huxley 1957, p. 455).

In Huxley’s view, the movement of a lineage towards a higher grade is attended by a stepwise improvement of adaptive characters, with each step precipitating a minor cladogenetic event (Huxley 1963). Once a higher grade is attained, the lineage—even if it ceases to experience significant anagenetic change—may nonetheless flourish “as a result of bountiful speciation and various modification in the basic adaptive theme of the grade” (Mayr 1976, p. 450).¹⁵ Consequently, “improvement of general organisation is brought about by a succession of [dominant] types,” each of which

achieves its evolutionary success by virtue of superior organisation, and as a result evolves into a new taxonomic group which radiates (undergoes cladogenesis) at the expense of the earlier groups in competition with it, including the group of similar taxonomic rank from which it has originated...This process appears to apply to the anagenesis of all taxa from genus upwards, and indeed inevitably results in a taxonomic hierarchy. (Huxley 1963, Prefix [not paginated])

What good did Huxley anticipate his gradal scheme would do within biology? First and most importantly, it would direct biologists’ attention to “the problem of progress”—and since “anagenesis” is just another word for “biological improvement,” different types of improvement could be seen to associate with different types of evolutionary outcome (e.g., limiting specialization, non-limiting progress). Second, it would foster an appreciation of two important truths: “[1] that many delimitable taxa are simultaneously grades and clades, and [2] that others are grades which may or may not also be single clades” (Huxley 1958, p. 455). The second point, concerning the multiple origins of grades, is especially important, and recapitulated in “a lucid and useful way” a piece of paleontological lore (Mayr

¹⁵ Here it bears mentioning that grades, in Huxley’s view, are *stable units* of anagenetic advance (Huxley 1957, p. 454). Grades are therefore attained *only when anagenesis is arrested*; that is, when progress is consolidated by “stasigenetic,” or stability inducing, evolutionary processes.

1963, p. 608). As Simpson observed in *The Major Features of Evolution* (1953), probably the majority of higher taxa “are polyphyletic in detail [with] more than one single lineage or specific line [having] crossed the arbitrary boundary as dawn by systematists” (p. 349). What Huxley accomplished when he equated certain important taxa with “grades” was to render this parallelism the expected result of anagenesis. Anagenesis produces biological improvement *by definition*, Huxley observed, and grades are stabilized units of anagenetic advance. Consequently, transspecific evolution must be understood in terms of biological improvement, leading severally to new and higher organizational levels.

But not just any biological improvement is competent to bring about *indefinite organizational advance* (which, in Huxley’s view, is the most important feature of evolution). For instance, “[the] particular improvement of a line in relation to a special way of life” leads most often to the “*restriction* of any further improvement...Specialization almost invariably forces organisms into a deepening evolutionary groove out of which it is increasingly impossible for them to climb” (Huxley 1954, p. 9, emphasis added). By contrast, “major anagenetic transformations, such as those leading to the formation of a new successful...Class or Subclass,” typically involve improvements in “all-round functional efficiency [i.e., general biological improvement]” (Huxley 1963, Prefix [not paginated]). The upshot of such transformations is an improved “general organisation,” which enables the favored lineage to radiate “at the expense of the earlier groups in competition with it, including the group of similar taxonomic rank from which it has originated” (ibid, p.).¹⁶ It is in this way that lineages undergoing biological improvement will gradually overtop their kin and competitors.

From these remarks it is clear that the gradal scheme is no mere system of classification; in addition, *it is a viewpoint regarding the nature of transspecific evolution* (Gould 1976, p. 120). The significant events in life’s history (which, by Huxley’s lights, are the major steps of anagenetic advance) proceed by the sequential improvement of important characters—a process Gavin de Beer called “mosaic evolution” (1954). Yet the lineages undergoing this process are *not* species, which are gradually transformed by natural selection operating within a single interbreeding community. Rather, they are higher taxa, which undergo anagenesis in virtue of the parallel transformation of many (but not all) species-lineages. Bobb Schaeffer (a vertebrate paleontologist, and Gould’s teacher at Columbia) summarizes this view as follows:

The transition from one higher level of organization [grade] to another always involves some form of biological improvement for the same or a new way of life. Except in rare cases when a single lineage attains a new level, the transition is expressed in terms of similar adaptations (broad adaptations) that

¹⁶ Notice that while this process will tend to produce monophyletic grades “near the level of the taxon actually arising” (e.g., orders, classes), it should *not* be assumed that these would qualify as monophyletic at lower taxonomic levels (e.g., species, genera). While anagenesis followed by cladogenesis sometimes produces monophyletic grades at the species level, this outcome requires that *no* other lineages independently achieve the same organizational level. And this Huxley and others presumed to be rare (see, e.g., Simpson 1953, p. 348; Mayr 1963, p. 609).

evolve more or less in parallel in lineages of common ancestry...The partly opportunistic nature of this process implies that these lineages will approach or enter a new level with varying degrees of success. (Schaeffer 1965, p. 318)

It should now be obvious why the gradal picture appealed so strongly to the young Stephen Jay Gould. In Gould's view, the history of "most major groups" is a history of mechanical improvement—that is, improvements of the engineering type that occur in relatively constant physical environments (Gould 1970a, p. 111). Now, since the solutions to the functional problems facing animals are limited (as Thompson argued, and Raup ostensibly demonstrated), it is expected that such improvement will produce massive parallelism and convergent evolution at high taxonomic levels (Gould 1968, p. 97). As Gould wrote in 1970: "A quantitative and functional science of form suggests that parallelism and convergence are *dominant phenomena* [in transspecific evolution], not mere taxonomic nuisances" (Gould 1970a, p. 78, emphasis added). And this is precisely what the gradal scheme leads us to expect (notwithstanding that it supplies no mechanism, comparable to the principle of limited solutions, to account for this pattern). Gould summarizes:

If efficient solutions to common problems of optimization are as limited as D'Arcy Thompson has claimed, then grades are levels of structural organization that may be reached independently by different lineages. Many higher taxa are not the monophyletic clades that most theories of classification require (or at least desire) but are grades of improvement attained in the same way by many lineages...When solutions to common problems are limited and success confers great advantages on lineages in competition, parallel evolution is rampant. A "phyletic bias"—and its metaphor, the evolutionary tree—has prevented proper assessment and understanding of the severe constraints that mechanical limits (including size itself) place on adaptive design. (Gould 1976, pp. 119–120)

Gould concludes with an affirmation of the gradal scheme's importance, which verges on a promise: "[The gradal scheme's] emphasis on resemblance and functional morphology may inspire a science of form as powerful as the current science of diversity...Long live the analog and its science of functional morphology" (Gould 1976, pp. 120–121).

4.3 Recapitulation

As I earlier remarked, the principle of limited solutions is the keystone of Gould's first macroevolutionary synthesis. Although somewhat impressionistic, it provides the prediction on which the whole enterprise is founded—in a world of limited solutions, transspecific evolution should be characterized by parallelism, convergence and "trends towards increased mechanical efficiency." Large-scale evolution is severely constrained by the principles of good design, and it is the charge of the evolutionary paleontologist to make use of these principles in his or her explanations. Successful explanations are those that *rationalize evident history*, either by displaying evidence of increased mechanical efficiency over time, or by

demonstrating that multiple lineages evolved the same (mandatory) solution to a shared functional problem. The principle of limited solutions thus supplies a mechanical explanation of paleontology's "distinctive contribution" to modern evolutionary theory: the recognition that parallelism and convergence are ubiquitous features of transspecific evolution (Sylvester-Bradley 1959).

Gould's "science of form" aimed to raise the status of invertebrate paleontology within evolutionary biology, and therefore to score a victory for paleontology as a whole. By attending carefully to the mechanics of adaptation, the science of form could throw new light on "paleontology's unique domain...transspecific evolution and major patterns in the history of life" (Gould 1970a, p. 80). But Gould had a problem. When he began making his case, he was barely out of graduate school—the author of a brilliant review paper, but still a relative unknown in the community of evolutionary biologists. Aware of this, Gould addressed his papers primarily to paleontologists, urging reforms that could transform paleontology into a science of good methodological, and philosophical, standing. It was a sincere strategy, but one that was unlikely to work its effects overnight. Gould, the freshly minted professor at Harvard, was digging in for a long battle.

"Punctuated equilibria" changed everything. After 1972, Gould's star was on the rise, and his audience grew exponentially (Sepkoski 2009b). Suddenly, Gould had the attention not only of paleontologists, but of evolutionary biologists as well. The majority of these were uninterested in the second-class status of invertebrate paleontologists within geology departments. To them, Gould was simply a *paleontologist* (and increasingly, an evolutionary theorist). Realizing this, Gould took up the mantle of paleontology-as-a-whole, and recalibrated his ambitions accordingly. For the next decade, he pursued two projects with enthusiasm: (1) the conversion of paleontology into a nomothetic (or law-making) discipline (ca. 1972-1980), and (2) the hierarchical expansion of evolutionary theory (1977-). Since the origin of the latter project involved the abandonment of his first macroevolutionary synthesis, it is important to explore the events surrounding this transition. What accounts for the downfall of Gould's first macroevolutionary synthesis?

5 The collapse of Gould's first macroevolutionary synthesis

5.1 A new criterion of adaptation

Perhaps Gould's finest scientific achievement is his book *Ontogeny and Phylogeny* (1977), which marks a major turning point in his career. Today it is little read (at least in its entirety), and is usually remembered as a historical study of the "structural tradition" in biology developed by Continental Europeans like K.E. von Baer (York and Clark 2011, p. 54). But *Ontogeny and Phylogeny* is not an attempt to challenge neo-Darwinism by highlighting the theoretical insights of an overlooked structuralist tradition. Rather, it is an exhaustive investigation of the evolutionary significance of *heterochrony*: "all directions of change in developmental timing and their evolutionary [adaptive, macroevolutionary] significance"

(Gould 1979, p. 126). Additionally, and no less important, it is an attempt to (re)synthesize over a decade of thought concerning themes of size, shape, development and adaptation. As Gould recalled in 1988, “I began *Ontogeny and Phylogeny* largely to show that all heterochronies could be interpreted as adaptations, once the proper ecological correlations were established” (Gould 1988, p. 11). And this was indeed the major accomplishment of the theoretical section of the book, which it achieved by drawing on contemporary developments in the theory of life history tactics (see, e.g., Stearns 1976).

There can be no doubt that *Ontogeny and Phylogeny* is adaptationist in conception (see Cain 1978, p. 758), and for this reason represents a continuation of Gould’s early interest in the adaptive aspects of development. Yet it is also a transitional work, standing Janus-faced between his first macroevolutionary synthesis and the hierarchical expansion of evolution theory. The reason is that while it retains an adaptationist commitment at the core of its theoretical section, the criterion of adaptation it employs is very different from the criterion employed in Gould’s early works. In “Evolutionary paleontology and the science of form,” for instance, Gould regarded “adaptations” as *any structures that confer mechanical fitness on an organism by an engineer’s criteria of good design* (Gould 1970a, p. 78). In other words, adaptations are those “morphological, physiological and behavioral traits” that constitute “superior a priori designs for living in [an] environment” (Gould 1977b, p. 42). By 1977, however, Gould realized that this criterion was too narrow to render all heterochronies in terms of immediate adaptation (his stated goal in *Ontogeny and Phylogeny*). For instance, selection for precocious sexual maturation (“progenesis”) can unbind morphology from selective control, unleashing cascades of morphological change that lead, under certain conditions, to the rapid and “fortuitous” origin of new designs (Gould 1977a, p. 339). These designs are not generated by mechanical exigencies, nor do they constitute “mechanical improvements of the engineering type that occur in a constant physical environment” (Gould 1968, p. 97). Evidently, an important class of macroevolutionary events does not involve selection on morphology, but instead involves selection on life history parameters (with essentially adventitious morphological consequences).

In Gould’s view, earlier work on the importance of heterochrony (especially neoteny) in evolution erred in focusing on the morphological significance of particular heterochronic episodes. “They look upon a case of neoteny *after its descendants have evolved* and attribute meaning in terms of the aggregate success [of the group]” (Gould 1977a, p. 285).¹⁷ “But what of the actual species that experience neoteny,” Gould asked. “[This species] did not realize that it would be the herald of future diversity because it had sloughed off some ancestral specializations.”¹⁸ Rather, “[it] became neotenic for its own immediate reasons—its own ecologic strategy in its own particular environment” (ibid, p. 285). To

¹⁷ Neoteny refers to the slowing of development, leading to the sexual maturity of an animal while it is still in a juvenile (or even larval) state.

¹⁸ A traditional assessment of the evolutionary significance of neoteny appealed to the ability of neotenic species to escape from ecological specialization—the putative enemy of diversification.

capture this aspect of “immediate [as opposed to retrospective] significance” Gould turned to theoretical population ecology, whose “rise” constituted “one of the most significant events in evolutionary theory during the past twenty years” (ibid, p. 289). In particular, Gould turned to the theory of life history tactics (e.g., Stearns 1976), which had recently supplied an entirely “new set of parameters for assessing adaptation” (ibid, p. 290):

Classical evolutionary theory portrayed adaptation in terms of morphology, physiology, and, perhaps, behavior. The size, structure, and dynamics of populations were very rarely considered...such an attitude does not invite attention to the individual advantages most readily inferred from population size, age structure, and turnover rates. As Cole wrote in his pioneering paper [1954]: “Comparative studies of life histories appear to be fully as meaningful as studies of comparative morphology, comparative psychology or comparative physiology. The former type of study has, however, been neglected from the evolutionary point of view, apparently because the adaptive values of life-history differences are almost entirely quantitative.” (Gould 1977a, p. 289).

According to the theory of life history tactics, the criterion of adaptation is contribution to reproductive success (“fitness” in the population geneticist’s sense). Without differences in fitness, natural selection cannot act and Darwinian evolution is stymied; hence, for a character to be considered an “adaptation,” its presence must enhance the ability of an organism to contribute genetically to the next generation.¹⁹ Applied to the problem of heterochrony, Gould’s new criterion of adaptation enabled him to interpret all heterochronies as adaptations to ambient ecological circumstances. Whereas heterochronies had earlier been analyzed “in terms of morphological results” (like all other adaptations), “yet the process that produces [them]—displacement in time by acceleration and retardation—...is a primary variable in setting life history strategies” (Gould 1977a, p. 290). We therefore “have a prima facie case for ascribing direct significance to the change in developmental timing itself, not only to its morphological consequence.” Heterochronies are adaptive because certain life history strategies are favored over others in particular environments, not because certain morphological changes produced by heterochrony increase the mechanical fitness of organisms to their abiotic conditions of life.

5.2 Constraint and hierarchy: materials for a new macroevolutionary synthesis

With the link between natural selection and mechanical adaptation broken, Gould’s first macroevolutionary synthesis was on the rocks. No longer was it possible to view macroevolution as a result of “phenotypic molding to better biomechanical design [by natural selection]”—a premise that buttressed his use of the principle of

¹⁹ Notice that the theory of life history tactics does *not* demand that adaptations constitute “superior *a priori* designs for living in [an] environment,” at least if superiority is cashed out in engineering terms. Indeed, certain changes may confer fitness by decreasing the mechanical efficiency of a structure, like the loss of eyes in cavefishes.

limited solutions (Gould 2002, p. 781). Instead, natural selection can sometimes *free* organisms from “rigid morphological monitoring,” leading (occasionally) to the origin of new and higher taxa (Gould 1988, p. 10, 1977a, p. 9). At these junctures, inherited patterns of growth “are as much a determinant of evolutionary pathways as any efficient cause of shaping by natural selection” (Gould 1988, p. 11). This was an important conceptual breakthrough, as Gould had earlier described inherited patterns of growth (allometries) *as consequences* of shaping by natural selection. As he wrote in “Allometry and size in ontogeny and phylogeny” (1966): “Some of the most important steps in the evolution of complex organisms may be attributed to the mechanical requirements of size increase [so-called ‘size-required allometry’].” But their ‘automatic’ nature “should not obscure the importance of such steps as biological improvements,” whose cause is natural selection (p. 591).²⁰

But there remained a further step to be taken before inherited patterns of growth could be admitted as “evolutionary force[s] in [their] own right”—an important element of Gould’s second macroevolutionary synthesis (Gould 1982b, p. 340). Specifically, it was necessary to conceptualize these patterns as *positive causes of morphological trajectories in evolution, which exert their effects independently of the operation of natural selection*. Despite a passing reference to “the constraints of design” in *Ontogeny and Phylogeny*, there is little reason to think that Gould formulated this notion of constraint in the book (p. 293).²¹ By “The spandrels of San Marco,” however, Gould was happy to proclaim that developmental constraints “may hold the most powerful reign of all over possible evolutionary pathways” (Gould and Lewontin 1979, p. 160). If development occurs in integrated packages...then the adaptationist programme cannot explain the alteration of developmental programs underlying nearly all changes of *Bauplan*.” Several years later, he built on this notion, and even suggested that “[m]any classic cases of convergence may have to be reinterpreted more as results of limited (albeit adaptive) variation than as multiple, unconstrained approaches to mechanical optima” (Gould 1982b, pp. 337–338).²² Clearly, Gould’s thinking had progressed considerably since the salad days of “Evolutionary paleontology and the science of form.”

And how could it not have? The decade from 1970 to 1979 was the most frenzied period of Gould’s career, as well as his most scientifically creative. In the first half

²⁰ Elsewhere, Gould seems to back off this statement, suggesting that size-imposed characters “merely [provide] the same efficiency for a primary adaptation of altered size,” and therefore do not constitute biological improvements (Gould 1970a, p. 110). Nonetheless, their importance for transspecific evolution is manifest: “the expanded potential for further progress...conferred upon organisms bearing [size-required adaptations] is a true and most significant evolutionary advance” (Gould 1966a, p. 591). If size-required adaptations do not *constitute* biological improvements, yet they set the stage for potential biological improvements in the future.

²¹ I owe this insight to Alan Love.

²² While Gould made superficially similar claims in *Ontogeny and Phylogeny*, his emphasis fell on the capacity of natural selection (acting on the life history parameter of “difficult transitions” between “fundamentally different designs in the origin of taxa,” not on positive channeling (Gould 1977a, p. 338). This phrasing betrays a concern for the original problematic of macroevolutionary studies: the origin of higher taxa or organizational types (e.g., Schaeffer 1965). By contrast, Gould’s later interest in the ability of constraints to “impart a preferred direction to evolutionary change not based on natural selection” is responsive to a new problematic: the causation of statistical trends within large taxa (e.g., Stanley 1975, p. 648; Gould 1982a, p. 385).

of the decade alone, Gould (1) announced his new science of form (Gould 1970a, 1971a), (2) co-authored the theory of punctuated equilibria (Eldredge and Gould 1972), (3) pioneered the use of stochastic models in paleontology (along with Raup, Schopf and Simberloff), and (4) began writing a monthly column for *Natural History* magazine (1974-).²³ Then, in 1975, a pair of watershed events took place. The first was the debut of Steven Stanley theory of “species selection,” which provided the conceptual basis of a fully generalized hierarchical theory of natural selection (Stanley 1975). The other was the publication of *Sociobiology*—E.O. Wilson’s controversial tome on the evolution of social behavior. Much has been made of the latter event, such that it is tempting to ascribe the collapse of Gould’s first macroevolutionary synthesis to the often heated “sociobiology debate” (Segerstråle 2000, p. 118, cf. Gould 1993, p. 319). But as Philip Kitcher observes, Gould’s early criticisms of sociobiology were actually “quite gentle and quite specific,” and had more to do with genetic determinism than adaptationism *per se* (Kitcher 2009, p. 208). Only *after* 1976 did Gould identify adaptationism as the besetting sin of sociobiology, and by this time, an expanded criterion of adaptation had damaged his first macroevolutionary synthesis beyond repair.

By contrast to the sociobiology debate, insufficient attention has been paid to Stanley’s paper, “A theory of evolution above the species level” (1975), in which it is claimed that “Macroevolution is *decoupled* from microevolution, and we must envision the process governing its course as being analogous to natural selection but operating at a higher level of biological organization” (p. 648, emphasis added). The importance of this claim lies in the implication that a theory of macroevolution needn’t appeal to adaptation in order to explain the phenomena typically ascribed to directional natural selection (see also Raup and Gould 1974).²⁴ Indeed, *adaptation can be effectively bracketed* within a macroevolutionary theory so long as the causal apparatus it employs can render “long term phyletic trends in evolution [i.e., patterns of directional change within large clades]” (Stanley 1975, p. 648). The key to this, Gould came to realize, is *hierarchy*—that is, “the previously unrecognized mode of operation for natural selection at hierarchical levels higher than the [individual organism]” (Gould and Eldredge 1977, p. 139).²⁵ But not just any higher-level ‘selection’ process can guarantee “that paleobiology...shall provide essential theory to any complete science of evolution” (ibid, p. 145). To ensure

²³ Sepkoski’s *Rereading the Fossil Record* contains an excellent account of this period in the history of paleobiology (see especially chapter 5, on the origins of “Punctuated equilibria,” and chapter 7, on the introduction of stochastic models). Further useful information can be found in chapters 11 and 16 of *The Paleobiological Revolution* (written by Todd Grantham and John Huss, respectively), and in Raup’s synopsis of the MBL project (Raup 1977).

²⁴ In 1974, Gould collaborated with David Raup on a series of stochastic simulations of morphological evolution—a project with distinct bearings on the problem of the causation of phyletic trends (Raup and Gould 1974). The results suggested that “trends in morphology” (“[even those] of outstanding duration and unreversed direction”) could occur in the absence of deterministic causes like directional natural selection (Raup and Gould 1974, p. 314). While Gould was wary of assigning too great a significance to these results (ibid, 321), yet he later enlisted them in his campaign for a hierarchically expanded evolutionary theory (e.g., Gould 2002, p. 741).

²⁵ I say “Gould” instead of “Gould and Eldredge (1977)” because, as Eldredge recounts, “Steven wrote the entire [1977] manuscript” (Eldredge 2013, p. 14).

paleontology's distinctive contribution to evolutionary theory, it is required that selection acts, at least some of the time, on irreducible species-level properties (like population size or environmental range).²⁶

That selection can act on irreducible species-level properties was Stanley's great contribution to macroevolutionary theory, and became a central element of Gould's second macroevolutionary synthesis. It was this insight that enabled Gould to bracket adaptation as a cause of macroevolutionary events without sacrificing any of his theory's explanatory power:

In the conventional model [of macroevolutionary change]...trends—since they represent unusually persistent directional selection within a single lineage—must record the increasing “perfection” of organic form, either in adaptation to changing local environments, or in the more cosmic sense of improved general design on engineering principles. *This severe restriction in modes of explanation has been a serious impediment to paleontologists*; for we can relate few trends to such improvement and have been reduced to pleading ignorance of functional morphology for excusing our lack of success. But if trends represent the differential survival of species, then a panoply of explanations becomes legitimate. Trends may arise simply because some kinds of species speciate more often, or because some kinds live longer than others. And the reasons for more frequent speciation or greater longevity may not reside in morphological superiority, but in characteristic habits, population sizes, geographic mobility, etc. Morphological shifts may be incidental to the reasons for trends and basically non-adaptive. (Gould 1980b, pp. 107–108).

In an earlier work, Gould had decried the inability of paleontologists “to offer functional explanations of...evident history [directional morphological change],” and immediately followed this with an adaptationist call to arms (Gould 1970a, p. 110). That we may formulate “functional explanations of...evident history...is the greatest promise of the [emerging science of form],” he declared, brimming with optimism. By 1980, little of this optimism remained. While the “flowering of functional morphology” had “yielded a panoply of elegant individual examples,” it had generated “few principles beyond the unenlightening conclusion that animals work well” (Gould 1980b, p. 101). “I, at least, once harbored the naïve belief that a simple enumeration of more and more cases would yield new principles for the study of form,” Gould reflected (see Gould 1970a, pp. 110–112). “But Newtonian procedures yield Newtonian answers and who doubts that animals tend to be well designed?” (Gould 1980b, p. 101). Functional morphology will fulfill its promise “[only] when it probes the situations in which animals are *not* well designed—development, phyletic and architectural constraints as marks of history.” Hence, we

²⁶ In their celebrated discussion of trends, Eldredge and Gould (1972, pp. 108–112) failed to consider that the differential success of species may owe to irreducible species-level properties, although they *did* recognize that certain species will outlast others in virtue of the superior adaptedness of their members. Years later, Gould would admit that this was indeed a major limitation of their earlier discussion (Gould 1982a, p. 101, 2002, p. 731), and one he did not fully appreciate until papers by Stanley (1975) and Gilinsky (1981).

come by hierarchy theory to a heightened appreciation of evolutionary constraint—the second great theme of Gould’s new macroevolutionary synthesis.

5.3 Recapitulation

In summary, Gould’s mounting interest in the theory of life history tactics, by occasioning an expansion in his criterion of adaptation, rapidly eroded the basis of his first macroevolutionary synthesis (the connection between adaptation, mechanical efficiency and the principle of limited solutions). Spurred on by sociobiology, and stimulated by Stanley’s suggestion that macroevolution is “decoupled” from microevolution, Gould gradually extricated himself from his adaptationist commitments (ca. 1974–1977). After all, they were no longer vital to securing paleontology’s distinctive contribution to evolutionary theory. By 1977, he had begun to articulate a new vision of macroevolution—one in which natural selection on organisms plays a markedly reduced role. With this conception in place, adaptation (even of the broad, life history variety) could be safely bracketed. Macroevolution did not consist in “the weeding out of unsuccessful designs and [the] multiple evolution of mechanical optima,” as Gould had supposed in “Evolutionary paleontology” (p. 111). Rather, it consisted in the higher-level sorting of species within large clades, often in virtue of species-level properties (Gould and Eldredge 1977). As Gould and Eldredge (1977) claim: “[the] virtual irrelevancy, in many cases, of morphological superiority to a clade’s success may largely explain the puzzling observation that so few stories of increasing perfection in design can be read from the history of life” (p. 144). These words proclaim the failure of Gould’s science of form, while nonetheless heralding the promise of paleontology’s bright future.

6 Conclusion

Among the few essays to critically explore Gould’s early career is Roger D.K. Thomas’s “Gould’s odyssey: Form may follow function, or former function, and all species are equal (especially bacteria) but history is trumps” (2009). In this piece, Thomas proposes that Gould’s early interest in D’Arcy Thompson stemmed from his realization that “Thompson’s emphasis on intrinsic formal properties of organic design was complementary to Darwinian evolutionary theory” (Thomas 2009, p. 281). I suspect that Gould’s commitment to Thompson ran even deeper—that it formed the very *matrix* of his science of form, and demanded even Darwinism be reinterpreted in its light. Nonetheless I agree with Thomas’s analysis of Gould’s change of heart, and his adoption of “contingency” as the cardinal theme of life’s history. As time bore on, Thomas, writes Gould became “increasingly unwilling to accept the determinism that is implicit in Thompson’s worldview”:

[He] preferred contingency to any sort of more general determinism on personal and ideological grounds. His rich and provocative evolutionary theory—at least the key punctuational and hierarchical parts of it—does not

require that the effects of natural selection, speciation, or extinction must be unbiased in their directions. But Steve's humanity, his commitment to free will and personal responsibility, did require this. It gave rise to a highly personal evolutionary synthesis in which historical contingency takes the dominant role. (Thomas 2009, p. 287)

In this paper, I have argued that Gould's first macroevolutionary synthesis collapsed in virtue of his adoption of an enlarged criterion of adaptation derived from the theory of life history tactics (ca. 1973–1975). I thought it important to emphasize this because it was Gould's *continuing commitment to adaptationism* that led him to dismantle his science of form, including the all-important connection between adaptation, mechanical fitness, and the principle of limited solutions. Hence, it is *not* the case that Gould abandoned his science of form because of the perceived connection between adaptation and determinism, as Thomas may be taken to suggest. But of course, Gould's deliberations about adaptation did not take place in a vacuum. The historian Myrna Perez Sheldon has recently detailed how Gould's role as a "New Left activist" informed his participation in a variety of scientific debates, including the debate over *Sociobiology* (see especially Perez 2013, Perez Sheldon 2014). More studies of this type may illuminate how Gould's involvement in these debates altered the contours of his theoretical commitments, in particular, those implicated in his second macroevolutionary synthesis (for one perspective, see Segerstråle 2003). In addition, they may show how his worldview mingled with his science to give rise to "a highly personal evolutionary synthesis"—one dominated by hierarchical vistas and ineliminable contingency.

Another topic deserving of increased attention is Gould's role in redefining "macroevolution" during the 1970s—a development that owes a great deal to the theory of punctuated equilibria (see Sepkoski 2012, Ch. 10, for a preliminary account). Recall that to an earlier generation of biologists, "transspecific (or macro-) evolution" concerned the origin of new and higher taxa, for instance, the rise of amphibians from rhipidistian fishes, or mammals from synapsid reptiles (see Schaeffer 1965). Viewed in this light, macroevolution is fundamentally about *origins*—specifically, the origin of "key innovations" whose appearance heralds the birth of new and higher taxa (Schaeffer 1947, Simpson 1953). During the 1970s, however, a group of ambitious paleontologists sought to reorganize macroevolutionary studies around the theme of differential species success (Stanley 1975; Gould and Eldredge 1977). Henceforth, macroevolution was to concern "the combination of features [that a clade possesses] and their differential spread"—not their origin and establishment (Gould 1982a, p. 385). Punctuated equilibria (a theory erected at the zenith of Gould's adaptationism) had improbably become the pivot of a new macroevolutionary synthesis; but before it could do this, it required to be significantly renovated. The story of this renovation, and its manifold implications, is the story of Gould's second macroevolutionary synthesis.

Acknowledgements I would like to thank Alan Love, Emilie Snell-Rood, Mark Borrello, Ruth Shaw and Staffan Müller-Wille for their keen editorial insights during the writing process. Dr. Love read the manuscript several times and provided invaluable feedback on its organization and scope. In addition, I would like to thank Niles Eldredge, Roger D.K. Thomas and Richard Lewontin for their generous

correspondence during various stages of this project. Last but not least, I owe a debt of gratitude to the participants of the 2015 MBL-ASU History of Biology Seminar (“Perspectives on Stephen Jay Gould”), and especially to the seminar organizers, John Beatty and David Sepkoski, for inviting me to participate.

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