Defining and Revising the Structure of Evolutionary Theory

Theories Need Both Essences and Histories

In a famous passage added to later editions of the Origin of Species, Charles Darwin (1872, p. 134) generalized his opening statement on the apparent absurdity of evolving a complex eye through a long series of gradual steps by reminding his readers that they should always treat "obvious" truths with skepticism. In so doing, Darwin also challenged the celebrated definition of science as "organized common sense," as championed by his dear friend Thomas Henry Huxley. Darwin wrote: "When it was first said that the sun stood still and world turned round, the common sense of mankind declared the doctrine false; but the old saying of Vox populi, vox Dei [the voice of the people is the voice of God], as every philosopher knows, cannot be trusted in science."

Despite his firm residence within England's higher social classes, Darwin took a fully egalitarian approach towards sources of expertise, knowing full well that the most dependable data on behavior and breeding of domesticated and cultivated organisms would be obtained from active farmers and husbandmen, not from lords of their manors or authors of theoretical treatises. As Ghiselin (1969) so cogently stated, Darwin maintained an uncompromisingly "aristocratic" set of values towards judgment of his work—that is, he cared not a whit for the outpourings of vox populi, but fretted endlessly and fearfully about the opinions of a very few key people blessed with the rare mix of intelligence, zeal, and attentive practice that we call expertise (a democratic human property, respecting only the requisite mental skills and emotional toughenes, and bearing no intrinsic correlation to class, profession or any other fortuit of social circumstance).

Darwin ranked Hugh Falconer, the Scottish surgeon, paleontologist, and Indian tea grower, within this most discriminating of all his social groups, a panel that included Hooker, Huxley and Lyell as the most prominent members. Thus, when Falconer wrote his important 1863 paper on American fossil elephants (see Chapter 9, pages 745–749, for full discussion of this incident), Darwin flooded himself with anticipatory fear, but then rejoiced in his critic's generally favorable reception of evolution, as embodied in the closing
THE STRUCTURE OF EVOLUTIONARY THEORY

Defining and Revising the Structure of Evolutionary Theory

overlying public structure. A framework, on the other hand, defines the basic form and outline of the public structure itself. Thus, the two men conjure up very different pictures in their crystal balls. Falconer expects that the underlying evolutionary principle of descent with modification will persist as a factual foundation for forthcoming theories devised to explain the genealogical tree of life. Darwin counters that the theory of natural selection will persist as a basic explanation of evolution, even though many details, and even some subsidiary generalities, cited within the Origin will later be rejected as false, or even illogical.

I stress this distinction, so verbally and disarmingly trivial at a first and superficial skim through Falconer’s and Darwin’s words, but so incisive and portentous as contrasting predictions about the history of evolutionary theory, because my own position—closer to Falconer than to Darwin, but in accord with Darwin on one key point—led me to write this book, while also supplying the organizing principle for the “one long argument” of its entirety. I do believe that the Darwinian framework, and not just the foundation, persists in the emerging structure of a more adequate evolutionary theory. But I also hold, with Falconers, that substantial changes, introduced during the last half of the 20th century, have built a structure so expanded beyond the original Darwinian core, and so enlarged by new principles of macroevolutionary explanation, that the full exposition, while remaining within the domain of Darwinian logic, must be construed as basically different from the canonical theory of natural selection, rather than simply extended.

A closer study of the material basis for Falconer and Darwin’s metaphors—the Duomo (or Cathedral) of Milan—might help to clarify this important distinction. As with so many buildings of such size, expense, and centrality (both geographically and spiritually), the construction of the Duomo occupied several centuries and included an amalgam of radically changing styles and purposes. Construction began at the chevet, or eastern end, of the cathedral in the late 14th century. The tall windows of the chevet, with their glorious flamboyant tracery, strike me as the finest achievement of the entire structure, and as the greatest artistic expression of this highly ornamented latest Gothic style. (The term “flamboyant” literally refers to the flame-shaped element so extensively used in the tracery, but the word then came to mean “richly decorated” and “showy,” initially as an apt description of the overall style, but then extended to the more general meaning used today.)

Coming now to the main point, construction then slowed considerably, and the main western façade and entrance way (Fig. 1-1) dates from the late 16th century, when stylistic preferences had changed drastically from the points, curves and traceries of Gothic to the orthogonal, low-angled or gently rounded lintels and pediments of classical Baroque preferences. Thus, the first two tiers of the main (western) entrance to the Duomo display a style that, in one sense, could not be more formally discordant with Gothic elements of design, but that somehow became integrated into an interesting coherence. (The third tier of the western façade, built much later, returned to a “retro” Gothic style, thus suggesting a metaphorical reversal of phylogenetic conventions, as
comparison with a discrete building that continually grew but did not change its location or basic function, then how shall we conceive "the structure of evolutionary theory" (chosen, in large measure, as the title for this book because I wanted to address, at least in practical terms, this central question in the history and content of science)? Shall we accept Darwin's triumphalist stance and hold that the framework remains basically fixed, with all visually substantial change analogous to the non-structural, and literally superficial, icing of topmost pinnacles? Or shall we embrace Falconer's richer and more critical, but still fully positive, concept of a structure that has changed in radi-

1-1. The west facade (main entrance) of Milan Cathedral, built in baroque style in the 16th century, with a retro-gothic third tier added later.

up leads to older—in style if not in actual time of emplacement! Finally, in a distinctive and controversial icing upon the entire structure (Fig. 1-2), the "wedding cake," or row-upon-row of Gothic pinnacles festooning the tops of all walls and arches with their purely ornamental forms, did not crown the edifice until the beginning of the 19th century, when Napoleon conquered the city and ordered their construction to complete the Duomo after so many centuries of work. (These pinnacle forests may amuse or disgust architectural purists, but no one can deny their unintended role in making the Duomo so uniquely and immediately recognizable as the "icon of the city").

How, then, shall we state the most appropriate contrast between the Duomo of Milan and the building of evolutionary theory since Darwin's Origin in 1859? If we grant continuity to the intellectual edifice (as implied by

1-2. The "wedding cake" pinnacles that festoon the top of Milan Cathedral, and that were not built until the first years of the 19th century after Napoleon conquered the city.
Defining and Revising the Structure of Evolutionary Theory

scribed as a different kind of mental "thing." How, in short, can such an intellectual entity be defined? And what degree of change can be tolerated or accommodated within the structure of such an entity before we must alter the name and declare the entity invalid or overthrown? Or do such questions just represent a fool's errand from the start, because intellectual positions can't be refuted into sufficient equivalents of buildings or organisms to bear the weight of such an inquiry?

As arrogant as I may be in general, I am not sufficiently delusional or vainglorious to imagine that I can meaningfully address the deep philosophical questions embedded within this general inquiry of our intellectual ages—that is, fruitful modes of analysis for the history of human thought. I shall therefore take refuge in an escape route that has traditionally been granted to scientists: the liberty to act as a practical philistine. Instead of suggesting a principled and general solution, I shall ask whether I can specify an operational way to define "Darwinism" (and other intellectual entities) in a manner specific enough to win shared agreement and understanding among readers, but broad enough to avoid the doctrinal quarrels about membership and allegiance that always seem to arise when we define intellectual commitments as pledges of fealty to lists of dogmata (not to mention initiation rites, secret handshakes and membership cards—in short, the intellectual paraphernalia that led Karl Marx to make his famous comment to a French journalist: "Je ne suis pas marxiste").

As a working proposal, and as so often in this book (and in human affairs in general), a "Goldlocks solution" embodies the blessedly practical kind of approach that permits contentious and self-serving human beings (God love us) to break intellectual bread together in pursuit of common goals rather than personal triumph. (For this reason, I have always preferred, as guides to human action, messy hypothetical imperatives like the Golden Rule, based on negotiation, compromise and general respect, to the Kantian categorical imperatives of absolute righteousness, in whose name we so often murder and maim until we decide that we had followed the wrong instantiation of the right generosity.) We must, in short and in this case, steer between the "too little" of refusing to grant any kind of "essence," or hard anatomy of defining concepts, to a theory like Darwinism; and the "too much" of an identification so burdened with a long checklist of exigent criteria that we will either spend all our time debating the status of particular items (and never addressing the heart or central meaning of the theory), or we will waste our efforts, and poison our communities, with arguments about credentials and anachronisms, applied to individual applicants for membership.

In his brilliant attempt to write a "living" history and philosophy of science about the contemporary restructuring of taxonomic theory by phenetic and cladistic approaches, Hull (1988) presents the most cogent argument I have ever read for "too little" on Goldlocks's continuum, as embodied in his defense of theories as "conceptual lineages" (1988, pp. 15-18). I enthusiastically support Hull's decision to treat theories as "things," or individuals in the crucial sense of coherent historical entities—and in opposition to the stan-
dard tactic, in conventional scholarship on the “history of ideas,” of tracing the chronology of expression for entirely abstract concepts defined only by formal similarity of content, and not at all by ties of historical continuity, or even of mutual awareness among defenders across centuries and varied cultures. (For example, Hull points our that such a conventional history of the “chain of being” would treat this notion as an invariant and disembodied Platonic archetype, independently “borrowed” from the eternal storehouse of potential models for natural reality, and then altered by scholars to fit local contexts across millennia and cultures.)

But I believe that Hull’s laudable desire to recast the history of ideas as a narrative of entities in historical continuity, rather than as a disconnected chronology of tidbits admitted into a class only by sufficient formal similarity with an abstract ideological archetype, then leads him to an overevaluation of actual content. Hull exemplifies his basic approach (1988, p. 17): “A consistent application of what Mayr has termed ‘population thinking’ requires that species be treated as lineages, spatiotemporally localized particulars, individuals. Hence, if conceptual change is to be viewed from an evolutionary perspective, concepts must be treated in the same way. In order to count as the ‘same concept,’ two terms must be part of the same conceptual lineage. Population thinking must be applied to thinking itself.”

So far, so good. But Hull now extends this good argument for the necessity of historical connectivity into a claim for sufficiency as well—thus springing a logical trap that leads him to debate, or even to ignore, the “morphology” (or idea content) of these conceptual lineages. He states that he wishes to “organize term-tokens into lineages, not into classes of similar term-types” (pp. 16-17). I can accept the necessity of such historical continuity, but neither I nor most scholars (including practicing scientists) will then follow Hull in his explicit and active rejection of similarity in content as an equally necessary criterion for continuing to apply the same name—Darwinian theory, for example—to a conceptual lineage. At an extreme that generates a reductio ad absurdum for rejecting Hull’s conclusion, but that Hull bravely owns as a logical entailment of his own prior decision, a pure criterion of continuity, imbued with no constraint of content, forces one to apply the same name to any conceptual lineage that has remained consciously intact and genealogically unbroken through several generations (of passage from teachers to students, for example), even if the current “morphology” of concepts directly inverts and contradicts the central arguments of the original theory. “A proposition can evolve into its contrary,” Hull allows (1988, p. 18). Thus, on this account, if the living intellectual descendants of Darwin, as defined by an unbroken chain of teaching, now believed that each species had been independently created within six days of 24 hours, this theory of biological order would legitimately bear the name of “Darwinism.” And I guess that I may call myself kosher, even though I and all members of my household, by conscious choice and with great ideological fervor, eat cheeseburgers for lunch every day—because we made this dietary decision in a macronutritional shift of content, but with no genealogical break in continuity, from ten previous generations of strict observers of kashrut.

The objections that most of us would raise to Hull’s interesting proposition include both intellectual and moral components. Certain kinds of systems are, and should be, defined purely by genealogy and not at all by content. I am my father’s son no matter how we interact. But such genealogical definitions, as validated by historical continuity, simply cannot adequately characterize a broad range of human groupings properly designated by similarity in content. When Cain mocked God’s inquiry about Abel’s whereabouts by explaining “Am I my brother’s keeper” (Genesis 4:9), he illustrated the appropriateness of either genealogy by historical connection or fealty by moral responsibility as the proper criterion for “brotherhood” in different kinds of categories. Cain could not deny his genealogical status as brother in one sense, but he derided a conceptual meaning, generally accorded higher moral worth as a consequence of choice rather than necessity of birth, in disclaiming any responsibility askeeper. As a sign that we have generally privileged the conceptual meaning, and that Cain’s story still haunts us, we need only remember Claudius’s lament that his murder of his own brother (and Hamlet’s father) “hath the primal eldest curse upon’s.”

Ordinary language, elementary logic, and a general sense of fairness all combine to favor such preeminence for a strong component of conceptual continuity in maintaining a name or label for a theory. Thus, if I wish to call myself a Darwinian in any justly or generally accepted sense of such a claim, I do not qualify merely by documenting my residence within an unbroken lineage of teachers and students who have transmitted a set of changing ideas organized around a common core, and who have continued to study, augment and improve the theory that bears such a longstanding and honorable label, I must also understand the content of this label myself, and I must agree with a set of basic precepts defining the broad ideas of a view of natural reality that I have freely chosen to embrace as my own. In calling myself a Darwinian I accept these minimal obligations (from which I remain always and entirely free to extract myself should my opinions or judgments change); but I do not become a Darwinian by the mere default of accidental location within a familial or educational lineage.

Thus, if we agree that a purely historical, entirely content-free definition of allegiance to a theory represents “too little” commitment to quality, and that we must buttress any genealogical criterion with a formal, logical, or anatomical definition framed in terms of a theory’s intellectual content, then what kind or level of agreement shall we require as a criterion of allegiance for inclusion? We now must face the opposite side of Goldilocks’s dilemma—for once we advocate criteria of content, we do not wish to impose such stringency and uniformity that membership becomes more like a sworn obedience to an unchanging religious creed than a freely chosen decision based on personal judgment and perception of intellectual merits. My allegiance to Dar-
winian theory, and my willingness to call myself a Darwinian biologist, must not depend on my subscription to all 95 articles that Martin Luther nailed to the Wittenberg church door in 1517 or to all 80 items in the Syllabus of Errors that Pio Nono (Pope Pius IX) proclaimed in 1864, including the "fal-
lacy," so defitionally unconceptual to science, that "the Romans Pointillist can and should reconcile himself to and agree with progress, liberalism and moder-
civilization"; or to all 39 articles of the Church of England, adopted by Queen Elizabeth in 1571 as a replacement for Archbishop Thomas Cranmer's 42 articles of 1535.

Goldstuck's "just right" position between these extremes will strike nearly all cooperatively minded intellectuals, committed to the operationality and advance of their disciplines, as eminently sensible: shared content, not only historical continuity, must define the structure of a scientific theory; but this shared content should be expressed as a minimal list of the free defining attributes of the theory's central logics— in other words, only the absolutely essential statements, absent which the theory would either collapse into fallacy or operate so differently that the mechanism would have to be granted an-
other name.

Now such a minimal list of such maximal centrality and importance bears a description in ordinary language—but its proper designation requires that evolutionary biologists utter a word rigorously expunged from our professional consciousness since day one of our preparatory course work: the concept that dare not speak its name—essence, essence, essence (say the word a few times our loud until the fear evaporates and the laughter recedes). It's high time that we repressed our aversion to this good and honorable word. Theories have essences. (So, by the way, and in a more restrictive and nuanced sense, do organisms—in their limitation and channeling by con-
straints of structure and history, expressed as Bauplätze of higher taxa. My critique of the second theme of Darwinian central logic, Chapters 4-5 and 10-11, will treat this subject in depth. Moreover, my partial defense of or-
ganic essences, expressed as support for structuralist versions of evolutionary causality as potential partners with the more conventional Darwinian func-
tionalism that understandably denies intelligibility to any notion of an es-
ence, also underlies the double entendre of this book's title, which honors the intellectual structure of evolutionary theory within Darwinian traditions and their alternatives, and which also urges support for a limited version of structuralist theory, in opposition to certain strict Darwinians verifies.)

Our unhinking rejection of essences can be muted, or even reversed into
propensity for a sympathetic hearing, when we understand that an invocation of
this word need not call down the full apparatus of an entirely abstract and
total Platonic eidos—a reading of "essence" admittedly outside the logic of
evolutionary theory, and historical modes of analysis in general. But the solu-
tion to a meaningful notion of essence in biology lies within an important epis-
dode in the history of emerging evolutionary views, a subject treated exten-
sively in Chapter 4 of this book, with Goethe, Etienne Geoffroy St. Hilaire, and
Richard Owen as chief protagonists. After all, the notion of a general anatomical blueprint that contains all par-
ticular incarnations by acting as a fundamental building block (Goethe's leaf or Geoffroy's vertebra) moved long ago from conceptualization as a disem-
bodied and nonmaterial archetype employed by a creator, to an actual struct-
ure (or inherited developmental pathway) present in a flesh and blood ances-
tor—a material basis for channeling, often in highly positive ways, the future
history of diversity within particular phylogenetic lineages. This switch from ar-
chetypal to ancestor permitted us to reformulate the idea of "essence" as
broad and fruitful commonalities that unite a set of particulars into the most
meaningful relationships of common causal structure and genesis. Our active
use of this good word should not be hampered by a shyness and disquietude
lacking any validity beyond the vestiges of suspicions originally set by battles
won so long ago that no one can remember the original reasons for antime-
thematization. Gracious (and confident) victors should always seek to revive
the valid and important aspects of defeated but honorable systems. And the tran-
scendental morphologists did understand the importance of designating a
small but overarching set of defining architectural properties as legitimate es-
ences of systems, both anatomical and conceptual.

Hull correctly defines theories as historical entities, properly subject to all
the principles of narrative explanation—and I shall so treat Darwinian logic
and its substantial improvements and changes throughout this book. But the-
ories of range and power also feature inherent "essences," implicit in their
logical structure, and operationally definable as minimal sets of proposi-
tions so crucial to the basic function of a system that their falsification must
undermine the entire structure, and also so necessary as an ensemble of
mutual implication that all essential components must work in concert to set
the theory's mechanisms into smooth operation as a generator and explana-
tion of nature's order. In staking out this middle Goldstuckean ground be-
tween (1) the "too little" of Hull's genealogical continuity without commit-
tment to a shared content of intellectual morphology and (2) the "too much"
of long lists of ideological fealty, superficially imbued or memorized, and
then invoked to define membership in ossified cults rather than thoughtful al-
legiance to developing theories, I will argue that a Darwinian essence can be
minimally (and properly) defined by three central principles constituting a tri-
pod of necessary support, and specifying the fundamental meaning of a pow-
eful system that Darwin famously described as the "grandeur in this view of
life."

I shall then show that this formulation of Darwinian minimal commit-
ments proves its merit on the most vital ground of maximal utility. For not
only do these three commitments build, in their ensemble, the full frame of
a comprehensive evolutionary worldview, but they have also defined the chief
obstructions and alternatives motivating all the most interesting debate within
evolutionary theory during its initial codification in the 19th century. More-
over, and continuing in our own time, these three themes continue to specify
the major weaknesses, the places in need of expansion or shoring up, and the
locus of unresolved issues that make evolutionary biology such a central and
exciting subject within the ever changing and ever expanding world of modern science.

The Structure of Evolutionary Theory: Revising the Three Central Features of Darwinian Logic

In the opening sentence of the Origin's final chapter (1859, p. 459), Darwin famously wrote that "this whole volume is one long argument." The present book, on "the structure of evolutionary theory," despite its extravagant length, is also a brief for an explicit interpretation that may be portrayed as a single extended argument. Although I feel that our best current formulation of evolutionary theory includes modes of reasoning and a set of mechanisms substantially at variance with strict Darwinian natural selection, the logical structure of the Darwinian foundation remains remarkably intact—a fascinating historical observation in itself, and a stunning tribute to the intellectual power of our profession's founder. Thus, and not only to indulge my personal propensities for historical analysis, I regard such analysis not as an antiquarian indulgence, but as an optimal path to proper understanding of our current commitments, and the underlying reasons for our decisions about them.

As a primary theme for this one long argument, I claim that an "essence" of Darwinian logic can be defined by the practical strategy defended in the first section of this chapter: by specifying a set of minimal commitments, or broad statements so essential to the central logic of the enterprise that disproof of any item will effectively destroy the theory, whereas a substantial change to any item will convert the theory into something still recognizable as within the Banquet of descent from its forebear, but as something sufficiently different to identify, if I may use the obvious taxonomic metaphor, as a new subclade within the monophyletic group. Using this premise, the long argument of this book then proceeds according to three sequential chapters that set the structure and order of my subsequent chapters:

1. Darwin himself formulated his central argument under these three basic premises. He understood his necessity within his system, and the difficulty that he would experience in convincing his contemporaries about such unfamiliar and radical notions. He therefore presented careful and explicit defenses of all three propositions in the Origin. I devote the first substantive chapter (number 2) to an exegesis of the Origin of Species as an embodiment of Darwin's defense for this central logic.

2. As evolutionary theory experienced its growing pains and pursued its founding arguments in the late 19th and early 20th centuries (and also in its pre-Darwinian struggles with more inchoate formulations before 1859), these three principles of central logic defined the themes of deepest and most persistent debate—as, in a sense, they must because they constitute the most interesting intellectual questions that any theory for causes of descent with modification must address. The historical chapters of this book's first half then treat the history of evolutionary theory as responses to the three central issues of Darwinian logic (Chapters 3–7).

3. As the strict Darwinism of the Modern Synthesis prevailed and "hardened," culminating in the overconfidences of the centennial celebrations of 1959, a new wave of discoveries and theoretical reformulations began to challenge aspects of the three central principles anew—thus leading to another fascinating round of development in basic evolutionary theory, extending throughout the last three decades of the 20th century and continuing today. But this second round has been pursued in an entirely different and more fruitful manner than the 19th century debates. The earlier questioning of Darwin's three central principles tried to disprove natural selection by offering alternative theories based on confutations of the three items of central logic. The modern versions accept the validity of the central logic as a foundation, and introduce their critiques as helpful auxiliaries or additions that enrich, or substantially alter, the original Darwinian formulation, but that leave the kernel of natural selection intact. Thus, the modern reformulations are helpful rather than destructive. For this reason, I regard our modern understanding of evolution as closer to Falcöen's metaphor, than to Darwin's, for the Duomo of Milan—a structure with a firm foundation and a fascinatingly different superstructure. (Chapters 8–12, the second half of this book on modern developments in evolutionary theory, treat this third theme.)

Thus, one might say, this book cycles through the three central themes of Darwinian logic at three scales—by brief mention of a framework in this chapter, by full exegesis of Darwin's presentation in Chapter 2, and by lengthy analysis of the major differences and effects in historical (Part 1) and modern critiques (Part 2) of these three themes in the rest of the volume.

The basic formulation, or bare-bones mechanics, of natural selection is a disarmingly simple argument, based on three undeniable facts (overproduction of offspring, variation, and heritability) and one syllogistic inference (natural selection, or the claim that organisms enjoying differential reproducive success will, on average, be those variants that are fortuitously better adapted to changing local environments, and that these variants will then pass their favored traits to offspring by inheritance). As Huxley famously, and ruefully, remarked (in self-reproach for failing to devise the theory himself), this argument must be deemed elementary (and had often been formulated "Two of these three ranked as "folk wisdom" in Darwin's day and needed no further justification—variation and inheritance (the mechanism of inheritance remained unknown, but its factuality could scarcely be doubted). Only the principle that all organisms produce more offspring than can possibly survive—superfluousness, in Darwin's lovely term—ran counter to popular assumptions about nature's benevolence, and required Darwin's specific defense in the Origin.

Defining and Revising the Structure of Evolutionary Theory
lated before, but in negative contexts, and with no appreciation of its power—see p. 137), and can only specify the guts of the operating machine, not the three principles that established the range and power of Darwin's evolu-

tion in human thought. Rather, these three larger principles, in defining the Darwinian essence, take the guts of the machine, and declare its simple operation sufficient to generate the entire history of life in a philosophical manner that could not have been more contrary to all previous, and cher-
hished, assumptions of Western life and science.

The three principles that elevated natural selection from the guts of a working machine to a radical explanation of the mechanism of life's history can best be exemplified under the general categories of agency, efficacy, and scope. I treat them in this specific order because the logic of Darwin's own de-

development proceeds (as I shall illustrate in Chapter 2), for the most radical claim comes first, with assertions of complete power and full range of appli-
cability then following.

Agency. The abstract mechanism requires a locus of action in a hierar-
chical world, and Darwin insisted that the apparently intentional "benevo-
lence" of nature (as embodied in the good design of organisms and the har-
mony of ecosystems) flowed entirely as side-consequences of this single causal locus, the most "reductionistic" account available to the biology of Darwin's time. Darwin insisted upon a virtually exceptionless, single-level theory, with organisms acting as the locus of selection, and all "higher" order emerging, by the analog of Adam Smith's invisible hand, from the (unconscious) "strug-
gles" of organisms for their own personal advantages as expressed in dif-
ferential reproductive success. One can hardly imagine a more radical reformu-
lization of a domain that had unhesitatingly been viewed as the primary mani-
festation for action of higher power in nature—and Darwin's brave and single-minded insistence on the exclusivity of the organismic level, although rarely appreciated by his contemporaries, ranks as the most radical and most distinctive feature of his theory.

Efficacy. Any reasonably honest and intelligent biologist could easily understand that Darwin had identified a vera causa (or true cause) in natural selection. Thus, the debate in his time (and, to some extent, in ours as well) was never centered upon the existence of natural selection as a genuine causal force in nature. Virtually all anti-Darwinian biologists accepted the reality and action of natural selection, but branded Darwin's force as a minor and negative mechanism, capable only of the headman's or executioner's role of removing the unfit, once the fit had arisen by some other route, as yet undeni-
tified. This other route, they believed, would provide the centerpiece of a "real" evolutionary theory, capable of explaining the origin of novelties. Dar-
win insisted that his admittedly weak and negative force of natural selection could, nonetheless, under certain assumptions (later proved valid) about the nature of variation, act as the positive mechanism of evolutionary novelty—
that is, could "create the fit" as well as eliminate the unfit—by slowly accu-
mulating the positive effects of favorable variations through innumerable genera-

sions.

Scope. Even the most favorably minded of contemporaries often admit-
ted that Darwin had developed a theory capable of building up small changes (of an admittedly and locally "positive" nature as adaptations to changing environments) within a "basic type"—the equivalent, for example, of making dogs from wolves or developing edible corn from teosinte. But these critics could not grasp how such a genuine microevolutionary process could be ex-
tended to produce the full panoply of taxonomic diversity and apparent "progress" in complexification of morphology through geological time. Dar-
win insisted on full sufficiency in extrapolation, arguing that his micro-
evolutary mechanism, extended through the immensity of geological time, would be fully capable of generating the entire pageant of life's history, both in anatomical complexity and taxonomic diversity—and that no further causal principles would be required.

Because primates are visual animals, complex arguments are best portrayed or epitomized in pictorial form. The search for an optimal icon to play such a role is therefore not trivial matter (although scholars rarely grant this issue the serious attention so richly merits)—especially since the dangers of confu-
sion, misplaced metaphor, and replacement of rigor with misleading "intui-
tion" stand so high. I knew from the beginning of this work that I needed a suitable image for conveying the central logic of Darwinian theory. As one of my humanistic concerns, I hoped to find a historically important scientific im-
age, drawn for a different reason, that might fortuitously capture the argu-
ment in pictorial form. But I had no expectation of success, and assumed that I would need to commission an expressly designed figure drawn to a long list of specifications.

The specific form of the image—in its central metaphorical content, if you will—plays an important role in channeling or redirecting our thoughts, and therefore also requires careful consideration. In the text of this book, I speak most often of a "tripod" since central Darwinian logic embodies three major propositions that I have always visualized as supports—perhaps be-
cause I have never been utterly confident about this entire project, and I needed some pictorial encouragement to keep me going for twenty years.

(And I much prefer tripods, which can hold up elegant objects, to buttresses, which may fly as they preserve great Gothic buildings, but which more often shoo crumbling edifices. Moreover, the image of a tripod suits my major claim particularly well—for I have argued, just above, that we should define the "essence" of a theory by an absolutely minimal set of truly necessary propositions. No structure, either of human building or of abstract form, captures this principle better than a tripod, based on its absolute minimum of three points for fully stable support in the dimensional world of our physical experience.)

But organic images have always appealed more strongly, and I preferred a biological icon. If the minimal logic can be represented by a tripod pointing downward, then the same topology can be inverted into a structure growing upward. Darwin's own favorite image of the tree of life immediately sug-
gested itself, and I long assumed that I would eventually settle on a botanical
icon. But I also remembered Darwin's first choice for an organic metaphor or picture of branching to capture his developing views about descent with modification and the causes of life's diversity—the "coral of life" of his "B Notebook" on transmutation, kept during the 1830's as he became an evolutionist and struggled towards the theory of natural selection (see Barrett et al., 1987).

As I began to write this summary chapter, I therefore aimlessly searched through images of Cnidaria from my collection of antiquarian books in paleontology. I claim no general significance whatsoever for my good fortune, but after a lifetime of failure in similar quirky quests, I was simply stunned to find a preexisting image—not altered one iota from its original form, I promise you, to suit my metaphorical purposes—that so stunningly embodied my needs, not only for a general form (an easy task), but down to the smallest details of placement and potential excision of branches (the feature that I had no right or expectation to discover and then to exapt from so different an original intent).

The following figure comes from the 1747 Latin version of one of the seminal works in the history of paleontology—the 1670 Italian treatise of the Sicilian savant and painter Agostino Scilla, La sana speculazione disingannata dal senso ("Vain speculation undeceived by the senses"—Scilla's defense, at the outset of "the scientific revolution" of Newton's generation, for empirical methods in the study of nature, and specifically, in this treatise, for a scientific paleontology and the need to recognize fossils as remains of ancient organisms, not as independent products of the mineral kingdom). This work, famous not only for its incisive text, but also for its beautiful plates (see Fig. 1-3), engraved by an author known primarily as an artist of substantial eminence, includes this figure, labeled Coralium articulatum quod copiosisissimum in raptibus et colibus Messanae repertum ("Articulated coral, found in great abundance in the cliffs and hills of Messina").

This model, and its organic features, work uncommonly well as a metaphor for the Goldilocks position of definition by a barest minimum of truly fundamental postulates. For Scilla's coral, with its branching structure (see Fig. 1-4)—particularly as expressed in the lessening consequences of excising branches at ever higher levels nearer the top (the analogs of disconfirming theoretical features of ever more specialized and less fundamental import)—so beautifully captures the nature and operation of the intellectual structure that I defended above for specifying the essences of theories. The uncanny appropriateness of Scilla's coral lies in the fortuity that this particular specimen (accurately drawn from nature by Scilla, I assume, and not altered to assert any general point) just happens to include exactly the same number of branches (three) as my Darwinian essential structure. (They terminate at the same upper level, so I could even turn the specimen over into a tolerably unwobbly tripod!) Moreover, since this particular genus of corals grows in discrete segments, the joining points correspond ideally with my metaphor of chopping planes for excising parts of structures at various levels of importance in an intellectual entity. But, most incredibly, the segmental junctions of
this particular specimen just happen to occupy the exact places that I needed a priori to make my central point about lower choppings that destroy theorems, middle choppings that change theories in a Falconerian way (major alterations in structure upon a preserved foundation), and upper choppings that change theories in the lesser manner of Darwin’s Milanese metaphor (smaller excisions that leave the framework intact as well).

The central trunk (the theory of natural selection) cannot be severed, or the creature (the theory) dies. (The roots, if you will, represent sources of evidence; any one may be excised, if recognized as incorrect by later study, so long as enough remain to anchor the structure.) This central trunk then divides into a limited number of major branches. These basic struts—the three branches of the Darwinian essence in this particular picture—are also so essential that any severing of a complete branch either kills, or so seriously compromises, the entire theory that a new name and basic structure becomes essential.

We now reach the interesting point where excisions and regraftings preserve the essential nature of an intellectual structure, but with two quite different levels of change and revision, as characterized by Falconer’s and Darwin’s competing metaphors for the Duomo of Milan. I would argue that a severing low on any one of the three major branches corresponds to a revision profound enough to validate the more interesting Falconerian version of major revision upon a preserved foundation. (The Falconerian model is, in this sense, a Goldilocksian solution itself, between the “too much” of full destruction and the “too little” of minor cosmetic revision.) On the other hand, the severing of a subbranch of one of the three branches symbolizes a less portentous change, closer to Darwinian models for the Milanese Duomo—an alteration of important visual elements, but without change in the basic framework.

My fascination with the current state of evolutionary theory, at least as I read current developments in both logic and empirics, lies in its close conformity to the Falconerian model—with enough continuity to make the past history of the field so informative (and so persistently, even emotionally, compelling), but with enough deep difference and intellectual fascination to stimulate anyone with a thirst for the intriguing mode of novelty that jars previous certainty, but does not throw a field into the total anarchy of complete rebuilding (not a bad thing either, but far from the actual circumstance in this case).

To summarize my views on the utility of such a model for the essence of Darwinian logic, I will designate three levels of potential cuts or excisions to this organic (and logical) coral of the structure of evolutionary theory, as originally formulated by Darwin in the Origin of Species, and as revised in a Falconerian way in recent decades. The most inclusive and most fundamental K-cuts (killing cuts) sever at least one of the three central principles of Darwinian logic and thereby destroy the theory tout court. The second level of R-cuts (revision cuts) removes enough of the original form on one of the three central branches to ensure that the new (and stronger or more arborescent) branch, in regrowing from the cut, will build a theory with an intact Darwinian foundation, but with a general form sufficiently expanded, revised or reconstructed to present an interestingly different structure of general explanation—the Falconerian model for the Duomo of Milan. Finally, the third level of S-cuts (subsidiary cuts) affects only a subbranch of one of the three major branches, and therefore reformulates the general theory in interesting ways, while leaving the basic structure of explanation intact—the Darwinian model for the Duomo of Milan.

I wrote this book because I believe that all three pillars, branches, or tripod legs, representing the three fundamental principles of Darwinian central logic, have been subjected to fascinating R-cuts that have given us at least the
firm outlines—for the revised structure of evolutionary explanation remains a work vigorously in progress, as only belies the nature of its subject, after all—of a far richer and fascinatingly different theory with a retained Darwinian core rooted in the principles of natural selection. In short, we live in the midst of a Falsenian remodelling of our growing and multifractal, yet coherently grounded, intellectual mansion.

I will not, in this chapter, detail the nature of the K-cuts that failed (thus preserving the central logic of Darwinism), the R-cuts that have succeeded in changing the structure of evolutionary theory in such interesting ways, and the S-cuts that have refurbished major rooms in particular wings of the edifice—for these specifications set the subject matter of all following chapters. But to provide a better opening sense of this book’s argument—and to clarify the nature of the three central claims of Darwinian logic—I shall at least distinguish, for each branch, the K-cuts that never prevailed (and therefore did not tell the structure) from the R-cuts that have affected each branch, and therefore provoked our current process of building an enriched structure for evolutionary theory.

Returning to Solla’s coral (Fig. 1-4), consider the central branch as the first leg of the tripod (agency, or the claim for organismal selection as the causal locus of the basic mechanism), the left branch as the second leg (efficacy, or the claim that selection acts as the primary creative force in building evolutionary novelties), and the right branch as the third leg (scope, or the claim that these macroevolutionary modes and processes can, by extrapolation through the vastness of geological time, explain the full panoply of life’s changes in form and diversity).

The cut labeled K1 on Figure 1-4 would have severed the entire coral by disproving natural selection as an evolutionary force at all. The cut labeled K2 would have fully severed the second branch, leaving natural selection as a legitimate cause, but denying it any creative role, and thereby deterring Darwinism as a major principle in explaining life’s history. (We shall see, in Chapters 3-6, that such a denial of creativity underlay the most common anti-Darwinian argument in the first generations of debate.) The cut labeled K3 would have fully severed the third branch, allowing that natural selection might craft some minor changes legitimately called “creative” in a local sense, but denying that Darwin’s mechanism could then be extended to explain the panoply of macroevolutionary processes, or the actual organic of history. The success of any one of these K-cuts would have destroyed Darwinian theory, plain and simple. None of them succeeded, and the foundation of Darwinian central logic remains intact and strong.

In striking, and most positive, contrast, I believe that higher R-cuts—leaving the base of each major branch intact, but requiring a substantial regrowth and regrafting of an enlarged structure upon the retained foundation—have been successfully wielded against all three branches of Darwinian logic, as the structure of evolutionary theory developed in the last third of the 20th century (following too rigid a calcification of the original structure, a good admiration of the coral metaphor), in the hardening of the Modern Synthesis that culminated in the Darwinian centennial celebrations of 1959, On the first branch of agency, the cut labeled R1 (see Fig. 1-4) expanded Darwin’s unidirectional theory of organismal selection into a hierarchical model of selection acting simultaneously on several legitimate levels of Darwinian individuality (genes, cell-lineages, organisms, demes, species, and clades). I shall show in Chapters 3, 8, and 9 how the logic of this pronounced expansion builds a theory fascinatingly different from, and not just a smooth extension of, Darwin’s single-level mechanism of agency—my reason for portraying the hierarchical model as a deeply interesting R-cut rather than a more superficial S-cut.

On the second branch of efficacy, the cut labeled R2 accepts the validity of Darwin’s argument for creativity (by leaving the base of the branch intact), but introduces a sufficient weight of formalist thinking—its renewed appreciation for the enormous importance of structural, historical, and developmental constraint in channeling the pathways of evolution, often in highly positive ways—that the pure functionalism of a strictly Darwinian (and externalist) approach to adaptation no longer suffices to explain the channeling of phylogenetic directions, and the clumping and inhomogeneous population of organic morphospace. The strict Darwinian form of explanation has thereby been greatly changed and enriched, but in no way defeated. I shall discuss the historical aspect of this branch in Chapters 4 and 5, and modern reformulations of this R2 cut in Chapters 10 and 11.

On the final branch of scope, the cut labeled R3 accepts the Darwinian contention that microevolutionary modes and principles can build grand patterns by cumulation through geological immensity, but rejects the argument that such extrapolations can render the entire panoply of phenomena in life’s history without adding explicitly macroevolutionary modes for distinctive expression of these processes at higher tiers of time—as in the explanation of cladal trends by species sorting under punctuated equilibrium, rather than by extended adaptive anageneis of purely organismal selection, and in the necessity of iterating adaptive microevolutionary accumulation with occasional resetting of rules and patterns by catastrophically triggered mass extinctions at time’s highest tides. Chapters 6 and 12 discuss historical and modern critiques of Darwinian extrapolationism.

For now, I will say little about the even higher and more superficial S-cuts of subbranches, but I will at least indicate how I construe this category by stating a hypothetical example for each branch: an S1 cut, for example, might accept the selective basis of evolutionary change in a purely mechanical sense, but then deny full force to Darwin’s deliciously radical philosophical claim that all apparent “higher level” harmony arises consequentially, through the invisible hand of lower levels acting for personal reproductive success. One might, in principle, propose such a revision by arguing that a higher force, operating by an overarching principle of order, “employs” natural selection as its mechanical agent. I speak only hypothetically here, for no such defendable scientific hypothesis now exists, although the concept certainly remains intelligible. Explicitly theological versions don’t count as science, whatever their kind or form of potential validity.) An S2 cut might be assayed by a
THE STRUCTURE OF EVOLUTIONARY THEORY

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developmental saltationist who accepted the selectionist basis of adaptive change but felt that, at a sufficient relative frequency to be counted as important, the initial steps of such changes may be larger than the pure continuous generation of Darwinian selection can admit. And an S3 cut might accept the full validity of microevolutionary extrapolationism, but deny the subsidiary defense of progress that Darwin granted onto this apparatus (see Chapter 6) with ecological arguments about plenitude and the priority of biotic over abiotic competition.

As a paleontologist and part-time historian of science by profession, my reading of these important R-cuts arose from a macroevolutionary perspective framed largely in terms of longstanding difficulties faced by Darwinism in extending its successes for explaining small changes in palpable time into equally adequate causal accounts for broader patterns and processes in geological history. I have, in this effort, also benefited from my personal study of Darwin’s life and times, and especially the late 19th century debates on mechanisms of population (as promulgated largely by professionals who could neither fully understand nor accept the radical philosophical commitments underlying Darwin’s view). This historical study allowed me to grasp the continuity in basic themes from Darwin’s own formulation, through these foundational debates, right down to the major theoretical struggles of our own time. An appreciation of this continuity allowed me to discern and define the distinctively Darwinian view of life.

But I recognize only too well that every strength comes paired with weaknesses. In my case, a paleontological focus leads me into relative ignorance for an equally important focus of reform in the structure of Darwinism—in increasing knowledge of the nature of genomes and the mechanics of development. To try to cover the outcomes of important theoretical critiques from this “opposite” realm I admit, in my characteristically brilliant way, to tie the diverse threads of his initiating argument into an overall view with a similarly tight structure—thus granting clear definition to his own commitments, and also permitting their revision in the form of an equally coherent “package.” I would argue, moreover, and without wishing to become extravagantly hagiographical (for I wrote this book after all, primarily to discuss a critique and revision of strict Darwinism), that our modern sense of limitations in the canonical version arises from decisions that Darwin made for tough and correct reasons in the context of his initiating times—reasons that made his account the first operational theory of evolution in modern science. In particular, as Chapter 2 will discuss in detail, Darwin converted evolution from untestable speculation to double science by breaking through the old paradox (as embedded most prominently in Lamarck’s system) of contrasting a palpable force of small-scale change that could do little in extension, with a basically nonoperational (and orthogonal) mechanism of large-scale change putatively responsible for all the interesting patterns of life’s history, but imperceptible and untestable from the uniformitarian study of modern organisms.

By claiming that the small-scale mechanics of modern change could, by extension, explain all of evolution, Darwin opened the entire field to empirical study. And yet, as Hegel and so many other students of change have noted, progress in human (and other) affairs tends to spiral upwards in cycles of proposal (thesis), then countered by opposition (antithesis), and finally leading to a new formulation combining the best aspects of both competitors (synthesis). Darwin’s thesis established evolution as a science, but his essential commitments, as expressed in the three legs of his necessary logical tripod (or the three branches of his conceptual tree or coral, as in the alternate metaphor of Fig. 1-1), eventually proved too narrow and confining, thus requiring an antithesis of extension and reformulation on each branch, and leading—or so this book maintains as a central thesis of its own—to a still newer and richer synthesis expressing our best current understanding of the structure of evolutionary theory.

In fact, and to repeat my summary in this different form, one might encapsulate the long argument of this book in a Hegelian format. Prec Darwinian concepts of evolution remained speculative and essentially non-operational, largely because (see Chapter 3) they fell into the disabling paradox of contrasting an effectively unknowable large-scale force of cosmic progress against an orthogonal, palpable, and testable small-scale force that could generate local adaptation and diversity, but that couldn’t, in principle, explain the macroevolutionary pattern of life. Then Darwin, in his thesis (also an antithesis to these earlier sterile constructions), brilliantly argued that the putative large-scale force did not exist, and that all evolution could be explained by upward extrapolation from the small-scale force, now properly understood as natural selection. In a first stage of debate during the late 19th and early 20th centuries (Chapters 3-6), most critiques of Darwinism—one might designate them as a first round of ultimately destructive antitheses—simply denied sufficient agency, efficacy and range to natural selection, and reasserted the old claims of dialectic, with selection relegated to triviality, and some truly contrary force sought as the explanation for major features of evolution. Strict Darwinism eventually fended off these destructive critiques, reasserted itself in the triumphant, and initially (and generously) pluralistic form of the Modern Synthesis, but eventually calved into a “hardened” version (Chapter 7).

Then, in a strikingly different, and ultimately fruitful, second round of antitheses, a renewed debate about central theoretical issues arose during the last three decades of the 20th century, and reshaped the field by recognizing
time to break down, and a time to build up... A time to rend, and a time to sew; a time to keep silence, and a time to speak." Evolutionary theory now stands in the happier second state of those genuine dichotomies (in part because the first state had been restricted to the limited extent of its utility): we live in a time for building up, for sewing together, and for speaking out.

Not all times are such good times, and not all scientists win the good fortune to live within these times of motion. For theories grow as organisms do, with periods of stasis and drift, long latencies of youth or ossifications of age, and some happy times of optimally productive motion in between (another Goldblatian phenomenon). I recently studied the life and career of E. Ray Lankester (Gould, 1999a), clearly the most talented evolutionary morphologist of the generation just after Darwin. He did "good" work and had a "good" career (see Chapter 10, pages 1069–1076 for his best theoretical efforts), but he never transcended the ordinary. Perhaps the limitation lay largely within his own abilities. However, I rather suspect that he did possess both the temperamental gumption and the requisite intellectual might—but that the tools of major empirical advance just didn't emerge in his generation, for he remained stuck in a relatively unproductive middle, as Darwin had seized the first fruits from traditional data of natural history, and the second plucking required a resolution of genetic mechanisms.

I felt a similar kind of frustration in 1977, after writing my first technical book, Ontogeny and Phylogeny (see Chapter 10, pages 1061–1063). I had spent the best years of a young career on a subject that I knew to be relevant (at a time when most of the profession had forgotten). But then defeat snatched my prize from the jaws of victory. I am proud of the book, and I do believe that it helped to focus interest on a subject that became double soon thereafter. But I ran up against a wall right at the end—for the genetics of development clearly held the key to any rapprochement of embryology and evolution, and we knew effectively nothing about eukaryotic regulation. Indeed, as we could then only characterize structural genes by electrophoretic techniques, our major "arguments" for regulatory effects (if they even merited such a positive designation) invoked such negative evidence as the virtual identity in structural genes between chimpanzees and humans, coupled with a fair visceral sense of extensive phenotypic disparity in anatomy and behavior—with the differences then attributed to regulatory genes that we could not, at the time, either study or even identify.

By sheer good fortune (altered in minuscule ways by my own pushes and those of my paleontological colleagues), the field moved fast and I lived long enough to witness a sea change (if I may cite Ariel yet again) towards potentiation on all three major intellectual and social substrates for converting a subject from great promise combined with even more frustrating inseparability, into a discipline bursting with new (and often utterly surprising) data that led directly to testable hypotheses about basic issues in the structure of evolutionary theory.

EMPIRE. During the last third of the 20th century, new techniques and conceptualizations opened up important sources of data that challenged or-
THE STRUCTURE OF EVOLUTIONARY THEORY

Alized at all. But, speaking parochially as a student of the fossil record, I can at least say that the conceptual revolution in macroevolutionary thinking re-

alized the field of palaeobiology (even creating the name as a subdiscipline of palaeontological endeavor). Whatever the varied value of different individ-

ual efforts in this burgeoning field, we may at least be confident that our pro-

fession will no longer be humiliated as a synecdoche for ossified boredom among the natural sciences—as Nature did in 1969 when editorializing about the salutary value of plate tectonics in revitalizing the geological sciences: “Scientists in general might be excused for assuming that most geologists are palaeontologists and most palaeontologists have staked out a square mile as their life’s work. A revamping of the geologist’s image is badly needed” (Anonymous, 1969, p. 903)

The intricate and multifaceted concepts that have nuanced and altered the central logic on all three branches of Darwinism’s essential postulates represent ideas of broad ramifications and often remarkably subtle complexity, as we vainly scientists soon discovered in our fractured bubbles of burst pride—

for we had been so accustomed to imagining that an evening in an armchair could conquer any merely conceptual issue, whereas we all acknowledge the substantial time and struggle that empirical problems, demanding collection and evaluation of data, often require. Yet, on these basic questions in formulating evolutionary theory, we often read and thought for months, and ended up more confused than when we began.

The general solution to such procedural dilemmas lies in a social and intellec-
tual activity that scientists do tend to understand and practice better than colleagues in most other academic disciplines—collaboration. For far more than most colleagues, I have tended to work alone in my professional life and pub-

lication. But for each of the conceptually difficult and intellectually manifold issues of reevaluation for the central logic of the three essential Darwinian postulates, I desperately needed advice, different skills, and the give and take of argument, from colleagues who complemented my limited expertise with their equally centered specialties and aptitudes for other aspects of these large and various problems. Thus, on the first leg or branch of hierarchy theory, I worked with Niles Eldredge on punctuated equilibrium, and with Elisabeth Vrba on levels of selection and sorting. On the second leg of structuralist alter-

native to adaptationist argument, I worked with Dick Lewontin on span-

drels, Elisabeth Vrba on exaptation, David Woodruff on the functional and structural morphology of Cenozo, and with “the gang of four” (increased to five with the later inclusion of Jack Sepkoski)—Dave Raup, Tom Schopf, Dan Simberloff, and me—on trying to specify how many aspects of apparently or-
dered phyletic patterns, heretofore confidently attributed to selection for little reason beyond the visual appearance of order itself, could plausibly be gener-

ated within purely random systems. And on the third leg of extrapolationism, my chief interests in the logic and justification of uniformitarianism in phi-

losophy, and of Lyellian perspectives in the history of science, could not have developed without advice and substantial aid (but not collaborative publica-

tion this time) with historians Martin Rudwick, Reijer Hooykaas, and Cecil
of philosophers of science that no scientists read their journals or even encounter their analyses. Several key achievements in modern evolutionary theory, particularly the successful resolution of conceptual difficulties in formulating a workable theory of hierarchical selection, have appeared as joint publications of biologists and philosophers, including the books of Sober and Wilson, 1998, and Eldredge and Gensler, 1992; and articles of Sober and Lewontin, 1982, and Mayo and Gilinsky, 1987. My own understanding of how to formulate an operational theory of hierarchical selection, and my "rescue" from a crucial conceptual error that had stymied my previous thinking (see Chapter 8, pages 656-673), emerged from joint work with Elisabeth Lloyd, a professional philosopher of science. I take great pride in our two joint articles (Lloyd and Gould, 1993; Gould and Lloyd, 1999), which, in my partisan judgment, resolve what may have been the last important impediment to the codification of a conceptually coherent and truly operational theory of hierarchical selection.

Zeitgeist. Although major revisions to the structure of evolutionary theory emerged mainly from the conventional substrates of novel data and clearer concepts, we should not neglect the admittedly fuzzier, but by no means unimportant, input from a distinctive social context, or intellectual "spirit of the times" (a literal meaning of Zeitgeist) that, at the dawn of a calendrical millennium, has suffused our general academic culture with a set of loosely coherent themes and concerns far more congenial with the broad revisions here proposed within evolutionary theory than any previous set of guiding concepts or presuppositions had been. Needless to say, Zeitgeists are two edged swords of special sharpness—for either they encourage sheeplike conformity with transient ghosts of time (another literal meaning of Zeitgeist) that will soon fade into oblivion, or they open up new paths to insights that previous ages could not even have conceptualized. Any intellectual would therefore be a fool to argue that conformity with a Zeitgeist manifests any preferential correlation with scientific veracity ipso facto. Zeitgeists can only suggest or facilitate.

Nonetheless, we would be equally foolish in our naive empiricism if we claimed that major advances in science must be entirely data driven, and that social contexts can only act as barriers to our vision of nature's factuality. Both the social and scientific world were "ready" for evolution in the mid 19th century. People of equal intelligence could neither have formulated nor owned such a concept in Newton's generation, even if some hypothetical Darwin had then advanced such a claim (and probably ended up in Bedlam for his troubles). In Chapter 2, I shall document not only this general readiness of Western science within the Zeitgeist of Darwin's time, but also the specific social imperatives that Darwin gained from studying the distinctive theories (also a product of the earlier Enlightenment Zeitgeist, and not accessible before) of Adam Smith and the Scottish economists. Thus, and by analogy a century later, the altered Zeitgeist of our own time may also facilitate a fruitful recon-
sideration of major evolutionary concepts that still bear the originating stamp of a Victorian scientific context strongly committed to unidirectional, single-level and deterministic views of natural causality—subtly controlling concepts that many scientists would now label as limiting and outmoded.

Although the next few paragraphs will be the most vague and impressionistic (I trust) of the entire book, I venture these ill-structured statements about Zeitgeist because I feel that something important lurks behind my inability to express these inchoate thoughts with precision. I argue above (page 14) that the key concerns of the three essential branches of Darwinian logic might be identified as agency, efficacy and scope of natural selection. In each of these domains, I believe, the revised structure of evolutionary theory, as presented in this book, might be characterized as expansion and revision according to a set of coordinated principles, all consonant with our altered Zeitgeist vs. the scientific spirit of Darwin’s own time. The modern revision seeks to replace Darwin’s un phased theory of organismic selection with a hierarchical account (leg one); his unidirectional theory of adaptational construction in the functionalist mode with a more balanced interaction of these external causes, treating internal (or structural) constraints primarily as positive channels, and not merely as limitations (leg two); his unlevel theory of micro-evolutionary extrapolation with a model of distinctive but interacting modes of change, each characteristic for its tier of time. In short, a hierarchy of interacting levels, each important in a distinctive way, for Darwin’s single locus; an interaction of environmental outcides with organic insides for Darwin’s single direction of causal flow; and a set of distinctive temporal tiers for Darwin’s attempt to situate all causality in the single microevolutionary world of our own palpable moments.

I do sense a common underlying vision behind all these proposed reforms. Strict Darwinism, although triumphant within mid 20th century evolutionary theory, embodied several broad commitments (philosophical or metaphysical, in the technical sense of these terms), more characteristic of 19th than of 20th century thought and, obviously, not necessarily wrong, or even to be discounted, for this reason—as nothing can be more dangerous to the progress of science than winds of fashion, and we do, after all, learn some things, and develop some fruitful approaches, with validity and staying power well beyond their time of origin and initial popularity. Some aspects of Darwin’s formulation broke philosophical ground in a sense quite consonant with our modern Zeitgeist of emphasis upon complexity and interaction—particularly, Darwin’s focus on the interplay of chance and necessity in sources of variation vs. mode of selection. Indeed, Darwin paid the usual price for such innovation in the failure of nearly all his colleagues, even the most intellectually acute, to grasp such a radical underlying philosophy. But, in many commanding respects, Darwinism follows the norms of favored scientific reasoning in his time.

The logic of Darwin’s formulation rests upon several preferences in scientific reasoning more characteristic of his time than of ours—preferences that many scientists would now view as unduly restrictive in their designation of a privileged locus of causality, a single direction of causal flow, and a smooth continuity in resulting effects. Classical Darwinism follows standard reductionist preferences in designating the lowest level then available—the organism, for Darwin—as an effectively unique locus of causality (the first leg of agency). In this sense, the efforts of Williams and Dawkins (see Chapter 6) to reduce the privileged locus even further to the genic level (perforce unavailable to Darwin) should be read as a furthering and intensification of Darwin’s intent—in other words, a basically conservative adumbration of Darwin’s own spirit and arguments, and not the radical conceptual revision that some have imagined.

At this single level of causality, classical Darwinism then envisages a similarly privileged direction of causal flow, as information from the environment (broadly construed, of course, to include other organisms as well as physical surroundings) must impact the causal agent (organisms struggling for reproductive success) and be translated, by natural selection, into evolutionary change. The organism supplies raw material in the form of “random” variation, but does not “push back” to direct the flow of its own alteration from inside. Darwinism, in this sense, is a functionalist theory, leading to local adaptation as the environment proposes and natural selection disposes. Finally, classical Darwinism completes a trio of privileged causal places and consequently directional flows by postulating strict continuity in results, as local selection scales smoothly through the immensity of geological time to engender life’s history by pure extrapolation of lowest-level modes and causes.

By contrast, the common themes behind the reformulations defended in this book all follow from serious engagement with complexity, interaction, multiple levels of causation, multidirectional flows of influence, and pluralistic approaches to explanation in general—a set of integrated approaches that strongly contribute to the Zeitgeist of our moment. To anticipate and make a preemptive strike against the obvious counterattack from Darwinian traditionalists, these alternative themes do not substitute a “faded back, laissez-faire, anything goes” kind of sloppy tolerance for contradiction and fuzziness in argument against the genuine rigor of old-line Darwinism. The social and psychological contributions of a Zeitgeist to the origin of hypotheses bear no logical relationship to any subsequent scientific defense and validation of the same hypotheses. Moreover, on this subject of test and confirmation, I expose a rigorously conventional and rather old-fashioned “realist” view that an objective factual world exists “out there,” and that science can access its ways and modes. Whatever the contribution of a Victorian Zeitgeist to Darwin’s thinking, or of a contemporary Zeitgeist to our revisions, the differences are testable and subject to validation or disproof by the usual armamentarium of scientific methods. That is, either Darwin is right and effectively all natural selection occurs at the organismic level (despite the logical conceivability of other levels), or the hierarchical theory is right and several levels make interestingly different and vastly important simultaneous con-
tributions to the overall pattern of evolution. The same ordinary form of testability can be applied to any other contrast between strict Darwinism and the revised and expanded formulations defended in this book.

As the most striking general contrast that might be illuminated by reference to the different Zeitgeists of Darwin's time and our own, modern revisions for each essential postulate of Darwinian logic substitute mechanics based on interaction for Darwin's single locus of causality and directional flow of effects. Thus, for Darwin's near exclusivity of organicistic selection, we now propose a hierarchical theory with selection acting simultaneously on a rising set of levels, each characterized by distinctive, but equally well-defined, Darwinian individuals within a genealogical hierarchy of gene, cell-lineage, organism, clade, species. The results of evolution then emerge from complex, yet intimately knowable, interactions among these potent levels, and do not simply flow out and up from a unique causal locus of organismal selection.

A similar substitution of interaction for directional flow then pervades the second branch of selection's efficacy, as Darwin's functionalist formulation— with unidirectional flow from an external environment into an isotropic organic substrate that supplies "random" raw material but imposes no directional vector of its own to "push back" from internal sources of constraint—yields to a truly interactive theory of balance between the functionalist Darwinian "outside" of natural selection generated by environmental pressures, and a formalism "inside" of strong, interesting and positive constraints generated by specific past histories and timeless structural principles. Finally, on the third and last branch of selection's range, the single and control- ling microevolutionary locus of Darwinian causality yields to a multileveled model of tiers of time, with a unified set of processes working in distinctive and characteristic ways at each scale, from allelic substitution in observable years to catastrophic climatic-scale changes. Thus, and in summary, for the unifocal and noninteractive Darwinian models of exclusively organismal selection, causation flow from an environmental outside to an organismal inside, and a microevolutionary locus for mechanisms of change that smoothly extrapolate to all scales, we substitute a hierarchical selectionist theory of numerous interacting levels, with balanced and bidirectional flow of causality between external selection and internal constraint (interaction of functionalist and structuralist perspectives), and causal interaction among tiers of time.

Among the many consequences of these interactionist reformulations, punctuational rather than continuumist models of change (with stronger structuralist components inevitably buttressing the punctuational versions) may emerge as the most prominent and most interesting. The Darwinian mechanics of functionalism yield an expectation of continuously improving local adaptation, with longterm stability representing the achievement of an optimum. But interactionist and multi-leveled models of causality reconcep-

ualize stasis as a balance, actively maintained among potentially competing forces at numerous levels, with change then regarded as exceptional rather than intrinsically tickling most of the time, and punctuational rather than

Defining and Revising the Structure of Evolutionary Theory

smoothly continuous when it does occur (representing the relatively quick transition that often accompanies a rebalancing of forces).

To end this admittedly vague section with the punch of paradox (and even with a soundbite), I would simply note the almost delicious irony that the formulation of a hierarchical theory of selection—the central concept of this book, and invoking a non-vernacular meaning of hierarchy in the purely structural sense of rising levels of inclusivity—engenders, as its most important consequence, the destruction of a different and more familiar meaning of hierarchy; that is, the hierarchy of relative value and importance embodied in Darwin's privileging of organismic selection as the ultimate source of evolutionary change at all scales. Thus, a structural and descriptive hierarchy of equally effective causal levels undermines a more conventional hierarchy of relative importance rooted in Darwin's exclusive emphasis on the micro-evolutionary mechanics of organismal selection. And so, this structuralist view of nature's order enriches the structure of evolutionary theory—carry-

ing the difference between strict Darwinism and our current understanding through more than enough metatheoretical fashion to fashion a Falconerian, not merely a Darwinian, rebuilding and extension for our edifice of coherent explanation.

A PERSONAL ODYSSEY

For reasons beyond mere self-indulgence or egotism, I believe that defenders of such general theories about large realms of nature owe their readers some explanation for the personal bases and ontogeny of their choices—for at this level of abstraction, no theory can claim derivation by simple logical or empirical necessity from observed results, and all commitments, however well defended against alternative possibilities, will also be influenced by author's preferences of a more contingent nature that must then be narrated in order to be understood. Moreover, and in this particular case, the structure of this book includes a set of vigorously idiosyncratic features that, if not acknowl-

edged and justified, might obscure the far more important raison d'être for its composition: the presentation of a tight brief for substantial reformulation in the structure of evolutionary theory, with all threads of revision conceptually united into an argument of different thrust and form, but still sufficiently con-

tinuous with its original Darwinian base to remain within the same intellect-

ual lineage and logic.

Two aspects of my idiosyncratic procedures require explicit commentary here because, at least as my intention, they should reinforce this book's cen-

tral argument for coherence (logical, historical and empirical) of the revised and general structure of evolutionary theory, and not further the opposite, al-

but customary, function of such "confessional" writing—namely, to stake

authorial egos, fight old battles, and relate twice-told tales to one's own ad-

vantage (although I claim no immunity from these all too human foibles).

This book will be published in the Spring of 2002, an auspicious and palindromic year just one step out of the starting gate for a new millennium.
two points that I regard as most crucial to understanding the general argument through (or despite) conscious idiosyncrasies in my presentation.

**History**

Many technical treatises in science begin with a short section on previous history of work in the field—usually written in the hagiographical mode to depict prior history as a march towards final truths revealed in the current volume. Sometimes, authors get a bit carried away, and these historical sections expand into substantial parts of the final book. Lest anyone make the false inference that my full first half of history arose in this kaphalized and initially unintended way, I hasten to assure readers that my final result was my intention from the start.

For several reasons, I always conceived this book as a smooth joining of two halves, roughly equal in length and importance. First, and ontogenetically, I had written my earlier technical book, Ontogeny and Phylogeny, in this admittedly unusual manner—and I remain pleased with both the distinctiveness and the efficacy of the result. Second, I believe that the history of evolutionary thought, and probably of any other subject imbued with such importance to our lives and to understanding of nature, constitutes an epic tale of fascinating, and mostly honorable, people engaged in a great struggle to comprehend something very deep and very difficult. Thus, such histories capture a bit of the best in us (also of the worst, but all human endeavors so compose—a bit, moreover, that cannot be expressed in any other way. We really do need to honor the temporal substance of our current understanding, not only as a guide to our continuing efforts, but also as a moral obligation to our forebears.

But a third and practical reason trumps all others. Although I would not state such a claim as a generality for all scientific analyses, in this particular case I do not see how the structure of evolutionary theory can be resolved and the appropriate weights of relative importance assigned to the different components thereof, absent such a historical perspective. (Would it be odd to claim, in any case, that the quintessential science for resolving the nature of life’s history can itself be understood as a pristine construction, a fully-formed conceptual entity drawn intact from some analog of Zeus’s brow, rather than an “organic” structure of ideas with its own ontogeny and history?)

To give one example at the largest and at the smallest scales of my argument, I don’t know how I could have properly defended my identification and exposition of the threefold essence of Darwinian logic without documenting the history of theoretical debate in order to tease out the components that have always been most troubling, most central, and most directive. A pure description of the theory’s abstract logic simply will not suffice. To epitomize, I have identified these essential components on three basic grounds: that logic compels (Chapter 2), that history validates (Chapters 3–7), and that current debate reafirms (Chapters 8–12). The middle term of this epitome unites the end members; I cannot present a coherent or compelling defense without this linkage. The three issues of agency, efficacy and scope build the Darwinian es-
The Structure of Evolutionary Theory

36

To complement this most general statement with just one example of the utility of historical analysis at the smaller scale of details, I offer the following case as the strongest argument for my central claim that Darwin's brave attempt to construct a single-level, exclusively organismic theory of natural selection must fail in principle, and that all selectionists must eventually own a hierarchical model. What better evidence can we cite than the historical demonstration (see Chapters 3 and 5 for details) that each of the only three foundational thinkers who truly understood the logic of selectionism—August Weismann, Hugo de Vries, and Charles Darwin himself—tried mightily to make the single-level version work as a fully sufficient explanation for evolution. And each failed, after intense intellectual struggle, and for fascinatingly different reasons documented later in the book—Darwin for explaining diversity by reluctant resort to species selection; Weismann for a stronger initial commitment to a single level, and an eventual recognition of full hierarchy as the most important and distinctive conclusion of his later career (by his own judgment); and de Vries for reconciling his largely physiological fealty to Darwin as his intellectual hero, with his clearly non-Darwinian account of the origin of species and the explanation of trends (including an explicit coinage of the term "species selection" for explaining cladal patterns).

One might cite various traits in people ignorant of history will be condemned to repeat its errors. But I would rather re-express this accurate and rueful observation in a more positive manner by illustrating the power of historical analysis to aid both our current understanding and the depth of our appreciation for the intellectual importance of our enterprise. Finally, and to loosen the rein on personal bravado that I usually try to hold at least somewhat in check, no scholar should impose a project of this length upon his colleagues unless he believes that some quirk of special skill or experience permits him to proceed in a unique manner that may offer some insight to others. In my case, and only by history's fortune of no immediate competition in a small field, I may be able to combine two areas of professional competence not otherwise confined among current evolutionaryists. I am not a credentialed historian of science, but I believe that I have done sufficient work in this field (with sufficient understanding of the difference between the Whiggish diatribe of most enthusiastic amateurs, and the rigorous methods applied by serious historians) to qualify as adequately knowledgeable. At least I can read all the major works in their original languages, and I stay close to the "internalist" style of analysis that people who understand the logic and history of theories, but cannot claim truly professional expertise in the "externalist" factors of general social and historical context, can usefully pursue.

Meanwhile I am, for my sins, a lifelong and active professional paleontologist, a commitment that began at age five as love at first sight with a dinosaur skeleton.

Many historians possess deeper knowledge and understanding of their immediate subject than I could ever hope to acquire, but none enjoy enough intimacy with the world of science (knowing its norms in their bones, and its quirks and foibles in their daily experience) to link this expertise to contemporary debates about causes of evolution. Many more scientists hold superb credentials as participants in current debates, but do not know the historical background. As I hope I demonstrated by practical utility in The Mismeasure of Man (Gould, 1981), a small and particular—but I think quite important—intellectual space exists, almost entirely unoccupied, for people who can use historical knowledge to enlighten (not merely to footnote or to pretty) current scientific debates, and who can then apply a professional's "feel" for the doing of science to grasp the technical complexities of past debates in a useful manner inaccessible to historians (who have therefore misinterpreted, in significant ways, some important incidents and trends in their subject). I only hope that I have not been wrong in believing that my devotion of a lifetime's enthusiasm to both pursuits might make my efforts useful, in a distinctive way, to my colleagues.

Theory

I admire my friend Oliver Sacks extravagantly as a writer, and I could never hope to match him in general quality or human compassion. He once said something that touched me deeply, despite my continuing firm disagreement with his claim (while acknowledging the validity of the single statement relevant to the present context), Oliver said that he envied me because, although we had both staked out a large and generous subject for our writing (he on the human mind, me on evolution), I had enjoyed the privilege of devising and developing a general theory that allowed me to coordinate all my work into a coherent and distinctive body, whereas he had only written descriptively and aimlessly, albeit with some insight, because no similar central focus underlay his work. I replied that he had surely sold himself short, because he had been beguiled by conventional views about the nature and limits of what may legitimately be called a central scientific theory—and that he certainly held such an organizing concept in his attempt to reintroduce the venerable "case study method" of attention to irreducible peculiarities of individual patients in the practice of cure and healing in medicine. Thus, I argued, he held a central theory about the importance of individuality and contingency in general medical theory, just as I and others had stressed the centrality of historical contingency in any theoretical analysis and understanding of evolution and its actual results.

Oliver saw the theory of punctuated equilibria, which I developed with Niles Eldredge and discuss at inordinate length in Chapter 9, as my coordinating centerpiece, and I would not deny this statement. But punctuated equilibria stands for a larger and coherent set of mostly iconoclastic concerns, and I must present some intellectual autobiography to explain the reasons and the coming together, as best I understand them myself—hence my flip-off of Cardinal Newman's famous title for the best similar effort ever made, albeit in a maximally different domain. In his Apologia Pro Vita Sua (an apology for one's own life), Newman intends the operative word as I do,
in its original and positive meaning, not in the currently more popular negative sense—"something said or written in defense or justification of what appears to others to be wrong or of what may be liable to disapprobation" (per Webster's).

As my first two scientific commitments, I fell in love with paleontology when I met Tyrannosaurus in the Museum of Natural History at age five, and with evolution at age 11, when I read G. G. Simpson's *The Meaning of Evolution*, with great excitement but minimal comprehension, after my parents, as members of a book club for folks with intellectual interests but little economic opportunity or formal credentials, forgot to send back the "we don't want anything this month" card, and received the book they would never have ordered (but that I begged them to keep because I saw the little stick figures of dinosaurs on the dust jacket). Thus, from day one, my developing professional interests united paleontology and evolution. For some reason still unclear to me, I always found the theory of how evolution works more fascinating than the realized pageant of its paleontological results, and my major interest therefore always focused upon principles of macroevolution.1 I did come to understand the vague feelings of dissatisfaction (despite Simpson's attempt to resolve them in an orthodox way by incorporating paleontology within the Modern Synthesis) that some paleontologists have always felt with the Darwinian premise that microevolutionary mechanics could construct their entire show just by accumulating incremental results through geological time.

As I began my professional preparation for a career in paleontology, this vague dissatisfaction coagulated into two operational foci of discontent. First (and with Niles Eldredge, for we worried this subject virtually to death as graduate students), I became deeply troubled by the Darwinian convention that attributed all non-gradualistic literal appearances to imperfections of the geological record. This traditional argument contained no logical holes, but the practical consequences struck me as unacceptable (especially at the outset of a career, full of enthusiasm for empirical work, and trained in statistical techniques that would permit the discernment of small evolutionary changes). For, by the conventional rationale, the study of microevolution became virtually nonoperational in paleontology—as one almost never found this anticipated form of gradual change up geological sections, and one therefore had to interpret the vastly predominant signal of stasis and geologically abrupt appearance as a sign of the record's imperfection, and therefore as no empirical guide to the nature of evolution. Second, I became increasingly disturbed that, at the higher level of evolutionary trends within clades, the majority of well-documented examples (reduction of stipe number in graptolites, increasing symmetry of crinoidal cups, growing complexity of ammonoid sutures, for example) had never been adequately explained in the terms demanded by Darwinian convention—that is, as adaptive improvements of constituent organisms in anagenetic sequences. Most so-called explanations amounted to little more than what Lewontin and I, following Kipling, would later call "just-so stories," or plausible claims without tested evidence, whereas other prominent trends couldn't even generate a plausible story in adaptationist terms at all.

As Eldredge and I devised punctuated equilibrium, I used the theory to resolve these two puzzles to my satisfaction, and each resolution, when finally generalized and further developed, led to my two major critiques of the first two branches of the essential triad of Darwinian central logic—so Oliver Sacks's identification of punctuated equilibrium as central to my theoretical world holds, although more as a starting point than as a coordinating focus. By accepting the geologically abrupt appearance and subsequent extended stasis of species as a fair description of an evolutionary reality, and not only as a sign of the poverty of paleontological data, we soon recognized that species met all criteria for definition and operation as genuine Darwinian individuals in the higher-level domain of macroevolution—and this insight (by complex routes discussed in Chapter 9) led to the concepts of species selection in particular and, eventually, to the full hierarchical model of selection as an interesting theoretical challenge and contrast to Darwinian convictions about the exclusivity of organismal selection. In this way, punctuated equilibrium led to the reformulation proposed herein for the first branch of essential Darwinian logic.

Meanwhile, in trying to understand the nature of stasis, we initially focused (largely in error, I now believe) upon internal constraints, as vaguely represented by various concepts of "homeostasis," and as exemplified in the model of Galton's polyhedron (see Chapter 4). These thoughts led me to extend my doubts about adaptation and the sufficiency of functionalist mechanisms in general—especially in conjunction with my old worries about paleontological failures to explain cladal trends along traditional adaptationist lines. Thus, these aspects of punctuated equilibrium strongly contributed to my developing critique of adaptationism and purely functional mechanisms on the second branch of essential Darwinian logic (although other arguments struck me as even more important, as discussed below).

Nonetheless, and despite the centrality of punctuated equilibrium in developing a broader critique of conventional Darwinism, my sources extended...
major at Antioch College, as his skepticism evoked my stronger insistence that our science matched his reductionistic rigor because "we" now knew for certain that natural selection built everything for optimal advantage, thus making evolution as quantifiable and predictive as classical physics. Second, as a somewhat more sophisticated, but still beguiled, assistant professor, I remember my profound feeling of sadness and disappointment, nearly amounting to an emotional sense of betrayal, upon learning that an anthropological colleague favored drift as the probable reason for apparently trivial genetic differences among isolated groups of Papua-New Guinea peoples. I remember remonstrating with him as follows: Of course your argument conforms to logic and empirical possibility, and I admit that we have no proof either way. But your results are also consistent with selection—and our panselective paradigm has forged a theory of such beauty and elegant simplicity that one should never favor exceptions for their mere plausibility, but only for documented necessity. I recall this discussion with special force because my emotional feelings were so strong, and my disappointment in his "unnecessary apology" so keen, even though I knew that neither of us had the empirical "goods.") Finally, if I could, in a species of Devil's bargain, wipe any of my publications off the face of the earth and out of all memory, I would gladly nominate my unfortunately rather popular review article on "Evolutionary paleontology and the science of form" (Gould, 1970a)—a ringing pan to selectionist absolutism, buttressed by the literary barbarism that a "group evolutionary functional" paleontology, combining the best of biometric and mechanical analyses, could prove panadaptationism even for fossils that could not be run through the hoops of actual experiments.

Against this orthodox background—or, rather, within it and quite unconsciously for many years—I worked piecemeal, producing a set of separate and continually accreting revisionary items along each of the branches of Darwinian central logic, until I realized that a "Platonic" something "up there" in ideological space could coordinate all these critiques and fascinations into a revised general theory with a retained Darwinian base. The first branch of levels in selection proceeded rather directly and linearly because the generality flowed so clearly from punctuated equilibrium itself, once Eldredge and I finally worked through the implications and extensions of our own formulations (Eldredge and Gould, 1972). Steve Stanley (1975) and Elisabeth Vrba (1980) helped to show us what we had missed in ramifications leading from the phenomenon of stasis and geologically abrupt appearance, to recognizing species as Darwinian individuals, to designating species as, therefore and potentially, the basic individuals of macroevolution (comparable with the role of the organism in microevolution), to the validity of species selection, and eventually to the full hierarchical model and its profound departure from the exclusively organismal accounts of conventional Darwinism (or the even more reduced and equally monostic genetic versions of Williams and Dawkins)—see Vrba and Gould, 1986. Finally, by adopting the interactor rather than the replicator approach to defining selection, and by recognizing emergent fitness, rather than emergent characters, as
the proper criterion for identifying higher-level selection (Lloyd and Gould, 1993; Gould and Lloyd, 1999), I think that we finally reached, by a circuitous route around many stumbling blocks of my previous stupidities, a consistent and truly operational theory of hierarchical selection (see Chapter 8).

I must confess to some preconditioning by punctuated equilibria. I had admired Wynne-Edwards's pluck (1962) from the start, even though I agreed with William's (1966) trenchant criticisms of his particular defense for group selection, rooted in the ability of populations to regulate their own numbers in the interests of group advantage. Still, I felt, for no reason beyond vague intuition, that group selection made logical sense and might well find other domains and formulations of greater validity—a feeling that has now been cashed out by modern reformulations of evolutionary theory (see especially Wilson and Sober, 1995, and Chapters 8 and 9 here).

My odyssey on the second branch of balancing internal constraint with external adaptation in understanding the patterning and creative population of novel places in evolutionary morphospace followed a much more complex, meandering and diverse set of pathways. As an undergraduate, I loved D'Arcy Thompson's Growth and Form (1917) for my first "literary" paper, and wrote a senior thesis on his theory of morphology. But I thought that I admired the book only for its incomparable prose, and I attacked the anti-Darwinian (and structuralist) components of his theory mercilessly. Then, too, it allometry for my first empirical studies, somehow fascinated by structural constraint and correlation of growth, but thinking all the while that my task must center on a restoration of adaptationist themes to this "holdout" bastion of formalist thought—particularly the achievement of biomechanical optima consistent with the Galilean principle of decreasing surface/volume ratios with increasing size in isometric forms. I remain proud of my first review article, dedicated to this subject (Gould, 1966), written when I was still a graduate student, but I am now embarrassed by the fervor of my adaptationist convictions.

I emphasized allometric analysis, now in a directly multivariate reformulation, in my first set of empirical studies on the Bermudan pulmonate snail Pseudobosminia (see especially Gould, 1969—the published version of my Ph.D. dissertation). And yet, of all the long and largely adaptationist treatises in this series, and for some reason that I could not identify at the time, the conclusion that I reached with most satisfaction, and that I somehow regarded as most theoretically innovative (without knowing why), resided in a short, and otherwise insignificant, article that I wrote for a specialized paleontological journal on a case of convergence produced by structural necessity, given modes of coiling and allometry in this genus, rather than by selectionist homing (for some cases rested upon ecophenotypic expression, others on pseudomorphosis, and still others on gradual change that could be read as conventionally adaptive): "Precise but fortuitous convergence in Pleistocene land snails" (Gould, 1971c).

Five disparate reasons underlie my more explicit recognition, during the 1970s and early 1980s, of the importance and theoretical interest (and iconoclasm versus Darwinian traditions) of nonadaptationist themes rooted in structural and historical constraint. First, I stood under the dome of San Marco during a meeting in Venice and then wrote a notorious paper with Dick Lewontin on the subject of speciﬁds, or nonadaptive sequelae of prior structural decisions (Gould and Lewontin, 1979—see Chapter 11, pp. 1246—1258). Second, I recognized, with Elizabeth Vrba, that the lexicon of evolutionary biology possessed no term for the evidently important phenomenon of structures coopted for utility from different sources of origin (including nonadaptive speciﬁds), and not directly built as adaptations for their current function. We therefore devised the term "exaptation" (Gould and Vrba, 1982) and explored its implications for structuralist revisions to pure Darwinian functionalism. Third, I worked with a group of paleontological colleagues (Raup et al., 1973; Raup and Gould, 1974; Gould et al., 1977) to develop more rigorous criteria for identifying the signals that required selectionist, rather than stochastic, explanation of apparent order in phylogenetic patterns. The work left me imbued by the insight that our brains seek pattern, while our cultures favor particular kinds of stories for explaining these patterns—thus imposing a powerful bias for ascribing conventional deterministic causes, particularly adaptationist scenarios in our Darwinian traditions, to patterns well within the range of expected outcomes in purely stochastic systems. This work sobered me against such a priori preferences for adaptationist solutions, so often based upon plausible stories about results, rather than rigorous documentation of mechanisms.

Fourth, and most importantly, I read the great European structuralist literatures in writing my book on Ontogeny and Phylogeny (Gould, 1977b). I don't see how anyone could read, from Goethe and Grell to through Servetto, Remane and Riedl, without developing some appreciation for the plausibility, or at least for the sheer intellectual power, of structuralist explanations outside the domain of Darwinian functionalism—although my resulting book, for the last time in my career, stuck closely to selectionist orthodoxy, while describing these alternatives in an accurate and sympathetic manner. Fifth, my my unhappy with the speculative character of many adaptationist scenarios increased when, starting in the mid 1970s, the growing vernacular (and some of the technical) literature on sociobiology touted conclusions that struck me as implausible, and that also (in some cases) ran counter to my political and social beliefs as well.

Personal disease, needless to say, bears no necessary relationship to scientific validity. After all, what could be more unpleasant, but also more factually undeniable, than personal mortality? But when distrustful conclusions gain popularity by appealing to supposedly scientific support, and when this "support" rests upon little more than favored speculation in an orthodoxy mode of increasing dubious status, then popular misuse can legitimately sharpen a scientist's sense of unhappiness with the flawed theoretical basis behind a particular misuse. In any case, I trust that this compendium of reasons will dispel Cairns's (1979) hurtful assertion that Lewontin, I, and other evolutionists who questioned early forms of sociobiology by developing a general
Defining and Revising the Structure of Evolutionary Theory

the classical texts of late 18th and early 19th century catastrophism in their original languages—and I could find no claim for supernatural influences upon the history of the earth. In fact, the catastrophists seemed to be advancing the opposite claim that we should base our causal conclusions upon a literal reading of the empirical record, whereas the uniformitarians (aka “good guys”) seemed to be arguing, in opposing claim less congenial with the stereotypical empiricism of science, that we must make hypothetical inferences about the gradualistic mechanics that a woefully imperfect record does not permit us to observe directly.

But, although I had developed and presented an iconoclastic exegesis of Lyell, I simply lacked the courage to state so general a claim for inverting the standard view about uniformitarians and catastrophists. I assumed that I must be wrong, and that I must have misunderstood catastrophism because I had not read enough, or could not comprehend, the subtleties at this fledgling state of a career. So I scoured the catastrophe literature again until I found a quote from William Buckland (both a leading divine and the first reader in geology at Oxford) that could be interpreted as a defense of supernaturalism. I cited the quotation (Gould, 1965, p. 223) and stuck to convention on this broader issue, while presenting an original analysis of multiple meanings—some valid (like the invariance of law) and some invalid (like my professor’s claim for constancy in range of rates)—subsumed by Lyell under the singular description of “uniformity” in nature.

This work led me, partly from shame at my initial cowardice, and as others reassessed the scientific character of catastrophism, to a more general analysis of the potential validity of catastrophic claims, and particularly to an understanding of how assumptions of gradualism had so stymied and constrained our comprehension of the earth’s much richer history. These ideas forced me to question the necessary basis for Darwin’s key assumption that observable, small-scale processes of microevolution could, by extension through the immense of geological time, explain all patterns in the history of life—namely, the Lyellian belief in uniformity of rate (one of the invalid meanings of the hybrid concept of uniformitarianism). This exegesis led to a technical book about concepts of time and direction in geology (Gould, 1987b), an enlarged view that encouraged the development of punctuated equilibrium, and to a position of cautious favor toward such truly catastrophic proposals as the Alvarez theory of mass extinction by extraterrestrial impact—a concept ridiculed by nearly all other paleontologists when first proposed (Alvarez et al., 1980), but now affirmed for the K-T event, and accepted as an empirical basis for expanding our range of scientifically legitimate hypotheses beyond the smooth extrapolationism demanded by this third branch of Darwinian central logic.

In addition to these disparate accretions of revisionism on the three branches of Darwinian central logic, one further domain—my studies in the history of evolutionary thought—served as a sine qua non for wresting a coherent critique from such an inchoate jumble of disparate items. Above all, if I had not studied Darwin’s persona and social context so intensely, I doubt
that I would ever have understood the motivations and consistencies—also the idiosyncrasies of time, place and manner—behind the abstract grandeur of his view of life. History, as I argued before (see p. 35), must not be dismissed as a humanistic frill upon the adamantine solidity of "real" science, but must be embraced as the coordinating context for any broad view of the logic and reasoning behind a subject so close to the bone of human concern as the science of life's nature and structure. Of the two great revolutions in scientific thought, Darwin surely trumps Copernicus in raw emotional impact, if only because the older transition spoke mainly of real estate, and the later of essence.

Some of my historical writing appeared in the standard professional literature, particularly my thesis about the "hardening" of the Modern Synthesis (Gould, 1980c, 1982a, 1983b), a trend (but also, in part, a drift) towards a stricter and less pluralistic Darwinism. Several full-time historians of science then affirmed this hypothesis (Provine, 1986; Beatty, 1988; Smocovitis, 1996). But much of the historical analysis behind the basic argument of this book had its roots (in my consciousness at least) in the 300 consecutive monthly essays that I wrote from 1974 to 2001 in the popular forum of Natural History magazine, where I tried to develop a distinctive style of "mini-intellectual biography" in essay form—attempts to epitomize the key ideas of a professional career in a biographical context, and within the strictures of a few thousand words. By thus focusing myself to emphasize essentials and to discard peripherals (while always searching out the truly lovely details that best exemplify any abstraction), I think that I came to understand the major ideological contrasts between the defining features of Darwinian theory and the centerpieces of alternative views. In this format, I first studied such structuralist alternatives as Goethe's theory of the archetypal leaf, Geoffroy's hypothesis on the vertebral underpinning of all animals, and on dorso-ventral inversion of arthropods and vertebrates, and Owen's uncharacteristic English support for this continental view of life. I also developed immense sympathy for the beauty and raw intellectual power of various alternatives, even if I eventually found them wanting in empirical terms. And I came to understand the partial validity, and even the moral sussue, in certain proposals unfairly ridiculed by history's later victors—as in reconsidering the great hippocampus debate between Huxley and Owen, and recognizing how Owen used his (ultimately false) view in the service of racial egalitarianism, while Huxley missed his (ultimately correct) interpretation in a fallacious defense of traditional racial ranking.

Finally, my general love of history in the broadest sense spilled over into my empirical work as I began to explore the role of history's great theoretical theme in my empirical work as well—contingency, or the tendency of complex systems with substantial stochastic components, and intricate nonlinear interactions among components, to be unpredictable in principle from full knowledge of antecedent conditions, but fully explainable after time's actual unfoldings. This work led to two books on the pageant of life's history (Gould, 1980c; Gould, 1996a). Although this book, by contrast, treats gen-

eral theory and its broad results (pattern vs. pageant in the terms of this text), rather than contingency and the explanation of life's particulars, the science of contingency must ultimately be integrated with the more conventional science of general theory as explored in this book—for we shall thus attain our best possible understanding of both pattern and pageant, and their different attributes and predictabilities. The closing section of the book (pp. 1332–1343 of Chapter 12) offers some suggestions for these future efforts.

When I ask myself how all these disparate thoughts and items fell together into the one long argument of this book, I can only cite—and I don't know how else to put this—my love of Darwin and the power of his genius. Only he could have presented such a seductive framework of a fully consistent theory, so radical in form, so complete in logic, and so expansive in implication. No other early evolutionary thinker ever developed such a rich and comprehensive starting point. From this inception, I only had to explicate the full original version, tease out the central elements and commitments, and discuss the subsequent history of debate and revision for these essential features, culminating in a consistent reformulation of the full corpus in a helpful way that leaves Darwin's foundation intact while constructing a larger edifice of interestingly different form thereupon. Clearly I do not honor Darwin by hagiography, if only because such obsessive efforts would make any honest character cringe (and would surely cause Darwin to spin in his grave, thus upsetting both the tourists in Westminster Abbey and the adjacent bones of Isaac Newton). I honor Darwin's struggles as much as his successes, and I focus on his few weaknesses as entry points for needed revisions—his acknowledged failure to solve the "problem of diversity," or his special pleading for progress in the absence of any explicit rationale from the operation of his central mechanism of natural selection.

As a final comment, if this section has violated the norms of scientific discourse (at least in our contemporary world, although not in Darwin's age) by the liberty that I have taken in explicating personal motives, errors and corrections, at least I have shown how we all grope upward from initial stupidity, and how we would never be able to climb without the help and collaboration of innumerable colleagues, all engaged in the intensely social enterprise called modern science. I experienced no eureka moment in developing the long argument of this book. I forged the chain link by link, from initial possession of a few separate items that I didn't even appreciate as pieces of a single chain, or of any chain at all. I made my linkages one by one, and then often cut the segments apart, in order to refashion the totality in a different order. So many people helped me along the way—from long dead antecedents by their wise words to younger colleagues by their witticisms—that I must view this outcome as a social project, even though I, the most arrogant of literati, insisted on writing every word. Perhaps I can best express my profound thanks to the members of such an intellectual collectivity by stating, in the most literal sense, that this book would not exist without their aid and suffering. My formal dedication to my two dearest and closest paleontological collaborators in this effort to formulate macroevolutionary theory records
the worthy apex of an extensive pyramid. Scientists fight and squabble as all folks do (and I have scarcely avoided a substantial documentation thereof in this book). But we are, in general, a reasonably honorable lot, and we do embrace a tendency to help each other because we really do revel in the understanding of nature's facts and ways—and most of us will even trade some personal acclaim for the goal of faster and firmer learning. For all the tensions and unhappinesses in any life, I can at least say, with all my heart, that I chose to work in the best of all enterprises at the best of all possible times. May our contingent future only improve this matrix for our successors.

Epitomes for a Long Development

LEVELS OF POTENTIAL ORIGINALITY

Most of this book can be described as extensive narration of work already done, and ideas already expounded elsewhere. But no one should write at such length merely to organize the conventional material of a field, and without an original structure, or a set of unconventional ideas, to propose. I wrote The Structure of Evolutionary Theory because I felt that I had followed a sufficiently idiosyncratic procedure to devise a sufficiently novel theoretical structure that then yielded a sufficient number of original insights on specific matters to qualify as a justification for spending so many years of a career, and daring to ask readers for such a non-trivial chunk of their attention.

As implied by the foregoing sentence, I think that whatever originality this work possesses might best be conceptualized at three levels of basic structure, primary justifications for the major components of theory, and specific insights or discoveries then developed under the aegis of this structure and theory. At the first level of basic structure, I believe that three features of organization set the novelty of presentation:

1. Developing an exegesis of essential components in the logic of Darwinian theory, as expressed in the agency, efficacy, and scope of selection as an evolutionary mechanism (Chapter 2).

2. Explicating the history of evolutionary thought as a complex and extended debate about these essential components, developed negatively at first by early evolutionists who sought alternative formulations to Darwinian (Chapters 3-6), and then positively in our times by scientists who recognized the need for extensive revisions and expansions that would build an enlarged structure upon a Darwinian foundation, rather than uproot the theoretical core of selectionism (Chapters 7-12).

3. Formulating an expanded theory that introduces substantial revisions on each branch of Darwinian central logic, but builds, in its ensemble, a coherently enlarged structure with a retained Darwinian base—moving from Darwin’s single level of agency to a hierarchical theory of selection on the first branch; balancing positive sources of internal constraint (for both structural and historical reasons) with the conventional externalization of natural selection on the second branch; and recognizing the disparate inputs of various tiers of time, rather than trying to explain all phylogenetic mechanics by uniformitarian extrapolation from microevolutionary processes, on the third branch.

At the second level of validation for proposed revisions in the structure of evolutionary theory, I have tried to develop broad arguments and empirical justifications for major changes and expansions on each of the three branches of Darwinian central logic. On the first branch of agency, the theory of punctuated equilibrium itself, initially formulated by Niles Eldredge and me, establishes the species as a true and potent Darwinian individual, and grants a minimal guarantee of descriptive independence to macroevolution by requiring a treatment of trends as the differential success of stable species rather than the adaptive anagenesis of lineages by accumulated and extrapolated organismal selection alone. Beyond punctuated equilibrium, the general rationale for a hierarchical theory of selection, as presented here through the interactor approach based on emergent fitnesses at higher levels, may establish a complete (and tolerably novel) framework not only for grasping the consistent logic of hierarchical selection, but also for viewing each level as potent in its own distinctive way, and for recognizing the totality of evolutionary outcomes as a realized balance among these potencies, and not as the achieved optimality of a single causal locus—a substantial difference from Darwinian traditions for conceiving the dynamics of evolutionary change.

In working through the differences among levels—see Chapter 8, pp. 714-744—I was particularly struck by the surprising, but accurate and challenging, analogies (Lamarckian inheritance at the organismal level with adaptive anagenesis at the species level, for example); and by the different modes of equally effective change implied by disparate structural reasons for the establishment of individuality at various levels particularly, the domination of selection over drift and drive at the organismal level vs. the potent balance among all three mechanisms at the species level.

On the second branch of efficacy, I have tried to make the most comprehensive case yet advanced for internal constraint as a positive director and channeler of evolutionary change, and not only as a negative brake upon pure Darwinian functionalism. I proceed by explicating two conceptually different forms of constraint—structural constraints as consequences of physical principles, and historical constraints as channels from particular pasts. I argue that each category challenges a different central tenet of Darwinism—structural constraint by establishing a substantial space for non-selectionist origin of important evolutionary features, and historical constraint for explaining the markedly inhomogeneous filling of morphospace as flow down ancient internal channels of deep homology, and not primarily as a mapping of adaptive design upon current ecological landscapes. Beyond any novelty in this general formulation, I have attempted to develop a conceptual space, and to establish practical criteria, for the identification of non-adaptive sequels (spandrels), the evolutionary importance of their later cooption for utility (exaptation), and the importance of such reservoirs of potential (exaptive pools) in explicating the important concept of “evolvability” in structural rather than purely adaptational terms.
On the third branch of scope, my contribution cannot claim much novelty, if only because I have not worked professionally in this area of paleontological research. But I do explicate, perhaps more fully than before, both the historical and conceptual reasons for regarding catastrophic mass extinction, and catastrophic mechanics in general (within their limited scope of validity), not as anti-selectionist per se, but rather as fracturing the extrapolationist premise of Darwinian central logic, and requiring that substantial aspects of phylogenetic pattern be explained as interaction between temporal extensions of microevolution and different processes that only become visible and effective at higher tiers of time. I try to resolve "the paradox of the first tier" (the empirical failure of Darwin's logically airtight argument for a vector of progress) by arguing that punctuated equilibrium at the second tier of phylogenetic trends, and mass extinction at the third tier of faunal turnover, impose enough of their own, distinctive and different, patterning to forestall the domination or pure imprint of extrapolated microevolutionary results upon the general pagant of life's history. Finally, at the third level of those lovely details (where both God and the devil dwell, and where, ultimately, both the joy and power of science reside), I trust that any originality I have introduced at "higher" levels of theoretical structure gains primary expression and utility in the resolution of previously puzzling details, and in the identification of "little things" that had escaped previous notice or explicit examination. For example, most original analyses and discoveries in the historical first half of this book flow directly from my organizing theme of identifying essential components in Darwinian logic, and then tracing both the early attempts to defeat, and our later efforts to modify and expand them through time. I was thus able to discover and identify Darwin's major encounter with higher level selection not in his recognized discussion of group selection for human altruism, but in his previously unexplained admission of species selection to resolve the problem of diversity (see Chapter 3, pp. 246–250). In this case, I "lacked out" through an odd reason for previous ignorance of such an important textual revision—for Darwin omitted this material in his compressed and hasty discussion of diversity in Chapter 4 of the Origin (on this subject, the only Darwinian source generally known to professional biologists, who would immediately highlight the importance of any acknowledgment of species selection). But Darwin signified over levels of selection at explicit length in the unpublished "long version" that only saw the light of printed day in 1975 (Stauffer, 1975); and that virtually no practicing biologist has ever read (whereas historians of science who do study this longer text usually lack sufficient knowledge of the technical debate about levels of selection to understand the meaning of Darwin's passages or to appreciate their import). The same context led me to appreciate the previously unanalyzed development of a full hierarchical model by Weismann in his later works (Chapter 3, pp. 223–224), a formulation that Weismann himself identified as the most important theoretical achievement of his later career. Previous historians had written about his much longer and earlier explications of lower level selection (genetical selection in his terms), if only in the context of modern reductionistic breakdowns of Darwinism to selection among "selfish genes." But they had missed his later reversal and expansion to a full hierarchical model, despite Weismann's own emphasis. Similarly, de Vries's clear understanding of Darwinian logic had also been ignored because de Vries, as an opponent of the efficacy of Darwinian organismal selection (a painful decision for him, given his psychological fealty to Darwin, also explored herein), applied the logic to higher levels, and even devised the term "species selection" (Chapter 5, pp. 446–451)—a concept and coining previously entirely unremarked by historians (much to the embarrassment of scientists, including yours truly, who coined and explicated the same term much later in full expectation of pristine originality). Similarly, my sense of the logic in conflicts between constraint and adaptation (or internal vs. external, or formal vs. functional approaches) on the second branch helped me to pinpoint, or to make sense of, several important historical events and arguments that have not been properly treated or understood. Historians of science had not previously discussed orthogenetic theories in this faintest light, and had not distinguished the very different formulations of Hyatt, Eimer, and Whitman in terms of their increasingly greater willingness to accommodate Darwinian themes as well (see Chapter 5). The same framework allowed me to identify the crucial importance, and brilliant epitomization, of this issue in the final paragraphs of Chapter 6 ("Difficulties on Theory") in Darwin's Origin, a significance that had not been highlighted before. I also traced the dichotomy of anglophonc preferences for functionalist accounts vs. continental leanings towards formalism back through the evolutionary reconstruction of the argument in the mid 19th century into the creationist formulations of Paley vs. Agassiz (Chapter 4), thus illustrating a pedigree for this fundamental issue in morphology that evolution may have recast in causal terms, but did not budge in basic commitments to the meaning of morphology. Among the little tidbits that emerge from such analyses, I even discovered that Darwin borrowed his clearest admission of co-opted utility from non-adaptive origins (unfused skull sutures in mammalian neonates, essential for passage through the birth canal, but also existing in birds and reptiles born from more capacious eggs) from the longer and more nuanced descriptions of Richard Owen, Britain's anomalous defender of formalism. I also included some historical analyses in the book's second half on modern advances because I thought they could make an original contribution to arguments usually developed only in contemporary terms and findings. I have already mentioned my analysis of the initial pluralism of the Modern Synthesis (embracing any mode of change consistent with known genetic mechanisms) hardened through subsequent editions of the founding volumes into pronounced preferences for adaptationist accounts framed only in terms of natural selection (Chapter 7). In addition, I think that my reexamination of the debate between Falconer and Darwin on fossil elephants provides a
good introduction to punctuated equilibrium (Chapter 9, pp. 745–749). The largely unknown paradox of Lankester's original definition of homoplasy as a category of homology, rather than in the opposite status held by the term today, provides the best entry I could devise for understanding the vital, but little appreciated and rarely acknowledged, theoretical differences between parallelism and convergence. In the absence of this context and distinction, the key importance of evo-devo and the discovery of deep homology among distant phyla cannot properly be grasped as a challenge and expansion of Darwinian expectations (Chapter 10).

I hope that my sympathetic portrayal of D'Arcy Thompson's theory of form (Chapter 11), despite my general disagreement with his argument, will help colleagues to understand the thrust and potential power of this unusual formulation of structuralist constraint on external grounds of universal physics. Although I am chagrined that I discovered Nietzsche's account of the distinction between current utility and historical origin so late in my work, I know no better introduction—form one of history's greatest philosophers to boot, and in his analysis of morality, not of any scientific subject—nor the theoretical importance of spandrels and exaptation in the rebalancing of constraint and adaptation within evolutionary theory (Chapter 11, pp. 1214–1218). In a final historical analysis of the second part, I think that Darwin's own rationale for progress (Chapter 12, pp. 1296–1303), rooted not in the mechanics of natural selection itself, but in an ecological argument for extrapolation of biotic competition through time in a perpetually crowded world—an aspect of Darwin's thought that has very rarely been appreciated, formulated, or discussed by historians—provided the best context I could devise for understanding why catastrophic mass extinction in particular, and non-extrapolation through tiers of time in general, play such havoc with Darwin's need for uniformity on the third branch of his essential logic.

The original claims in the book's second half on modern reformulations of evolutionary theory rest, necessarily and primarily, on theoretical insights and unusual conceptual parsings, rather than on novel data—if only because custom dictates that my extensive empirical documentation be presented in a "review" format by collating published studies in support or refutation of general themes under discussion. But I have sometimes presented existing data in novel contexts—as in my analysis of the proper category for understanding the expatriate value of genes lost by founder drift in establishing the social cohesion (albeit transient) that has made the Argentine ant Linepithema humile such a successful invader of non-native Californian habitats (Chapter 11, pp. 1282–1284). I have also cited my own empirical studies, previously published but original in the more conventional sense, to support important pieces of more general arguments, including validation of punctuated equilibrium by dissection of a single bedding plane to reveal transition by absolute age dating of individual shells (Goodfriend and Gould, 1996), the "employment" of constraint by selection to yield several adaptive features by one heterochronic change in a case of neoteny in Graphea (Jones and Gould, 1999), and the explanation of most ordered geographic variation within a major subregion of Corvus as consequences of allometric correlations in growth (Gould, 1984b).

I tried (and utterly failed) to compose a selective listing, as provided above for the book's historical half, for original ideas about theoretical details developed in revising the three branches of Darwinian central logic in the book's second half on modern reformulations of evolutionary theory. I ripped up several attempts that read like the hodge-podge of a random laundry list rather than the ordered "sweet places" on a logical continuum. These highlights, I finally recognized, have little meaning outside the broader context of a linearly developing argument for each branch, and I will therefore make a second attempt, within the more detailed epilogue of the next and final section of this chapter, to designate the points that struck me with the force of "aha," or that conveyed a hint of deeper, surprising, or more radical implications for reasons that I couldn't quite fathom directly, but that tickled my intuition at the edge of that wonderful, if elongate, German word: Finger spitzengefühl, or feeling at the tip of one's finger. Most inchoate excitations of this sort lead to nowhere but foolishness and waste of time, but every once in a while, the following of one's nose catches a whiff of novelty. At least we must trust ourselves enough to try—and not take ourselves so seriously that we forget to laugh at our more frequent and inevitable stumbles.

**AN ABSTRACT OF ONE LONG ARGUMENT**

I have insisted, borrowing Darwin's famous line in my arrogance, that this "whole volume is one long argument," flowing logically and sequentially from a clear beginning in Darwin's Origin to our current reformulations of evolutionary theory. But this structural thread of Ariadne can easily become lost in the labyrinth of my tendencies to expatiate on little factual gems, or to follow the thoughts of leading scientists into small, if lovely, byways of their mental complexities. Hence, I need to present summaries and epiphanies as guidelines.

Long books, like large bureaucracies, can easily get bogged down in a baroque layering of summary within summary. The United States House of Representatives has a Committee on Committees (I kid you not), undoubtedly embellished with subcommittees thereof. And we must not forget Jonathan Swift's famous verse on the frailty of growing triviality in scholarly commentary:

So, naturalists observe, a flea

Hath smaller fleas that on him prey;

And these have smaller still to bite 'em

And so proceed ad infinitum.

Thus every poet, in his kind,

Is bit by him that comes behind.

I wrote, on page 13, that this book includes three levels of embedding for this long argument—the summary in this chapter, the epilogue of Darwin in
Chapter 2, and the development of the totality. Now, and most sheeplishly, I add two more, for a fractal total of five—the listed abstract, in pure "book order," of this section, and (God help us) the epilogue of this epilogue, presented now to introduce and guide the list.

I develop my argument throughout this book by asserting, first, that the central logic of Darwinism can be depicted as a branching tree with three major limbs devoted to selection's agency, efficacy and scope. Second, that Darwin, despite his heroic and explicit efforts, could not fully "cash out" his theory in terms of the stated commitments on each branch—and that he had to allow crucial exceptions, or at least express substantial fears, in each domain (admitting species selection to resolve the problem of diversity; permitting an uncomfortably large role for formalist correlations of growth as commitments of strict adaptationism; expressing worry that mass extinction, if more than an artifact of an imperfect fossil record, would dwarf the extrapolationist premise of his system). Third, that the subsequent history of evolutionary debate has focused so strongly upon the key claims of these three essential branches that we may use engagement with them as a primary criterion for distinguishing the central from the secondary when we need to gauge the importance of challenges to the Darwinian consensus. Fourth, that we should not be surprised by the prominence of these three themes, for they embody (in their biological specificity) the broadest underlying issues in scientific explanation, and in the nature of change and history (of levels of structure and causality, rates of alteration, directions of causal flow, the possibility of causal uniformity by reduction to the lowest level as autonomy and interaction of irreducible levels, punctuational vs. gradual change, causal and temporal hierarchies, smooth extrapolation). Fifth, that the most interesting and important debates in our contemporary science continue to engage the same three themes, thus requiring the vista of history to appreciate the continuity and logical ordering that extends right back to Darwinian beginnings. Sixth, that our best modern understanding of the structure of evolutionary theory has reversed the harmful dichotomization of earlier debates (Darwinian fealty vs. destructive attempts to trivialize or overturn the mechanism of selection) by confronting the same inadequacies of strict Darwinism, but this time introducing important additions and revised formulations that preserve the Darwinian foundation but build a theory of substantial expansion and novelty upon a retained selectionist core.

This logic and development may be defended as tolerably impersonal and universal, but any book of this length and complexity, and of so idiosyncratic a style and structure, must also own its authorial singularities. The Structure of Evolutionary Theory emerges, first of all, from my professional focus as a paleontologist and student of macroevolution, defined, as explained on page 38, as descriptive phenomenology prior to any decision about the need for distinctive theory (my view) or the possibility of full subsumption under microevolutionary principles (the view of Darwin and the Modern Synthesis). The contingency of history guarantees that any body of theory will underdetermine important details, and even general flows, in the realized pageant of life's phylogeny on Earth—and such a claim for nontheoretical independence of macroevolution generates no dispute, even between rigid reductionists who grant no separate theoretical space to macroevolution, and biologists, like myself, who envisage an important role for distinctive macroevolutionary theory within an expanded and reformulated Darwinian view of life.

In his description of the reductionist view of classical Darwinism—his own opinion in positive support, not a simplistic caricature in opposition—Hoffman (1989, p. 39) writes: "The neodarwinian paradigm therefore asserts that this history of life at all levels—including and even beyond the level of speciation and species extinction events, embracing all macroevolutionary phenomena—is fully accounted for by the processes that regulate within populations and species." I dedicate my book to refuting this traditional claim, and to advocating a helpful role for an independent set of macroevolutionary principles that expand, reformulate, operate in harmony with, or (at most) work orthogonally as additions to, the extrapolated, and persistently relevant (but not exclusive, or even dominant) forces of Darwinian microevolution.

This perspective of synergy confutes the contrary, and ultimately destructive, attempts by late 19th and early 20th century macroevolutionists to develop substitute mechanisms that would disprove or trivialize Darwinism, and that spread such a pall of suspicion over the important search for non-reductionistic and expansive evolutionary theories—a most unfortunate (if historically understandable) trend that stifled, for several generations, the unification and fruitful expansion of evolutionary theory to all levels and temporal tiers of biology. Thus, for example, my attempt to develop a spatio-temporal theory of macroevolution (Chapters 8 and 9), with species treated as irreducible Darwinian individuals playing causal roles analogous to those occupied by organisms in Darwinian micromutation, represents an extension of Darwinian styles of explanation to another hierarchical level of analysis (with interestingly different causal twists and resulting patterns), not a refutation of natural selection from an alien realm. (Such a spatio-temporal theory, however, does counter Hoffman's reductionistic claim of full theoretical sufficiency for "processes that operate within populations and species"—for, given the status of species under punctuated equilibrium, such macroevolutionary patterns originate by higher-order sorting among stable species, and not primarily by processes occurring asexuagenetically within the lifetime of these higher-level Darwinian individuals.) Similarly, the different rules of catastrophic mass extinctions require additions to the extrapolated Darwinian and microevolutionary causes of phyletic patterns, but do not refute or deny the relevance of conventional uniformitarian accretions through geological time. (In fact, a more comprehensive theory that seeks to integrate the relative strengths, and interestingly disparate effects, of such different levels and forms of continuationist vs. catastrophic causality offers greater richness to Darwinian perspectives as both underpinnings and important contributors to a larger totality.)

A second authorial input must arise from the distinctive ontogeny of past
work. The Structure of Evolutionary Theory occupies a much broader territory than my first lengthy technical book of an earlier career, Ontogeny and Phylogeny (1977b). The motivating concept of the first book rested upon my choice of a much smaller compass defined by a much clearer tradition of definition and research. I thought—thus my designation of this strategy as a concept—that I could quote, in extenso and from original sources, every important statement, from von Baer and before to de Beer and after, on the relationship between development and evolution. This potential for comprehensiveness brought me much pleasure and operational motivation.

In fact, I soon realized that I could not succeed, even within this limited sphere—and I therefore punted shamelessly in the final result. I did manage to quote every important passage on the theoretical relationship between these central subjects of biology, but I passed, nearly completely, on the actual use of these putative relationships in specific proposals for phylogenetic reconstructions. And, as all historians of science and practitioners of evolutionary biology know, this genre of “phylogenizing” represented by far (at least by weight) the dominant expression of this theoretical rubric in the technical literature. I would, by the way, defend my decision as entirely reasonable and proper, and not merely as practically necessary, because these specific phylogenetic invocations made effective no contribution to the development of evolutionary theory—my central concern in the book—and remained both speculative and transient to boot. But I do remember the humbling experience of realizing that a truly full coverage could only represent a pipe dream, if applied to any important subject in a vigorous domain of research!

My personal love of such thoroughness (with the necessary trade-off of limitation in domain) posed a substantial problem when I decided to expand my range from ontogeny and phylogeny to the structure of evolutionary theory. Of all genres in scholarship, I stand most strongly out of personal sympathy with broad-brush views that attempt to encompass entire fields (the history of philosophy from Plato to Pogo, or of transportation from Noah to NASA) in a breathless summary paragraph for each of many thousand incidents. Even the most honorable efforts by great scholars—former Librarian of Congress Daniel Boorstin’s The Explorers, for instance—make me cringe for simplistic legends repeated and interesting complexities omitted. At some level, truly important and subtle themes can only be misrepresented by such a strategy.

But how then to treat the structure of evolutionary theory in a repeatable, even an enlightening, way? Surely we cannot abandon all hope for writing honorably about such broad subjects simply because the genre of comprehensive listing by executive summary must propagate more mythology and misinformation than intrigue or understanding. As a personal solution to this crucial scholarly dilemma, and in developing the distinctive strategy of this book, I employed a device that I learned by doing, through many years of composing essays—a genre that I pursued by writing comprehensive personal treatments of small details, fully documentable in the space available, but also conveying important and general principles in their cascading implications. I vowed that I would try to encompass the structure of evolutionary theory in its proper intellectual richness, but that I would do so by exhaustive treatment of well-chosen exemplifying details, not by rapid summaries of inadequate bits and pieces catalogued for all relevant participants.

Under this premise, the central task then evolves (if I may use such a metaphor) into an extended exercise in discrimination. The solution may be labeled as elitist, but how else can selection in intellectual history be undertaken? One must choose the best and the brightest, the movers and shakers by the sieve of history’s harsh judgment (and not by the transiency of immediate popularity)—and let their subtle and detailed formulations stand as a series of episodes, each conveyed by an essay of adequate coverage. Luckily, the history of evolutionary thought—as one of the truly thrilling and expansive subjects of our mental lives—has attracted some of the most brilliant and fascinating doers and thinkers of intellectual history. Thus, we are blessed with more than adequate material to light the pathway of this particular odyssey in science. Luckily too, the founding figure of Darwin himself established such a clear basis of brave commitment that I could characterize, and then trace down to our own times, an essential logic that has defined and directed one of the most important and wide-ranging debates in the history of science into a coherent structure, ripe for treatment by my favored method of full coverage for the few truly central items (by knowing them through their fruits and legacies, and by leaving less important, if gaudy, swatches gently aside in order to devote adequate attention to essential threads).

A third, and final, authorial distinction—my treatment of history and my integration of the history of science with contemporary research on evolutionary theory—emerges directly from this strategy of coverage in depth for a small subset of essential items and episodes. My historical treatments tend to resolve themselves into a set of mini intellectual biographies (as exemplified and defended on page 46) for almost all the central players in the history of Darwinian traditions in evolutionary thought. I can only hope that this peculiar kind of intellectual comprehensiveness will strike some readers as enlightening for the “quick entry” thus provided into the essential work of the people who led, and the concepts that defined, the history of the greatest and most consequential revolution in the history of biological science. (In most cases—a Goethe, Cuvier, Weismann, de Vries, Fisher or Simpson, for example—I chose people for their intrinsic and transcendent excellence. In fewer instances—in Eimer or Hyatt as proponents of orthogenesis, for example—I selected eminently worthy scientists not as great general thinkers, but as best exponents of a distinctive approach to an important subject in the history of debate on essentials of evolutionary theory.)

A few figures in history have been so prescient in their principal contributions, and so acute and broad-ranging in their general perceptions, that they define (or at least intrigue upon) almost any major piece of a comprehensive discussion (A. N. Whitehead famously remarked, for example, that all philos-
Defining and Revising the Structure of Evolutionary Theory

3. Darwin famously characterized the Origin as "one long argument" without explicitly stating "for what?" Assumptions about the focus of this long argument have ranged from the restrictively narrow (for natural selection, or even for evolution) to the overly broad (for application of the most general hypothetico-deductive model in scientific argument, as Ghiselin has claimed). I take a middle position and characterize the "long argument" as an attempt to establish a methodological approach and intellectual foundation for rigorous analysis in historical science—a foundation that could then be used to validate evolution.

4. The "long argument" for historical science operates at two poles—methodological and theoretical. The methodological pole includes a set of procedures for making strong inferences about phylogenetic history from data of an imperfect record that cannot, in any case, "see" past causes directly, but can only draw conclusions from preserved results of these causes. Darwin develops four general procedures, all based on one of the three essential premises of his theory's central logic: the explanation of large-scale results by extrapolation from short-term processes. In order of decreasing information available for making the required inference, these four procedures include: (1) extrapolation to longer times and effects of evolutionary changes actually observed in historic times (usually by analogy to domestication and horticulture); (2) exemplification and ordering of several phenomena as sequential stages of a single historical process (forming reefs, barrier reefs and atolls as stages in the formation of coral reefs by subsidence of central islands, for example); (3) inference as history, the only conceivable coordinating explanation for a large set of otherwise disparate observations (consilience); and (4) inference of history from single objects based on quirks, oddities and imperfections that must denote pathways of prior change.

5. The theoretical pole rests upon the three essential components of Darwinian logic: (1) agency, or organismal struggle as the appropriate (and nearly exclusive) level of operation for natural selection; (2) efficacy, or natural selection as the creative force of evolutionary change (with complexly coordinated sequelae of inferred principles about the nature of variation, and of commitments to gradualism and adaptationism as (s) of evolutionary analysis); and (3) scope, or extrapolation (as described in point 4 just above).

The logical coordination of these commitments, and their establishment as a brilliantly coherent and intellectually radical theory of evolution, can best be understood by recognizing that Darwin transferred the paradoxical argument of Adam Smith's economics into biology (best organization for the general polity arising as a side consequence of permitting individuals to struggle for themselves alone) in order to devise a mechanism—natural selection—that would acknowledge Paley's phenomenology (the good design of organisms and harmony of ecosystems), while inverting its causal basis in the most radical of all conceivable ways (explaining the central phenomenon of adaptation by historical evolution rather than by immediate creation, and recognizing nature's sensible order as a side consequence of unfettered struggle among individuals, rather than a sign of divine intent and benevolence).
6. The first theme of agency: Darwin's commitment to the organismal level as the effectively exclusive locus of natural selection occupies a more central, and truly defining, role than most historians and evolutionists have recognized. Invocation of this most reductionistic locus then available (in ignorance of the mechanism of inheritance) embodies the intellectual radicalism of Darwin's theory—using Adam Smith to overturn Paley, and holding that all higher-order harmony, previously attributed to divine intention, arises only as a side-consequence of selfish "struggle" for personal advantage at the lowest organismal level. Darwin devoted far more of the Origin to defending this organismal locus than most exegetes have acknowledged, particularly in centering his only two chapters on specific difficulties in natural selection (7 on Instinct and 8 on Hybridism) to resolutions provided by insistence upon organismal agency—explaining the establishment of adaptive sterile castes in social insects by selection upon queens as individuals, and resolving sterility in interspecific crosses as an unselected sequel of differences accumulated by organismal selection in each of two isolated populations, rather than as a direct result of higher-level species selection, as Wallace affirmed and as Darwin strove mightily and consciously to avoid. We can also trace his struggle to affirm organismal exclusivity in his reluctance, underplayings and walking off (as unique and untreated elsewhere in nature) of the one exception (for human altruism) that the logic of his system forced upon his preferences.

7. For his defense of the second theme of efficacy—his assertion of natural selection as the only potent source of evolutionary change—Darwin recognized that his weak and negative force, although surely a vera causa (true cause), could only play this creative role if variation met three crucial requirements: copious in extent, small in range of departure from the mean, and isotropic (or undirected towards adaptive needs of the organism). I would argue that Darwin's most brilliant intellectual move lay in his accurate identification, through the logical needs of his theory and not from any actual knowledge of heredity's mechanism, of these three major attributes of variation—because he recognized that natural selection could not otherwise operate as a creative force in the evolution of novelties.

8. Gradualism enters Darwin's system as another deductive intellectual consequence of asserting that natural selection acts as the creative mechanism of evolutionary change. Gradualism has three distinct meanings in Darwinian traditions, with only the second (or intermediate) statement relevant to the central assertion of selection's creativity. First, gradualism as simple historical continuity of stuff or information underlies the basic factuality of evolution vs. creation, and does not validate any particular mechanism of evolutionary change. Second, gradualism as insensible intermediary of transitional forms specifies the Goldlochinean "middle position" required by the mechanism of natural selection to refute the possibility that substantial variation might engender creative change all at once, thus relegating selection to a negative role of removing the unfit. Third, gradualism as a geological claim for slowness and smoothness (but not constancy) of rate plays a crucial role in the third theme (see point 10 of this list) of selection's scope, or the extrapolarability of microevolution to explain all patterns in geological time—and is therefore the aspect of gradualism that punctuated equilibrium refutes (for punctuated equilibrium questions Darwin's uniformitarian and catastrophism beliefs, but not his mechanism of natural selection). This parsing of three distinctly different forms of gradualism, all embraced by Darwin for different reasons, alleviates the misunderstanding behind some unfortunate terminological wrangles without substance that have generated much heat (but little light) in recent debates.

9. The adaptationism program as a primary strategy of research emerges as the third major implication of advocating natural selection as the primary creative force in evolutionary change—for this Darwinian style of evolution must proceed step by step, with each tiny increment of change rendering organisms better adapted to alterations in local environments. To summarize all the key implications of this second theme of explanation, the creativity of natural selection makes adaptation central, isotropy of variation necessary, and gradualism pervasive.

10. Restriction of agency to the organismal level, and assertions of selection's creativity, set a biological basis for the third essential claim of Darwinian logic—selection's scope, or the argument that this incremental and gradualistic style of microevolution can, by smooth extrapolation through the immensity of geological time, build the full extent of life's anatomical change and taxonomic diversity by simple accumulation. I focus my shorter discussion of this third essential theme not upon biological needs (already covered in the first two themes), but upon the requirement of creative gradualistic styles of change in the geological stage that must present the evolutionary play—particularly in Darwin's embrace of Lyellian uniformity, and his denial of catastrophism (through arguments about the imperfection of the fossil record to alyx the literal appearance of such rapidity in geological data), for even a fully consistent, intellectually sound, and operationally potent theory will not regulate actual events if surrounding conditions debar its operation.

11. I use Kellogg's brilliant approach to the evaluation of Darwinian theory (published in 1907 in anticipation of centennial celebrations for Darwin's birth and the sesquicentenary of the Origin) to distinguish alternatives that deny the fundamental postulate of selection from auxiliaries that enlarge, adumbrate, or reformulate the theory of natural selection in basically helpful and consistent ways. I show that Darwinism may be epitomized by its three essential claims of agency, efficacy, and scope—and that the history of debate has always centered upon these themes, with critiques focusing upon destructive alternatives or constructive auxiliaries. I argue, as the major thesis of this book, that modern debates have developed important and coherent auxiliary critiques on all three branches of essential Darwinian logic, and that these debates may lead to a fundamentally revised evolutionary theory with a retained Darwinian core.

Chapter 3: Seeds of hierarchy

1. Nearly all scientific revolutions originate as replacements and refutations of previous explanatory schemes, not as pure additions to a former state
of acknowledged ignorance. Lamarck's evolutionary theory, known to anglo-
phonic readers as a full-fledged account of the kind but critical descriptions
of Lyell (in Volume 2, 1832, of the Principles of Geology), and from Cham-
ber's promotion in the Vestiges of 1844, provided a context for Darwin's ref-
utation. Darwin's single-level theory, based on the full efficacy of locally
adaptive changes at the smallest scale, countered the only available alter-
native of Lamarckianism by relocating the major phenomenon that generated
change and required explanation (local adaptation for Darwin, general prog-
gress for Lamarck), and (far more radically) by reversing the conventional
Paleyan explanation for the good design of organisms and the harmony of
ecosystems (direct divine construction at the highest level vs. sequence of nat-
ural selection working at the lowest level of organismal advantage).

2. Lamarck, a dedicated materialist with a two-factor theory of evolution
as a contrast between linear progress up life's ladder and tangential deflec-
tions of diversity through local adaptation, has been widely misunderstood
(and revised), both in Darwin's time and today, as a vitalist and pure expo-
ponent of "soft" or Lamarckian inheritance (which he accepted as the "folk
wisdom" of his day, and invoked primarily to explain the secondary process
of lateral adaptation).

3. Darwin's theory of natural selection shared a functionalist basis with
Lamarck in joint emphasis upon adaptation to external environment as the
instigator of evolutionary change. But the two theories differ most radically
in Darwin's citation of a single locus and mechanism of change—with the full
range of evolutionary results proceeding by natural selection for local adapta-
tion of populations to changing immediate environments, and all higher-level
phenomenology emerging by sequential accumulation of such tiny incre-
ments through the immensity of geological time. By contrast, Lamarck advo-
cated a two-factor theory, with local adaptation as a merely secondary and
diverging process (and, as we all know of course, arising by soft inheritance
of acquired features generated by adaptive effort during an organism's life,
rather than by natural selection of fortuitous variation), set against a primary
process of progressive complexification up the ladder of life. Thus, Darwin
embraced Lamarck's secondary force (instantiated by a different mechanism),
denied the existence of Lamarck's primary force, and argued that the sec-
ondary force of local adaptation also produced the large-scale results attributed
by Lamarck to the primary force. Thus, this first major debate between evolu-
tionary alternatives contrasted Lamarck's hierarchical theory with Darwin's
single-level account. Hierarchy has been an important issue from the start (al-
though, obviously, modern versions of hierarchical selection theory, advo-
cated as the centerpiece of this book, bear no relationship, either genealogical
or ideological, to this false, but fascinating, Lamarckian original).

4. Darwin explicitly rejected Lamarck's two-factor theory, correctly identi-
fying the disabling paradox that rendered the theory nonoperational: "what
is important cannot be observed or manipulated (the higher-level force of
progress), and what can be observed and manipulated (the tangential force of
local adaptation) cannot explain the most important phenomenon (progress
in complexification)," Darwin developed the first testable and operational
theory of evolution by locating all causality in the palpable mechanism of
natural selection.

5. In the first generation of Darwinian debate, August Weismann, clearly
the most brilliant theorist of his time, and the only biologist (besides Darwin)
who fully grasped the logic and implications of selection, wrestled with levels
of selection throughout his career, and along an interesting path, finally de-
veloping a full hierarchical theory that he explicitly identified as the most impor-
tant conclusion of his later work. He began by trying to refute Lamarckian
inheritance (and Herbert Spencer's vigorous defense thereof) by advocating
the Allmacht (omnipotence, or literally "all might" or complete sufficiency)
of natural selection. He first attributed the degeneration of previously useful
structures (a bigger problem for Darwinism than the explanation of adaptive
features) to what he called "pannixia" (not the modern meaning of the term,
but the effect of recombination, in sexual reproduction, between adaptive ele-
ments and inadaptive elements no longer subject to negative selection), then
realized that this process could not explain complete elimination, thus lead-
ing him to propose a lower level of subcellular selection, potentially acting
in opposition to organismal selection, and called "germinal selection;", and
finally recognized that if levels of selection existed below the organismal, then
the same logic implies the existence and potency of supraorganismal levels
as well.

6. Darwin himself provides the best 19th century example—previously un-
recognized because Darwin omitted this material, originally written for the
unpublished "long version," from the Origin—of the need for a hierarchical
theory of selection in any full account of the phenomenology of evolution.
Entirely consistent single-level theories cannot be carried through to comple-
tion. Darwin admitted important components of species selection in capping
his (still unsatisfactory) explanation for an issue that he ranked second in im-
portance only to explaining the anagenesis of populations by natural selec-
tion: the resolution of organic variety and plurality by a "principle of dver-
gence" (his terminology). I document the largely unrecognized emphasis that
he placed upon this principle of divergence (for example, the Origin's famous
single figure does not illustrate natural selection, as generally misinterpreted,
but rather the principle of divergence). Darwin struggled to explain this de-
scriptively higher-level phenomenon of taxonomic diversification as a fully
predictable consequence of ordinary organismal selection, but he could not
proceed beyond an argument that he himself finally recognized as forced, and
even a bit hokey: the claim that natural selection will always favor extreme
variants at the tails of a distribution for a local population in a particular
ecology (the Origin's diagram represents an exemplification of this claim).
Eventually, Darwin realized that he needed to invoke species selection for a
full explanation of the success of speciose clades—and this unknown argu-
ment, rather than his well-documented defense of group selection for hu-
man altruism, represents Darwin's most generalized invocation of selection at
supraorganismal levels.
7. Hierarchical models of evolutionary processes (at least descriptively so, but causally as well) have been feared and defended by evolutionary theorists from the beginning of our science, although not always by good or valid arguments. This inadequately recognized theme explains the major contrast between Lamarck and Darwin, and coordinates the various disputes between Wallace and Darwin. Wallace simply didn’t grasp the concept of levels at all, and remained so committed to adaptationism that he ranged up and down the hierarchy, oblivious of the conceptual problems thus entailed, until he found a level to justify his adaptationism bent. Darwin, by contrast, completely understood the problem of levels, and the reasons behind his strong preference for a reductionist and single-level theory of organisal agency—although he reluctantly admitted a need for species selection to resolve the problem of divergence. We can also understand why Wallace’s 1858 Ternate paper, sent to Darwin and precipitating the “delicate arrangement,” did not proceed as far to a resolution as later tradition holds, when we recognize Wallace’s conceptual confusion about levels of selection.

Chapter 4: Internalism and laws of form: pre-Darwinian alternatives

1. In a brilliant closing section to his general chapter 6, entitled “difficulties on theory,” Darwin summarized the logical structure of the most important challenge to his system, and organized his most cogent defense for his functionalist theory of selection, by explicating the classical dichotomy between “unity of type” and “conditions of existence”—or the formalism of Geoffroy vs. the functionalism of Cuvier—entirely in selectionist terms, and to his advantage. He attributed “conditions of existence” to immediate adaptation by natural selection, and then explicited “unity of type” as constraints of inheritance of homologous structures, originally evolved as adaptations in a distant ancestor. Thus, he identified natural selection as the underlying “higher law” for explaining all morphology as present adaptation or as constraint based on past adaptation. He also admitted, while clearly restricting their range and complexity, a few other factors and forces in evolutionary explanation.

2. A fascinating, and previously unexplored, contrast may be drawn between the strikingly similar dichotomy, although rooted in creationists’ explanations, of Paley’s functionalist and adaptationist theory of divine construction for individualized biomechanical optimality vs. Agassiz’s formalist theory of divine ordination of taxonomic structure as an incarnation of God’s thoughts according to “laws of form” reflecting modes and categories of eternal thought. Clearly, this ancient (and still continuing) contrast between structural and functional conceptions of morphology transcends and predates any particular mechanism, even the supposedly primary contrast of creation vs. evolution, proposed to explain the actual construction of organic diversity.

3. In the late 18th century, the great poet (and naturalist) Goethe developed a fascinating (and, in the light of modern discoveries in evo-devo, more than partly correct) archetypal theory in the structuralist or formalist mode—and explicitly critical of functionalist, teleological and adaptationist alternatives—

4. The famous early 19th century argument, culminating in the public debate of 1830 between Georges Cuvier and Etienne Geoffroy St. Hilaire (and analyzed by Goethe in his final paper before his death), did not, as commonly misinterpreted, pit evolutionary theories against creationist accounts (although Geoffroy favored a limited theory of evolution, while Cuvier remained strongly opposed), but rather represented the most striking and enduring incident in this older and persistent struggle between formalist (Geoffroy) and functionalist (Cuvier) explanations of morphology and taxonomic order. Geoffroy advocated the abstract vertebrata as an archetype for all animals, beginning (largely successfully) with a common basis for anatomical differences between teleosts and tetrapods, moving to the putatively common design of insects and vertebrates (still with some success, partly confirmed by the Zoology of modern evo-devo, but also including some “howlers” like the homology of arthropod limbs with vertebrate ribs), and crashing with the proposed homology of vertebrates and a cephalopod doubled back upon itself (the comparison that sufficiently aroused Cuvier’s growing ire into a call for public debate). Geoffroy’s theory of dorso-ventral inversion between insects and vertebrates was not a silly evolutionary conjecture about “the worm that turned” (as later caricatures often portray), and did not represent an evolutionary explanation at all, but rather expressed a formalist comparison based upon a common underlying structure, ecologically oriented one way in vertebrates (central nervous system up), and the other way in arthropods. The common impression of Cuvier’s victory must be reassessed as a complex “draw,” with Geoffroy’s position abetted by the fortuity of his longer life and his courting of prominent literary friends as supporters (including Balzac and Georges Sand).

5. Adaptationist preferences have enjoyed a long anglophonetic tradition, beginning with the treatises of Ray and Boyle, in Newton’s founding generation, on final causality; then extending, in creationist terms, through Paley and the Bridgewater Treatises; and finally culminating in the radically reversed evolutionary explanations (but still retaining the same functionalist and adaptationist commitments) of Darwin, extending forward to Fisher and the Modern Synthesis. By contrast, continental traditions have favored formalist and structuralist explanations of morphology, from the creationist accounts of Agassiz, through the transitional systems of Goethe and Geoffroy, to the fully evolutionary accounts of Goldschmidt and Schindewolf in the mid 20th century. Interestingly, the complex views of Richard Owen, so widely misunderstood as an opponent of evolution (when he only rejected the predominant formalism of traditional British approaches to morphology), may best be grasped when we understand him as a rare anglophonetic exponent of a predominantly formalist theory. Owen, following Geoffroy, tried to explain the entire vertebrate skeleton, including the skull and limbs, as a set of modifications upon a vertebral archetype.

6. Darwin maintained a genuine interest in formalist constraints upon
adaptationist optimism for individualized features of anatomy—a theme that he epitomized as "correlations of growth." But he developed an explicit framework and rationale, most thoroughly discussed not in the Origin but in his longest 1868 book on *The Variation of Animals and Plants Under Domestication*, that relegated such formalist effects to a clearly subservient and secondary status, compared with natural selection and adaptation, in evolutionary causality.

**Chapter 5: Channels and saltations in post-Darwinian formalism**

1. Galton's Polyhedron, the metaphor and model devised by Darwin's brilliant and eccentric cousin Francis Galton, and then fruitfully used by many evolutionary critics of Darwinism, including St. George Mivart, W. K. Brooks, Hugo de Vries, and Richard Goldschmidt, clearly expresses the two great, and both logically and historically conjoined, themes of formalism (or structuralist, or internalist, in other terminologies) challenges to functionalist (or adaptationist, or externalist) theories in the Darwinian tradition. This model of evolution by face-forwarding to limited possibilities of adjacent plates in inherited structure stresses the two themes—channels set by internal constraint, and evolutionary transition by discontinuous saltation—that structuralist alternatives tend to embrace and that pure Darwinism must combat as challenges to basic components of its essential logic (for channels direct the pathways of evolutionary change from the inside, albeit in potentially positive and adaptive ways, even though some external force, like natural selection, may be required as an initiating impulse; whereas saltational change violates the Darwinian requirement for selection's creativity by vesting the scope and direction of change in the nature and magnitude of internal jumps, and not in sequences of adaptive accumulations mediated by natural selection at each step).

2. Orthogenesis, as a general term for evolutionary directionality along channels of internal constraint, rather than external pathways of natural selection, existed in several versions, ranging from helpful auxiliaries to Darwinism, to outright alternatives that denied any creative potency to selection. Theodor Eimer, who coined the term orthogenesis, presented a middle version that tried to integrate internal channels of orthogenesis with external pathways of functionalist determination. But Eimer defended Lamarckian mechanisms for his functionalism, thus leading him to oppose natural selection (the "Ahrmacht," or "without power," of selection, contrasted with Weismann's "Almacht," or "all power") despite his pluralistic linkage of formalist and functionalist explanations.

3. The orthogenetic theory of the late 19th century American paleontologist Alpheus Hyatt embodied maximal opposition to natural selection, and must be viewed as alternative, rather than auxiliary, to Darwinism. Hyatt conceived the pathway of orthogeny, modified only by heterochronic changes permitted under the biogenetic law, as the internal directing channel that natural selection could tweak, but not derail. Illustrating the influence of theory over perception, Hyatt found several parallel lineages of nautiloids, running along different segments of a common pathway, but all supposedly living in an identical environment—where others had reconstructed typical Darwinian morphophletic trees of phylogeny from the same stratigraphic section of fresh-water planorbids. Hyatt, who engaged in a long and ultimately frustrating correspondence with Darwin on this subject, believed that lineages followed a preordained "ontogeny" of phyletic youth, maturity and old age, thus attributing the different internal responses of lineages living in the same environment to their residence in different stages of an ontogenetically fixed and shared phyletic pathway (a preset internal channel with a vengeance).

4. Charles Ors Whitman, a great early 20th century American naturalist, developed the most congenial auxiliary theory (to Darwinism) of orthogenetic in his extensive work on the evolution of color patterns in Darwin's own favorite organism, the domestic pigeon. Whitman argued that domestic pigeons in particular, and dove-like birds in general, followed a strong channel of internal predisposition leading in one direction from checkers to bars, and eventually to the obliteration of all color. (Darwin, by interesting contrast, argued for a reverse tendency from bars to checkers, but also held, as his basic theory obviously implies, that selection largely determines any particular event and that no internal predisposition can trump the dictates of immediate function.)

5. In his 1894 book on *Materials for the Study of Variation* (where he coined the term orthogeny), William Bateson presented an extensive catalog of cases in discontinuous variation among individuals in a population and between populations of closely related organisms. He used these examples to develop a formalist theory of saltational evolution, strongly opposed to the adaptationist assumptions of Darwinian accounts. (Bateson's acerbic criticism of adaptationist scenario-building and story-telling in the speculative mode emphasizes a common linkage between structuralist preferences for mechanical explanation, and distaste for the adaptationist assumption that functional necessity leads and the evolution of form follows.) Although Bateson coined the term genetics, his personal commitment to a "vibratory" theory of inheritance, based on physical laws of classical mechanics—an intuition that he could never "cash out" as a testable theory—prevented his allegiance to the growing influence of Mendelian principles.

6. Hugo de Vries, the brilliant Dutch botanist who understood the logic of selection so thoroughly and acutely (but largely in contrast with the only other biologists, Weismann and Darwin himself, who also grasped all the richness and range of implications, but with favor), developed a saltational theory of evolution, but explicitly denied any predisposition of lineages to follow internal channels of constraint. (He thus showed the potential independence of the frequently-linked formalist themes of channeling and saltation, a conjunction espoused by Bateson and Goldschmidt for example, but denied in the other direction by Whitman, who favored channeling but denied saltation by supporting a gradualist theory of orthogenetic change.) This fascinating scholar regarded Darwin as his intellectual hero and never forgot the kindness and encouragement conveyed by his mentor and guru during
their one personal meeting early in de Vries's career. But de Vries, who developed the theory of intracellular pangeneses (the ultimate source for the term "gene") in the late 19th century, and then (quite fortuitously and long after he had reached salientional conclusions for other reasons) became one of Mendel's rediscoverers, based his true salientional theory of immediate macromutation of origin of species on his work with the evening primrose, *Oenothera* *lamarckiana*, where he mistook an odd chromosomal organization that generates occasional saltations for a biological generality. De Vries, who understood the logic of selectionism so well, who knew that his macromutation theory refuted several essential components of Darwinian logic, but who could not bear (for largely psychological reasons) to forsake his intellectual and personal hero, insisted upon his larger factal to Darwin, even though he had banned Darwinian mechanisms from the master's own realm of the origin of species. So de Vries developed a hierarchical theory that, while denying selection for the origin of species, restored selectionist logic at the higher level of phyletic trends by explicitly proposing "species selection" (his term) as a mechanism for generating broader phylogenetic patterns.

7. By proposing a comprehensive formalist theory in the heyday of developing Darwinian orthodoxy, Richard Goldschmidt became the whipping boy of the Modern Synthesis—and for entirely understandable reasons. Goldschmidt showed his grasp, and his keen ability to utilize, microevolutionary theory by supporting this approach and philosophy in his work on variation and intraspecific evolution within the gymnophyllum, *Lamotraria dispar*. But he then expressed his apostasy by advocating discontinuity of causality, and proposing a largely nonselectionist and formalist approach for macromutation from the origin of species to higher levels of phyletic pattern. Goldschmidt integrated both themes of saltation (in his concept of "systemic mutation" based on his increasingly lonely, and ultimately indefensible, battle to deny the corpuscular gene) and channeling (in his more famous, if ridiculed, idea of "hopeful monsters," or macromutants channeled along viable lines set by internal pathways of ontogeny, sexual differences, etc.). The developmental theme of the "hopeful monster" (despite its inappropriate name, virtually guaranteed to inspire ridicule and opposition), based on the important concept of "race genes," came first in Goldschmidt's thought, and always occupied more of his attention and research. Unfortunately, he bound this interesting challenge from development, a partially valid concept that could have been incorporated into a Darwinian framework as an auxiliary hypothesis (and now has been accepted, to a large extent, if under different names), to his truly oppositional and ultimately incorrect theory of systemic mutation, therefore winning anathema for his entire system. Goldschmidt may have acted as the architect of his own undoing, but much of his work should evoke sympathetic attention today.

**Chapter 6: Pattern and progress on the geological stage**

1. Darwin based his argument for a broad and general vector of progress in life's history not on the "bare bones" operation of natural selection (where he had explicitly denied such an outcome as the most radical implication of his theory), but on subsidiary ecological claims for the predominance of biotic over abiotic competition, and for a geological history of plentitude in a persistently crowded ecological world, where one species must displace another to gain entry into ecosystems (the metaphor of the wedge). Darwin used these ecological sequellae, along with the gradualist and incrementalist logic of natural selection itself, as primary justifications for his third essential claim of selection's scope, or the uniformitarian extension of small-scale microevolution, in a smoothly continuationist manner, to explain all patterns of macro-evolution by accumulation of increments through the immensity of geological time.

2. Such a claim requires that the geological stage operate in an appropriately, and "Goldilocksian," manner—not too much change to debar the operation and domination of this slowly and smoothly accumulative biological mode, and not too little to provide insufficient impetus (within Darwin's externalist and functionalist theory) for attributing the amount of change actually observed to natural selection.

3. The primary claim of "too much" derived from the school of "catastrophe" in geology—a movement that has been unfairly stigmatized by later history, following Lyell's successful and largely rhetorical mischaracterization (he was a lawyer by profession), as an unscientific defense of supernaturalism to cram the observed structure of geologic history into the narrow confines of geologic chronology, but that actually took the opposite position of strict empirical literalism (whereas uniformitarianists argued that the numerous literal appearances of rapidity in the geological record must be "interpreted" as misleading consequences of how gradual change must be expressed in a usefully imperfect set of strata). The great catastrophist Cuvier, in particular, was an Enlightenment rationalist, not a theological apologue—and he based his defense of catastrophism upon his literalist reading of the paleontological and geological record.

4. The primary claim of "too little" geology followed Lord Kelvin's increasingly diminished estimates for the age of the earth (incorrectly made—although Kelvin accurately described the necessary, but as it turned out) empirically false, logic required to validate his views—by assuming that heat now flowing from the earth represented a continuing loss from an originally molten state). Darwin worried intensely over Kelvin's claims, even referring to him as an "odious spectre" in a letter to Wallace. Darwin feared that Kelvin's low estimates would not permit enough time to generate the history of life under his slowly acting theory of gradualistic and accumulative change. Although this story has been told often, and has become familiar to scientists, an important (and decisive) aspect of the tale has rarely been exposed: Darwin fought this battle alone, and his strong distress illustrates the maximal, and unique, extent of his gradualistic and continuationist commitments. His closest colleagues, Wallace and Huxley, did not find Kelvin's low estimates unacceptable, but argued that we had only been led to expect such slow change from our previous conception of the earth's age, and that faster rates
of phyletic change, implied by Kelvin's dates, were entirely acceptable under their reading of evolution.

Chapter 7: The modern synthesis as a limited consensus

1. From the anachronic situation that prevailed at the Darwinian centennial celebrations of 1909 (confidence in the factuality of evolution, linked with agnosticism about theories and mechanics, as the first fruits of Mendelian seemed, initially, to refute the gradualism and incrementalism of natural selection), the Modern Synthesis eventually emerged in two stages (following the union of Darwinian and Mendelian perspectives in the work of Fisher and others): first, by a welcome restriction that eliminated Kellogg's three al ternatives in oppositional modes that would have destroyed Darwinism ( Lamarckism as a substitute functionalism, and saltationism and orthogene sis as formalist alternatives), and reasserted, now in a context of Mendelian particulate inheritance, the adequacy of natural selection as a creative force; and second, by an increasingly dubious hardening, culminating in centennial celebrations for the Origin in 1959, that substituted an increasingly rigid adaptationism for an earlier pluralism that embraced all mechanisms (including genetic drift) consistent with known genetic principles, while favoring selection as a primary force.

2. In his founding book of 1930, The Genetical Theory of Natural Selection, R. A. Fisher showed how slow, gradual evolution in large, panmictic populations (treated as asexual and nonmeiotic system, analogous to effectively infinite populations of identical gas molecules free to move and diffuse by physical principles) could validate strict Darwinism under Mendelian particulate inheritance (with Darwin's own acceptance of blending inheritance exposed as a more serious impediment than Darwin himself had realized), and disprove saltationist alternatives by the inverse correlation of frequency and magnitude in variation. To these mathematical and general chapters, Fisher appended a long closing section devoted to his eugenic theory that Western society had begun to degenerate seriously as a consequence of the social promotion of infertility (the rise in class level of "good" genetic stock, largely by their correlated tendency to fewer children, thereby husbanding their economic resources to potentiate their social elevation). Fisher conceived this eugenic "blight" as entirely Darwinian in character—visible in its gradual expression generation by generation, but ultimately more deadly than the explicit saltational degenerescence stressed by most eugenacists.

3. In contrast with the initial pluralism of Haldane and Huxley (in the book that coined the Modern Synthesis), and of the first editions of founding documents for the second phase of the Synthesis (Dobzhansky's 1937 Genetics and the Origin of Species, Mayr's 1942 Systematics and the Origin of Species, and Simpson's 1944 Tempo and Mode in Evolution), later editions of these three documents encapsulated the hardening of this second phase, as initial pluralism yielded to an increasingly firm and exclusive commitment to adaptationist scenarios, and to natural selection as a virtually exclusive mechanism of change. Even Sewall Wright's views on genetic drift and shifting bal
particular, and by these criteria, species must be construed not only as classes (as traditionally conceived), but also as distinct historical entities acting as good Darwinian individuals—and therefore potentially subject to selection. In fact, a full and logical hierarchy of inclusion—with rising levels of genes, cell lineages, organisms, demes, species and clades—features clearly definable Darwinian individuals, subject to processes of selection, at each level, thus validating (in logic and theory, but not necessarily in the potency of actual practice in nature) an extension and reformulation of Darwin's exclusively organismal theory into a fully hierarchical theory of selection.

2. The validity of the "interactor approach" to defining the mechanics of selection, and the fallacy of the "replicator approach" expose, as logically invalid, all modern attempts to preserve Darwinian exclusivity of level, but to offer an even more reductionistic account in terms of genes, rather than organisms, as agents—with organisms construed as passive containers for the genes that operate as exclusive agents of natural selection. This argument, based upon the true but irrelevant identification of genes as faithful replicators, must be replaced by the conceptually opposite formulation of a hierarchical theory of selection, with genes identified as only one valid, and lowest, level in a hierarchy of equally potent, and interestingly different, levels of Darwinian individuality: genes, cell lineages, organisms, demes, species and clades. Replication identifies a valid and important criterion for the crucial task of bookkeeping or tracing evolutionary change; but replicators cannot specify the causality of selectionist processes, which must be based upon the recognition and definition of interactors with environments. Even Williams and Dawkins, the two leading exponents of exclusive gene selectionism, have acknowledged and properly described the hierarchical causality of interaction (while preferring increasingly elaborate and implausible verbal defenses of gene selection in arguments about parallel hierarchies and Nelder cubing of legitimate alternatives rooted in criteria of replication vs. interaction). Thus, Williams and Dawkins seem to grasp the validity of hierarchical interaction through a glass darkly, while still trying explicitly to defend their increasingly indefensible preferences for exclusive gene selectionism.

3. The logic of hierarchical selection cannot be gainsaid, and even Fisher admitted the consistency, even the theoretical necessity, while denying the empirical potency, of species selection. Fisher based his interesting and powerful argument on his assumption that low N for species in clades (relative to organisms in populations) must debar any efficacy for species selection in a world of continuous and gradulastic anagenesis rooted in organismal selection. However, Fisher's argument, although logically tight, fails empirically because species tend to be stable and directionally unchanging (however fluctuating) during their geological lifetimes, and the theoretically "weaker" force of species selection may therefore operate as the "only game in town" for macroevolution. The arguments for potentiality of species selection are stronger than corresponding assertions for interdemic selection (largely because species actively maintain their boundaries as Darwinian individuals, whereas demes remain subject to breakup and invasion). But, despite these intrinsic weaknesses and problems, interdemic selection has now been empirically validated as an important force in evolution—thus strengthening a prima facie case for the even greater importance of species selection in macroevolution.

4. Two theoretical results have long been the basis of contemporary biogeography: the sound theoretical basis, and a strong argument for the empirical potency, of species selection as an important component of macroevolution; first, the recognition of differential proliferation rather than downward effect as the most operational criterion for defining and recognizing species selection; second, the acknowledgment that emergent fitnesses under the interactor approach, rather than emergent features treated as active adaptations of the species, constitute the proper criterion for identifying species selection. The former insistence upon emergent features (by me and other researchers, and in error), while logically sound and properly identifying a small subset of best and most interesting cases, relegated the subject to infrequent operational utility, and thus to relative impotence. The proper criterion (under the interactor approach) of emergent fitness universalizes the subject by permitting general identification in the immediacy of the current mechanics of selection, and not requiring knowledge—often unavailable given the limits of historical archives—of adaptive construction and utility in ancestral states.

5. The six levels recognized for convenience, and not accompanied by any claim of completion or exclusivity—gene, cell lineage, organism, deme, species and clade—feature two important principles that make the theory of hierarchical selection so different from, while still in the lineage and tradition of, exclusivist Darwinian organismal selection. First, adjacent levels may interact in the full range of conceivable ways—in synergy, orthogonal, or in opposition. Opposition has been stressed in the existing literature, but only because this mode is easier to recognize, and not for any argument of greater importance in principle. Second, the levels operate non-fractally, with fascinating and distinguishing differences in mode of functioning, and relative importance of components, for each level. For example, the different mechanisms by which organisms and species maintain their equally strong individuality dictate that selection should dominate at the organismal level, while selection, drift, and drive should dominate the current important and balanced roles at the species level.

6. To cite just one difference (from conventions of the organismal level) for each nonstandard level, and to make the key point about distinctiveness of levels in an almost anecdotal manner: random change may be most prominent in relative frequency at the level of the gene and individual; true gene selection also plays an important, if limited, role (largely in the mode that has been given the unfortunate name—for its implication of opposition, almost in ethical terms, to the supposed standard of proper organismal selection—of "selfish DNA"); however, the Dawkinesque argument for exclusivity of genic selection only records the confutation of a preferred level of bookkeeping with an erroneous claim for a privileged locus of selection. Selection among cell-lineages, although ancestrally important in the evolution of multicellular organisms, has largely been suppressed by the organismal level in the interests
of its own integrity; failure of this suppression leads to the pyrrhic victory of cell-lines that we call cancer. Interdecim selection, although once so widely rejected, probably plays an essential role in the evolution of social cooperation in general, and not only for such specific phenomena as human altruism. Species-level selection, combined with other species-level properties of drive and drift, establishes the independent basis for a distinctive speciation theory and reformulation of macroevolution. The highest level of clade selection, although sometimes operative, may be relatively weak by an extension of Fisher's argument about low N.

7. I explore the distinctive differences between levels of selection by trying to exemplify and "play out" the detailed disparities in a "grand analogy" between the conventional operation of organismic selection and the relative conceptual novelty of species selection. As an idiosyncratic sample of potential reforms and surprises, consider the following claims: First, the formulation of a general taxonomy for sources of change in hierarchically ordered systems, based on a primary distinction of "drive" for directed changes arising within an individual, based on change among lower-level individuals as constituent parts; and "sorting," with two causally distinct subcategories of "selection" and "drift" for change based on alterations of relative frequencies among individuals at the focal level itself. Second, the recognition, by following the logic of the analogy, of some strikingly counterintuitive comparisons that become both interesting and revealing upon subsequent reflection—including the likeness of Lamarckian change, construed as ontogenetic drive at the organismal level, with standard anagenetic transformation as organismal drive at the species level (transformation by directional change of constituent parts of a higher-level individual, in this case the organisms of a species); this similarity may also highlight the rather different reasons for general unimportance of both levels of drive—Lamarckism for the well-known reason of the theoretical non-occurrence in a Mendelian world, and anagenesis based on the controversial claim for its evident plausibility in theory (as a basic Darwinian process), but rarity in fact, given the dominant relative frequency of punctuated equilibrium. Third, the establishment of a framework for distinguishing directional speciation as a form of reproductive drive (inherently biased differences in autapomorphies of descendant species vs. ancestral states) from true species selection as a higher order sorting among daughter species that arise with phenotypic differences randomly distributed among parental means. I believe that we have missed this crucial distinction because the analogy of directional speciation at the organismal level—drives induced by mutation pressure—occur so rarely (for conventional reasons of organismal selection's power to suppress them) that we haven't considered the greater potency of analogous processes at other levels. Fourth, the importance of testing "Wright's Rule"—the claim that speciation is random with respect to the direction of evolutionary trends within clades—because the major alternative of directional speciation as the cause of trends holds such potential power at the species level, whereas its analog (drives of mutation pressure) assumes so little importance at the organismal level. Fifth, the potentially far greater impor-

portance of drift (both species drift and founder drift) vs. selection as a mechanism of sorting at the species level, but not at the organismal level, where selection predominates in standard formulations. Sixth, the identification of an intrinsically, and probably unbreakable (in most cases), negative correlation between speciation and extinction propensities as the primary constraint operating to prevent the takeover of life by a few megaclasses (which might dominate by enhancing speciation while retarding extinction among constituent species—or perhaps the Collembola have prevailed by this means), Seventh, the recognition that the organismal level operates uniquely in securing the integrity of its individuals by devices (physiological homostasis among organs, and spatial bounding by an external surface) that "clear out" both drive from below and drift at its own level as mechanisms operating at a high relative frequency—thus leaving selection in its most dominant position at this level. Perhaps our Darwinian prejudice for regarding selection as by far the most effective, or virtually the only important, process of evolutionary change arises more from the parochialism of our organismal focus (given our own personal residence in this category) than from any universal characterization of all levels in evolution.

Chapter 9: Punctuated equilibrium and the validation of macroevolutionary theory

1. The clear predominance of an empirical pattern of stasis and abrupt geological appearance as the history of most fossil species has always been acknowledged by paleontologists, and remains the standard testimony (as documented herein) of the best specialists in nearly every taxonomic group. In Darwinian traditions, this pattern has been attributed to imperfections of the geological record that impose this false signal upon the norm of a truly gradualistic history. Darwin's argument may work as a principle for punctuational origin, but stasis is data and cannot be so encompassed.

2. This traditional argument from imperfection has stymied the study of evolution by paleontologists because the record's primary (and operational) signal has been dismissed as misleading, or as "no data." Punctuated equilibrium, while not denying imperfection, regards this signal as a basically accurate record of evolution's standard mode at the level of the origin of species. In particular, before the formulation of punctuated equilibrium, stasis had been read as an embarrassing indication of absence of evidence for the desired subject of study—that is, of data for evolution itself, falsely defined as gradual change—and the prominently testable, fully operational, and intellectually fascinating (and positive) subject of stasis had never been subjected to quantitative empirical study, a situation that has changed dramatically during the last 25 years.

3. The key empirical ingredients of punctuated equilibrium—punctuation, stasis, and their relative frequencies—can be made testable and defined operationally. The theory only refers to the origin and development of species in geological time, and must not be misconstrued (as so often done) as a claim for true salination at a lower organismal level, or for catastrophic mass extinc-
tion at a higher faunal level. Punctuation must be scaled relative to the later duration of species in stasis, and we suggest 1–2 percent (analogous to human gestation), the length of human life) as an upper bound. Punctuated equilibria can be distinguished from other causes of rapid change (including anagenetic passage through bottlenecks and the traditional claim of imperfect preservation for a truly gradualistic event) by the criterion of ancestral survival following the branching of a descendant. Punctuations can be revealed by positive evidence (rather than inferred from compression on a single bedding plane) in admittedly rare situations, but not so infrequent in absolute number, of unusual fineness of stratigraphic resolution or ability to date the individual specimens of a single bedding plane. Stasis is not defined as absolute phenotypic immobility, but as fluctuation of means through time at a magnitude not statistically broader than the range of geographic variation among modern populations of similar species, and not directional in any preferred way, especially not towards the phenotype of descendants. Punctuated equilibrium will be validated, as all such theories in natural history must be (including natural selection itself), by predominant relative frequency, not by exclusivity. Gradualism certainly can and does occur, but at very low relative frequencies when all species of a fauna are tabulated, and when we overcome our conventional bias for studying only the small percentage of species qualitatively recognized beforehand as having changed through time.

4. Punctuated equilibrium emerges as the expected scaling of ordinary allopatric speciation into geological time, and does not suggest or imply radically different evolutionary mechanisms at the level of the origin of species. (Other proposed mechanisms of speciation, including most sympatric modes, envision rates of speciation even faster than conventional allopatry, and are therefore even more consistent with punctuated equilibrium.) The theoretically radical features of punctuated equilibrium flow from its proposals for macroevolution, with species treated as higher-level Darwinian individuals analogous to organisms in microevolution.

5. The difficulty of defining species in the fossil record does not threaten the validity of punctuated equilibrium for several reasons. First, in the few studies with adequate data for genetic and experimental resolution, paleo-species (even for such difficult and morphologically labile species as colonial cheilosomate bryozoans) have been documented as excellent surrogates, comparable as units to conventional biospecies. Second, the potential underestimation of biospecies by paleospecies only imposes a bias that makes punctuated equilibrium harder to recognize. The fossil record's strongly positive signal for punctuated equilibrium, in the light of this bias, only increases the probability of the pattern's importance and high relative frequency. Third, the potential overestimation of biospecies by paleospecies is probably false in any case, and also of little practical concern because no paleontologist would assert punctuated equilibrium from the evidence of oversplit taxa in faunal lists, but only from direct biometric study of stasis and punctuation in actual data.

6. We originally, and probably wrongly, tried to validate punctuated equilibrium by asserting that, in principle, most evolutionary change should be concentrated at events of speciation. Subsequent work in evolutionary biology has not confirmed any a priori preference for concentration in such episodes. Futuyma's incisive macroevolutionary argument—that realized change will not become geologically stabilized and conserved unless such change be "tied up" in the unalterable individuality of a new species—offers a far richer, far more interesting, and theoretically justified rationale for correlating episodes of evolutionary change with speciation.

7. Section III presents a wide-ranging discussion of why proposed empirical refutations of punctuated equilibrium either do not hold in fact, or do not bear the logical weight claimed in their presentation. Refutations for single cases are often valid, but do not challenge the general hypothesis because we anticipate a lower relative frequency for gradualism, and these cases may reside in this minor category. Claims for predominant gradualism in the entire clade of planktonic forams may hold as exceptional (although, even here, the majority of lineages remain unstudied, in large part because they seem, at least subjectively, to remain in stasis, and have therefore not attracted the attention of traditional researchers, who wish to study evolution, but then equate evolution with gradualism). However, in these asexual forms with vast populations, gradualism at this level may just represent the expected higher-level expression of punctuational clade selection, as Lenski has affirmed in the most thorough study of evolution in a modern bacterial species—and just as gradual cladal trends in multicellular lineages emerge as the expected consequences of sequential punctuated equilibrium at the species level (trends as stasis rather than inclined planes, so to speak). Claims for genetic gradualism do not challenge punctuated equilibrium, and may well be anticipated as the proper expression at the genic level (especially given the high relative frequency of random nucleotide substitutions) of morphological stasis in the phenotypic history of species. Punctuated equilibrium has done well in tests of conformity with general models, particularly in the conclusion that extensive polyphyly in cladistic models may arise not only (as usually interpreted) from insufficient data to resolve a sequence of close dichotomies, but also as the expectation of punctuated equilibrium for successive branching of daughter species from an unchanged parental form in stasis. In fact, the frequency of polyphyly vs. dichotomy may be used as a test for the relative frequency of punctuated equilibrium in well resolved cladograms—a test well passed in data presented by Wagner and Erwin.

8. Section IV then summarizes the data on empirical affirmations of punctuated equilibrium, first on documented patterns of stasis in unbranched lineages; second on punctuational cladogenesis affirmed by the criterion of ancestral survival; third on predominant relative frequencies for punctuated equilibrium in entire biotas (with particularly impressive affirmations by Hallock, Kellogg, and Stanley and Yang for mollusks; and by Prothero and Heaton for Oligocene Big Bull Island mammals, where a study of all taxa yielded 177 species that followed the expectations of punctuated equilibrium and three cases of potential gradualism, only one significant); fourth on predominant relative frequencies for punctuated equilibrium in entire clades, with empha-
In the structure of evolutionary theory, perhaps the best documented and most impressive case of exclusive punctuated equilibrium ever developed. Finally, we can learn much from variation in relative frequencies among taxa, times, and environments—and interesting inferences have been drawn from recorded differences, particularly in Sheldon's counterintuitive linkage of stasis to rapidly changing, and gradualism to stable, environments.

9. Among many reasons proposed to explain the predominance of stasis, a phenomenon not even acknowledged as a "real" and positive aspect of evolution before punctuated equilibrium gave it some appropriate theoretical space, habitat tracking (favored by Eldredge), constraints imposed by the nature of subdivided populations (favored by Lieberman), and normalizing clade selection (proposed by Williams) represent the most novel and interesting proposals.

10. Among the implications of a predominantly punctuational origin of stable species—individuals for macroevolutionary theory, we must rethink trends (the primary phenomenon of macroevolution, at least in terms of dedicated discussion in existing literature) as products of the differential success of certain kinds of species, rather than as the adaptive anagenesis of lineages—a radical reformulation with consequent extending to a new set of explanations no longer rooted (as in all traditional resolutions) in the adaptive advantages conferred upon organisms, but potentially vested in such structural principles as sequelae (by hitchhiking or as end products) of fortuitous phenotypic linkage to higher speciation rates of certain taxa. In further extensions, macroevolution itself must be reconfigured in speciation terms, with attendant implications for a wide range of phenomena, including Cope's rule (structurally ordained biases of speciation away from a lower size limit occupied by founding members of the clade, rather than adaptive anagenesis towards organismal benefits of large size), living fossils (members of clades with persistently minimal rates of speciation, and therefore no capacity for ever generating much change in a speciation scheme, rather than forms that are either depository of variation, or have occupied morphological optima for untold ages), and reinterpretation of cladal trends long mistranslated as triumphs of progressive evolution (and now reevaluated in terms of variational range in species numbers, rather than vectors of mean morphology across all species at any time—leading, for example, to a recognition that modern horses represent the single surviving twig of a once luxuriant, and now depleted, clade, and not the apex of a continually progressing trend). By the same argument, generalized to all of life, we understand the stability and continued domination of bacteria as the outstanding feature of life's history, with the much vaunted progress of complexity towards mammalian elegance reinterpreted as a limited drift of a minor component of diversity into the only open space of complexity's theoretical distribution. But, to encompass this reformation, we need to focus upon the diversity and variation among life's species, not upon the supposed vectors of its central tendencies, or even its peripheral superiorities. Hominid evolution must also be rethought as reduction of diversity to a single species of admittedly spectacular (but perhaps quite transient) current success. In addition, the last 50,000 years or more of human phenotypic stability becomes a theoretical expectation under punctuated equilibrium, and not the anomaly so often envisaged (and attributed to the suppression of natural selection by cultural evolution) both by the lay public and by many professionals as well.

11. Further extensions of punctuated equilibrium include the controversial phenomenon of "coordinated stasis," or the proposition that entire faunas, and not merely their component species, tend to remain surprisingly stable in composition over durations far longer than any model based on independent behavior of species (even under punctuated equilibrium) would allow, although other researchers attribute the same results to extended consequences of sudden external pulses and resulting faunal turnovers, while still others deny the empiricals of coordination and continue to view species as more independent, one from the other, even in the classical faunas (like the Devonian Hamilton Group) that serve as "types" for coordinated stasis.

12. Punctuated equilibrium has inspired several attempts, of varying success, in my limited judgment, to construct mathematical models (or to simulate its central phenomena in simple computer systems of evolving "artificial life") that may help us to identify the degree of generality in modes of change that this particular biological system, at this particular level of speciation, exemplifies and records. Punctuated equilibrium has also proved its utility in extending by meaningful analogy (based on common underlying principles of change) to the generation of punctuational hypotheses at other levels, and for other kinds of phenomena, where similar gradualistic biases had prevailed and had stymied new approaches to research. These extensions range from phylic and ecological examples below the species level to interesting analogs of both stasis and punctation above the species level. Non-trending, the analog of stasis in large clades, for example, had been previously disregarded—following the same fate as stasis in species—as a boring manifestation of non-evolution, but has now been recognized and documented as a real and fascinating phenomenon in itself. Punctuational analogs have proven their utility for understanding the differential pace of morphological innovation within large clades, and for resolving a variety of punctuational phenomena in ecological systems, including such issues of the immediate moment as rates of change in benthic faunas (previously the province of hypotheses about glacially slow and steady change in constantly depauperate environments), and such questions of broad geological scale as the newly recognized stepped and punctuational "morphology" (correcting the hypothetical growth through substantial time of all previous gradualistic accounts) of mutual biomechanical improvement in competing clades involved in "arms races," and generating a pattern known as "escalation."

13. Punctuational models have also been useful, even innovative in breaking conceptual logjams, in nonbiological fields ranging from closely cognate studies of the history of human tools (including extended stasis in the Homo
erectus toolkit), and nontreading, despite classical (and false) claims to the contrary by both experts, the Abbé Breuil and André Leroi-Gourhan, for the 23,000 year history of elegance in parietal cave art of France and Spain—and extending into more distant fields like learning theory (plateaus and innovative punctuations), studies of the dynamics of human organizations, patterns of human history, and the evolution of technologies, including a fascinating account of the history of books, through punctuations of the clay tablet, the scroll, the codex, and our current electronic formatting (wherever it may lead), and long periods of morphological stasis (graced with such vital innovations as printing, imposed upon the unalterable phenotype of the codex, or standard “book”).

14. In a long and final section, I indulge myself, and perhaps provide some useful primary source material for future historians of scientific conflicts, by recording the plethora of non-scientific citations, ranging from the absurd to the insightful, for punctuated equilibrium (including creationist misuses and their politically effective exposure by scientists in courtroom trials that defeated creationist legislative initiatives; and the treatment of punctuated equilibrium, often very good but sometimes very bad, by journalists and by authors of textbooks—the primary arenas of vernacular passage). I also trace and repudiate the “dark side” of non-scientific reactions by professional colleagues who enoted at challenges to their comfort, rather than reacting critically and sharply (as most others did), and as discussed extensively in the main body of the chapter) to the interesting novelty, accompanied by some prominent errors of inevitable and initial groping upon our part, spawned by the basic hypothesis and cascading implications of punctuated equilibrium.

Chapter 10: The integration of constraint and adaptation: historical constraint and the evolution of development.

1. Although the directing of evolutionary change by forces other than natural selection has loosely been described as “constraint,” the term, even while acknowledged as a domain for exceptions to standard Darwinian mechanisms, has almost always been conceived as a “negative” force or phenomenon, a mode of preventing (through lack of variation, for example) a population’s attainment of greater adaptability. But constraint, both in our science (and in vernacular English as well), also has strongly positive meanings in two quite different senses: first, or empirically, as channeled directionality for recovery of past history (conserved as homology) or physical principles; and second, or conceptually, as a nonstandard force (therefore interesting pro facto) acting differently from what orthodoxy would predict.

2. The classical and most familiar category of internal channeling (the first, or empirical, citation of constraint as a positive theme) resides in preferred directions for evolutionary change supplied by inherited allometries and their phylogenetic potentiation by heterochrony. As “place holders” for an extensive literature, I present two examples from my own work: first, the illustration of synergy with natural selection (to exemplify the positive, rather than oppositional, meaning), where an inherited internal channel builds two important adaptations by means of one heterochronic alteration, as neoteny in descendant Gephyra species of the English Jurassic produces shells of both markedly increased size (by retention of juvenile growth rates over an unchanged lifetime) and stabilised shape to prevent foundering in muddy environments achieved by “bringing forward” the proportions of attached juveniles into the unattached stage of adult ontogeny; second, an illustration of pervasiveness and equal (or greater) power than selective forces (to exemplify the strength and high relative frequency of such positive influences), as geographic variation of the type species, Cerion sexa, on Aruba, Bonaire, and Curacao, a subject of intense quantitative study and disagreement in the past, becomes resolved in multivariate terms, with clear distinction between local adaptive differences and the pervasive general pattern of an extensive suite of automatic sequelae, generated by nonadaptive variation in the geometry of coiling a continuous tube, under defined allometric regularities for the genus, around an axis.

3. For the second, or conceptually positive, meaning of constraint as a term for nonstandard causes of evolutionary change, I present a model that compares the conventional outcomes of direct natural selection, leading to local adaptation, with two sources that can also yield adaptive results, but for reasons of channeling by internal constraints rather than by direct construction under external forces of natural selection. In this triangular model for aptive structures, the functional vertex represents features conventionally built by natural selection for current utilities. At the historical vertex, currently aptive features probably originated for conventionally adaptive reasons in distant ancestors; but these features are now developmentally channeled as homologies that constrain and positively direct both patterns of immediate change and the inhomogeneous occupation of morphospace (especially as indicated by “deep homologies” of retained developmental patterns among phyla that diverged from common ancestry more than 500 million years ago). At the structural vertex, two very different reasons underlie the origin of potentially aptive features for initially nonadaptive reasons: physical principles that build “good” form by the direct action of physical laws upon plastic material (as in D’Arcy Thompson’s theory of form), and architectural sequelae (spandrels) that arise as nonadaptive consequences of other features, and then become available for later cooption (as expatiations) to aptive ends in descendant taxa. These two structural reasons differ strongly in the historical implications of direct physical production independent of phyletic context vs. the explicit historical analysis needed to identify the particular foundation for the origin of spandrels in any individual lineage.

4. As a conceptual basis for understanding the importance of recent advances in evo-devo (the study of the evolution of development), the largely unknown history of debate about categories of homology, particularly the distinction between convergence and parallelism, provides our best ordering device—for we then learn to recognize the key contrast between parallelism as a positive deep constraint of homology in underlying generators (and therefore as a structuralist theme in evolution) and convergence as the oppo-
site sign of domination for external natural selection upon a yielding internal substrate that imposes no constraint (and therefore as a functionalist theme in evolution). As a beginning paradox, we must grasp why E. Ray Lankester coined the term homology as a category of homology, whereas today's terminology ranks the concepts as polar opposites. Lankester wanted to contrast homology of overt structure (homology in his terms, or homology sensu stricto) with homology of underlying generators (later called parallelism) building the same structure in two separate lineages (homoplasy, or homology sensu latu, in Lankester's terms). Because parallelism could not be cashed out in operational terms (as science had no way, until our current revolution in evo-devo, to characterize, or even to recognize, these underlying generators), proper conceptual distinctions between parallelism and convergence have generally not been made, and the two terms have even (and often) been united as subtypes of homoplasy (now defined in the current, and utterly non-Lankesterian sense, as opposed to homology). I trace the complex and confused history of this discussion, and show that structuralist thinkers, with doubts about panadaptationism, have always been most sensitive to this issue, and most insistent upon separating and distinguishing parallelism as the chief category of positive developmental constraint—a category that has now, for the first time, become scientifically operational.

5. I summarize the evolutionary empirics and conceptualizations of evo-devo in four themes, united by a common goal to reconcile constraint and adaptation as causes and forces of evolution, and to acknowledge the pervasiveness and importance—also the synergy with natural selection, rather than opposition to Darwinian themes—of developmental constraint as a positive, structuralist, and internal force. The first theme explores the implications for internally directed evolutionary pathways and consequent clumping of taxa in morphospace—of the remarkable and utterly unanticipated discovery of extensive "deep homology" among phyla separated at least since the Cambrian explosion, as expressed by shared and highly conserved genes regulating fundamental processes of development. I first discuss the role and action of some of these developmental systems—the ABC genes of Arabidopsis in regulating circles of structures in floral morphology, the Hox genes of Drosophila in regulating differentiation of organs along the AP axis, and the role of the Pax-6 system in the development of eyes—in validating (only partially, of course) the archetypal theories of 19th century transcendental morphology, long regarded as contrary to strictly selectionist views of life's history—particularly Goethe's theory of the leaf archetype, and Geoffroy's idea of the vertebral groundplan of AP differentiation. I then discuss the even more exciting subject of homologically conserved systems across distant phyla, as expressed in high sequence similarity of important regulators, common rules of development (particularly the "Hoxology" followed in both arthropod and vertebrate ontology), and similar action of homoeotic mutations that impact Hoxological rules by loss or gain of function. Geoffroy was partially right in asserting segmental homology between arthropods and vertebrates, particularly for the comparison of insect metameres with rhom-
evolution based upon mutations in rate genes that control ontogenetic trajectories; I discuss the false arguments often invoked to infer such saltational changes, but these are related forms of some limited, but occasionally important, cases of such discontinuous, but strongly channelled, change in macroevolution.

8. The fourth theme of top-down channeling from full ancestral complements, rather than bottom-up accretion along effectively unconstrained pathways of local adaptation, explores the role of positive constraint in establishing the markedly non-random and inhomogeneous population of potential morphospace by actual organisms throughout the history of life. Ed Lewis, in brilliantly elucidating the action of Hox genes in the development of Drosophila, quite understandably assumed (albeit falsely, as we later discovered to our surprise) that evolution from initial homonomy to increasing complexity of AP differentiation had been achieved by addition of Hox genes, particularly to suppress abdominal legs and convert the second pair of wings to halteres. In fact, the opposite process of tinkering with established rules, primarily by increased localization of action and differentiation in timing (and also by duplication of sets, at least for vertebrate Hox genes), has largely established the increasing diversity and complexity in bilateral phyla. The (presumably quite homonomous) common ancestor of arthropods and vertebrates already possessed a full complement of Hox genes, and even the bilateral common ancestor already possessed at least seven elements of the set. Moreover, the genomes of the most homonomous modern groups of oncyophores and urochordates (phyla that do not include a full set of Hox genes)—so differentiation of phenotypic complexity must originate as a derived feature of Hox action, adapted from a different initial role. The Cambrian explosion remains a crucial and genuine phenomenon of phenotypic diversification, a conclusion unthreatened by a putatively earlier common ancestry of animal phyla in a strictly genealogical (not phenotypic) sense. The further evolution of admittedly luxuriant, even awesome, variety in major phyla of complex animals has followed definite pathways of internal channeling, positively abetted (as much as negatively constrained) by homologous developmental rules acting as potentiation for more rapid and effective selection (as in the loss of snake limbs and iteration of pre-pelvic segments), and not as brakes or limitations upon Darwinian efficacy.

Chapter 11: The integration of constraint and adaptation: structural constraints, spurces, and exaptation

1. D'Arcy Thompson's idiosyncratic, but brilliantly crafted and expressed, theory of form (1917, 1942) presents a 20th century prototype for the generalist, or ahistorical, form of structural constraint: adaptation produced not by a functionalist mechanism like natural selection (or Lamarckism), but directly and automatically imposed by physical forces operating under invariant laws of nature. This theory enjoyed some success in explaining the correlation of form and function in very simple and labile forms (particularly as influenced by scale-bound changes in surface/volume ratios). But similarly nongenetic (and nonphyletic) explanations do not apply to complex cre-
of their final form, they might still have arisen by natural selection for a dif-
ferent initial utility (feathers first evolved for thermoregulation and later co-
opted for flight, for example). Darwin used this principle of cooption, or
functional shift, in two important ways that enriched and expanded his the-
ory away from a caricatured panselectionist version—as the primary ground
of historical contingency in phyletic sequences (for one cannot predict the di-
rection of subsequent cooption from different primary utilities), and as a
source of structural constraint upon evolutionary pathways. But these Dar-
winian invocations stopped short of a radical claim for frequent and impor-
tant nonadaptive origins of structures coopted to later utility. That is, Darwin
rarely proceeded beyond the principle of originally adaptive origin for differ-
ent function, with later cooption to altered utility.

5. This important principle of cooption of preexisting structures origi-
nally built for different reasons has been so underemphasized in Darwinian
traditions that the language of evolutionary theory does not even include a
term for this central process—which Elisabeth Vrba and I called “exaptation”
(Gould and Vrba, 1982). (The available, but generally disfavored, term “pre-
adaptation” only speaks of potential before the fact, and has been widely re-
jected in any case for its unfortunate, but inevitable, linguistic implication of
foreordination in evolution, the very opposite of the intended meaning!)

6. I present a list of criteria for recognizing exaptations and separating
them from true adaptations. I also discuss some outstanding examples of
exaptation from the recent literature, with particular emphasis on the multi-
ple exaptation of lens crystallins (in part for their fortuitous transparency, but
for many other cooptable characteristics as well) in so many vertebrates and
from so many independent and different original functions.

7. The exaptation of structures that arose for different adaptive reasons re-
mains within selectionist orthodoxy (while granting structural constraint a
large influence over historical pathways, in contrast with crude panadapta-
tionism) by confirming a Darwinian basis for the adaptive origin of struc-
tures, whatever their later history of exaptive shift. On the other hand, the
theoretically radical version of this second, or historicist, style of structural
constraint in evolution posits an important role for an additional phenome-
non in macroevolution: the truly nonadaptive origin of structures that may
later be exapted for subsequent utility. Many sources of such nonadaptive
origin may be specified (see point 10 below), but inevitable architectural con-
sequences of other features—the spandrels of Gould and Lewontin’s termi-
nology (1979)—probably rank as most frequent and most important in the
history of lineages.

8. Spandrels (although unnamed and ungeneralized) have been acknowl-
dged in Darwinian traditions, but relegated to insignificant relative frequen-
cies by invalid arguments for their rarity, their structural inconsequentiality
(the mold marks on an old bottle, for example), or their temporally subse-
quently status as sequelae—with the first two claims empirically false, and the
last claim logically false as a further confusion between historical origin and
current utility.

9. I affirm the importance and high relative frequency of spandrels, and
therefore of nonadaptive origin, in evolutionary theory by two major argu-
ments for ubiquity. First, for intrinsic structural reasons, the number of po-
tential spandrels greatly increases as organisms and their traits become more
complex. (The spandrels of the human brain must greatly outnumber the im-
mediately adaptive reasons for increase in size; the spandrels of the cylindri-
cal umbilical space of a gastropod shell, by contrast, may be far more limited,
although exaptive use as a brooding chamber has been important in several
lineages.) Second, under hierarchical models of selection, features evolved for
any reason at one level generate automatic consequences at other levels—and
these consequences can only be classified as cross-level spandrels (since they are
“injected into” the new level, rather than actively evolved there).

10. The full classification of spandrels and modes of exaptation offers a re-
versing taxonomy and solution—primarily through the key concept of the
“exaptive pool”—for the compelling and heretofore confusing (yet much
discussed) problem of “evolvability.” Former confusion has centered upon
the apparent paradox that ordinary organismal selection, the supposed ca-
nomical mechanism of evolutionary change, would seem (at least in its pri-
mary overt effect) to restrict and limit future possibilities by specializing
forms to complexities of immediate environments, and therefore to act
against an “evolvability” that largely defines the future macroevolutionary
prospects of any lineage. The solution lies in recognizing that spandrels, al-
though architecturally consequential, are not doomed to a secondary or un-
important status thereby: Spandrels, and all other forms of exaptive potential,
define the ground of evolvability, and play as important a role in macro-
evolutionary potential as conventional adaptation does for the immediacy
of microevolutionary success. I emphasize the centrality of the exaptive pool for
solving the problem of evolvability by presenting a full taxonomy of catego-
ries for the pool’s richness, focusing on a primary distinction between “fran-
klins” (or inherent potentials of structures evolved for other adaptive roles—
that is, the classical Darwinian functional shifts that do not depart from adapta-
tionism), and “miltons” (or true nonadaptations, arising from several
sources, with spandrels as a primary category, and then available for later
cooption from the exaptive pool—that is, the class of nonadaptive origins
that does challenge the dominant role of panadaptationism in evolutionary
theory).

11. I argue that the concept of cross-level spandrels vastly increases the
range, power and importance of nonadaptation in evolution, and also unites
the two central themes of this book by showing how the hierarchically ex-
tended theory of selection also implies a greatly increased scope for non-
adaptive structural constraint as an important factor in the potentiation of
macroevolution.

Chapter 12: Tiers of time and trials of extrapolationism

1. Darwin clearly recognized the threat of catastrophic mass extinction to
the extrapolationist and uniformitarian premises underlying his claim for full
explanation of macroevolutionary results by microevolutionary causes (and not as a challenge to the efficacy of natural selection itself). Darwin therefore employed his usual argument about the imperfection of geological records to “spread out” apparent mass extinction over sufficient time for resolution by ordinary processes working at maximal rates (and therefore only increasing the intensity of selection).

2. The transition of the impact scenario (as a catastrophic trigger for the K-T extinction) from apostasy at its proposal in 1980 to effective factuality (based on the concurrence of disparate evidence from iridium layers, shocked quartz and, especially, the discovery of a crater of appropriate size and age at Chicxulub) has reinvigorated the global paroxysms of classical catastrophism (in its genuinely scientific form, not its dismissive Lyellian caricature) as a legitimate scientific mechanism outside the Darwinian paradigm, but operating in conjunction with Darwinian forces to generate the full pattern of life’s history, and not, as previously (and unhelpfully) formulated, as an exclusive alternative to disproving or to trivializing Darwinian mechanisms.

3. If catastrophic causes and triggers for mass extinction prove to be general, or at least predominant in relative frequency (and not just peculiar to the K-T event), then this macroevolutionary phenomenon will challenge the crucial extrapolationalist premise of Darwinism by being more frequent, more rapid, more intense and more different in effect than Darwinian biology (and Lyellian geology) can allow. Under truly catastrophic models, two sets of reasons, inconsistent with Darwinian extrapolations by microevolutionary accumulation, become potentially important agents of macroevolutionary patterning: effectively random extinction (for clades of low N), and, more importantly, extinction under “different rules” from reasons regulating the adaptive origin and success of autapomorphic cladal features in normal times.

4. Catastrophic mass extinction, while breaking the extrapolationist credo, may suggest an overly simplified and dichotomous macroevolutionary model based on alternating regimes of “background” vs. “mass” extinction. Rather, we should expand this insight about distinctive mechanisms at different scales into a more general model of several rising tiers of time—with conventional Darwinian microevolution dominating at the ecological tier of short times and intraspecific dynamics; punctuated equilibrium dominating at the geological tier of phyletic trends based on interspecific dynamics (with species arising in geological moments, and then treated as stable “atoms,” or basic units of macroevolution, analogous to organisms in microevolution); and mass extinction (perhaps often catastrophic) acting as a major force of overall macroevolutionary pattern in the global history of relative waxing and waning of clades. I also contrast this preferred model of time’s tiering with the other possible style of explanation, which I reject but find interesting nonetheless, for denying full generality to smooth Darwinian upward extrapolation from the lowest level—namely, an equally smooth and monistic downward extrapolation from catastrophic mortality in mass extinction to diminishing, but equally random and sudden, effects at all scales, as proposed in Raup’s “field of bullets” model.

5. In a paradoxical epilogue, I argue (despite my role as a long-term champion of the importance and scientific respectability of unpredictable contingency in the explanation of historical patterns) that the enlargement and reformulation of Darwinism, as proposed in this book, will recapture for general theory (by adding a distinctive and irreducible set of macroevolutionary causes to our armamentarium of evolutionary principles) a large part of macroevolutionary pattern that Darwin himself, as an equally firm supporter of contingency, willingly granted to the realm of historical unpredictability because he could not encompass these results within his own limited causal structure of strict reliance upon smooth extrapolation from microevolutionary processes by accumulation through the immensity of geological time.

A FINAL THOUGHT. May I simply end by quoting the line that I wrote at the completion of a similar abstract (but vastly shorter, in a much less weighty book) for my first technical tome, Ontogeny and Phylogeny (1977b, p. 9): “This epitome is a pitiful abbreviation of a much longer and, I hope, more subtle development. Please read the book!”