CHAPTER TWO

The Essence of Darwinism and the Basis of Modern Orthodoxy: An Exegesis of the *Origin of Species*

A Revolution in the Small

Our theatrical and literary standards recognize only a few basic types of heroes. Most are preeminently strong and brave; some, in an occasional bone thrown to the marginal world of intellectuals, may even be allowed to triumph by brilliance. But one small section of the pantheon has long been reserved for a sideshow of improbables: the meek, the mild, the foolish, the insignificant, the ornamental—in short, for characters so disdained that they pass beneath notice and become demons of effectiveness by their invisibility. Consider the secretaries or chauffeurs who learn essential secrets because patrician bosses scarcely acknowledge their personhood and say almost anything in their presence; or the pageboys and schoolgirls who walk unnoticed through enemy lines with essential messages to partisans in conquered territories.

Though few scholars have considered the issue in this light, I would argue that the intellectual agent of Darwin's victory falls into this anomalous category. To be sure, Darwin succeeded because he devised a mechanism, natural selection, that possessed an unbeatable combination of testability and truth. But, at a more general level, Darwin triumphed by allowing the formerly meek to inherit the entire world of evolutionary theory.

Darwin's theory explicitly rejected and overturned the two evolutionary systems well known in Britain during his time (see next chapter for details)—Lamarck's (via Lyell's exegesis in the *Principles of Geology*) and Chambers's (in the anonymously printed *Vestiges of the Natural History of Creation*). Both these theories sunk a deep root in the most powerful of cultural biases by describing evolution as an interaction of two opposing forces. The first—considered dominant, intrinsic and fundamental—yielded progress on the old euphonious (and sexist) theme of "the march from monad to man." The second—designated as secondary, diversionary and superimposed—interrupted the upward flow and produced lateral dead-ends of specialized adaptations, from eyeless moles to long-necked giraffes. Darwin, in his greatest stroke of genius, took this secondary force, proposed a new mechanism for its operation (natural selection), and then redefined this former source for superficial tinkering as fully sufficient to render *all* of evolution—thus branding the separate and more exalted force of progress as illusory.

Such an argument poses an obvious logical dilemma: how can such power be granted to a force formerly viewed as so inconsequential? After all, evolution must still construct the full pageant of life's history and the entire taxonomic panorama, even if we abandon the concept of linear order. Darwin's answer records the depth of his debt to Lyell, the man more responsible than any other for shaping Darwin's basic view of nature. Time, just time! (provided that the "inconsequential" force of adaptation can work without limit, accumulating its tiny effects through geological immensity). The theory's full richness cannot be exhausted by the common statement that Darwinism presents a biological version of the "uniformitarianism" championed by Lyell for geology, but I cannot think of a more accurate or more encompassing one-liner. (In a revealing letter to Leonard Horner, written in 1844, Darwin exclaimed: "I always feel as if my books came half out of Lyell's brains . . . for I have always thought that the great merit of the Principles [of Geology], was that it altered the whole tone of one's mind and therefore that when seeing a thing never seen by Lyell, one yet saw it partially through his eyes" (cited in Darwin, 1987, p. 55).)

Darwin, in his struggle to formulate an evolutionary mechanism during his *annus mirabilis* (actually a bit more than two years) between the docking of the *Beagle* and the Malthusian insight of late 1838, had embraced, but ultimately rejected, a variety of contrary theories—including saltation, inherently adaptive variation, and intrinsic senescence of species (see Gruber and Barrett, 1974; Kohn, 1980). A common thread unites all these abandoned approaches: for they all postulate an internal drive based either on large pushes from variation (saltationism) or on inherent directionality of change. Most use ontogenetic metaphors, and make evolution as inevitable and as purposeful as development. Natural selection, by contrast, relies entirely upon small, isotropic, nondirectional variation as raw material, and views extensive transformation as the accumulation of tiny changes wrought by struggle between organisms and their (largely biotic) environment. Trial and error, one step at a time, becomes the central metaphor of Darwinism.

This theme of relentless accumulation of tiny changes through immense time, the uniformitarian doctrine of Charles Lyell, served as Darwin's touchstone throughout his intellectual life. Uniformitarianism provides the key to his first scientific book (Darwin, 1842) on the formation of coral atolls by gradual subsidence of oceanic islands, long continued. And the same theme defines the central subject of his parting shot (1881), a book on the formation of vegetable mould by earthworms. Darwin, for lifelong reasons of personal style, did not choose to write a summary or confessional in lofty philosophical terms, but he did want to make an exit with guns blazing on his favorite topic. Ironically, Darwin's overt subject of worms has led to a common interpretation quite opposite to his own intent—his misrepresentation as a doddering old naturalist who couldn't judge the difference in importance between fishbait and fomenting revolution, and who, in recognizing evolution, just happened to be in the right place at the right time. In fact, Darwin's worm book presents an artfully chosen example of the deeper principle that underlay all his work, including the discovery of evolution—the uniformitarian power of small changes cumulated over great durations. What better example than the humble worm, working literally beneath our notice, but making, grain by grain, both our best soils and the topography of England. In the preface (1881, p. 6), Darwin explicitly draws the analogy to evolution by refuting the opinions of a certain Mr. Fish (wonderful name, given the context), who denied that worms could account for much "considering their weakness and their size": "Here we have an instance of that inability to sum up the effects of a continually recurrent cause, which has often retarded the progress of science, as formerly in the case of geology, and more recently in that of the principle of evolution."

Darwin waxed almost messianic in advancing this theme in the *Origin of Species,* for he understood that readers could not grasp his argument for evolution until they embraced this uniformitarian vision with their hearts. He confessed the *a priori* improbability of his assertion, given the norms and traditions of western thought: "Nothing at first can appear more difficult to believe than that the more complex organs and instincts should have been perfected, not by means superior to, though analogous with, human reason, but by the accumulation of innumerable slight variations, each good for the individual possessor" (1859, p. 459). In his short concluding section on our general reluctance to accept evolution, he did not—probably for diplomatic reasons—identify specific cultural or religious barriers; instead, he spoke of our unfamiliarity with the crucial uniformitarian postulate: "But the chief cause of our natural unwillingness to admit that one species has given birth to other and distinct species, is that we are always slow in admitting any great change of which we do not see the intermediate steps . . . the mind cannot possibly grasp the full meaning of the term of a hundred million years; it cannot add up and perceive the full effects of many slight variations, accumulated during an almost infinite number of generations" (1859, p. 481).

To impress readers with the power of natural selection, Darwin continually stressed the cumulative effect of small changes. He reserved his best literary lines, his finest metaphors, for this linchpin of his argument—as in this familiar passage: "It may be said that natural selection is daily and hourly scrutinizing, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages" (1859, p. 84). Examine the smallest changes and variations, Darwin almost begs us. Let nothing pass beneath your notice. Cumulate, cumulate, cumulate:

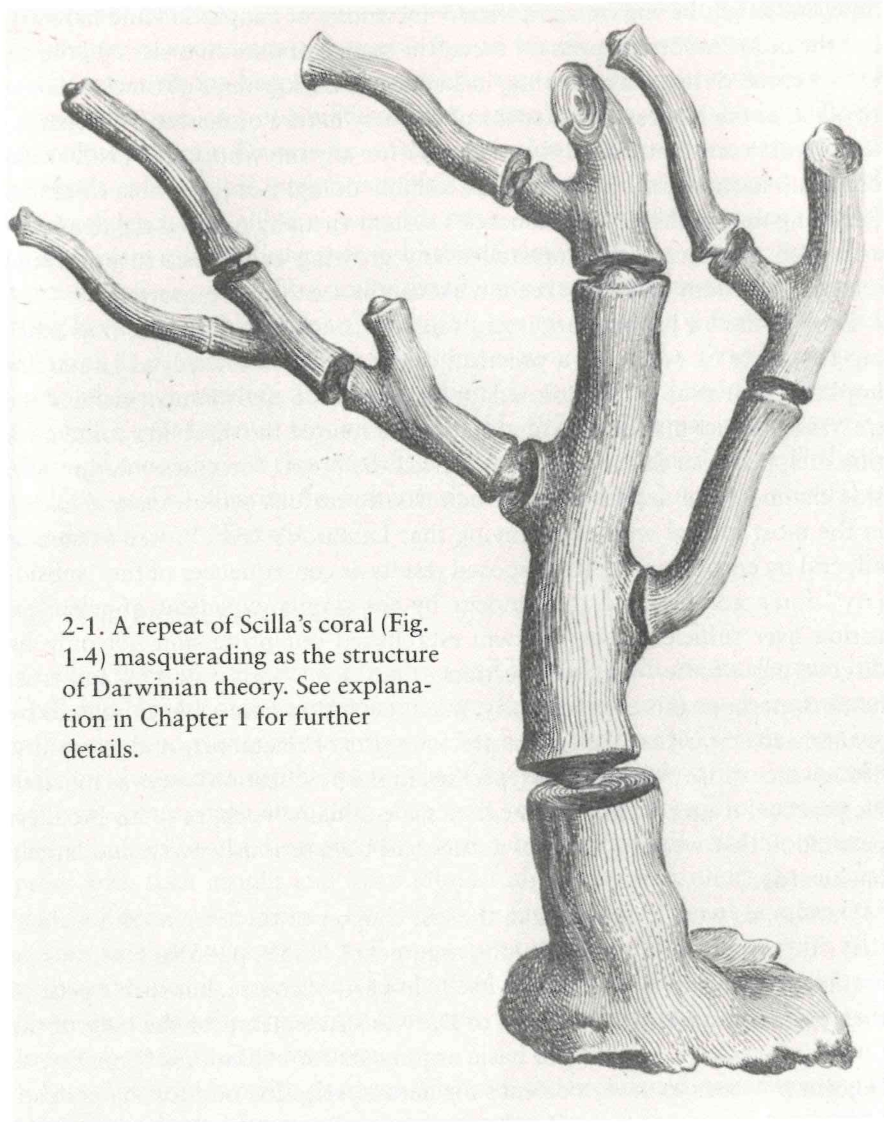
> Certainly no clear line of demarcation has as yet been drawn between species and sub-species . . . ; or, again, between sub-species and well-

marked varieties, or between lesser varieties and individual differences. These differences blend into each other in an insensible series; and a series impresses the mind with the idea of an actual passage. Hence I look at individual differences, though of small interest to the systematist, as of high importance for us, as being the first step towards such slight varieties as are barely thought worth recording in works on natural history (1859, p. 51).

I need hardly stress Darwin's impact as one of the half dozen or so most revolutionary thinkers in western history. I want, instead, to emphasize a more curious aspect of his status—his continuing relevance, indeed his benevolent hovering over almost all our current proceedings. We may revere Newton and Lavoisier as men of equal impact, but do modern physicists and chemists actively engage the ideas of these founders, as they pursue their daily work? Darwin, on the other hand, continues to bestride our world like a colossus—so much so that I can only begin this book on the structure of evolutionary theory by laying out Darwin's detailed vision as a *modern* starting point, a *current* orthodoxy only lightly modified by more than a century of work. I do, in this book, advocate some major restructuring, in the light of new concepts and findings, and with the approbation of more and more colleagues as our understanding of evolution broadens. But Darwin remains our context—and my proposed restructuring represents an extension, not a replacement, of his vision. The hierarchical theory of selection builds a world different from Darwin's in many important respects, but we do so by extending his mechanism of selection to a larger realm than he acknowledged—that is, to levels both below and above his focus on the struggle among organisms.

When Cassius spoke his words about Caesar (paraphrased above), he added his puzzlement at Caesar's extraordinary success: "Upon what meat doth this our Caesar feed, that he is grown so great." I shall argue in this chapter that Darwin's continued, pervasive relevance arises from his capacity for revolutionary innovation at two opposite poles of scientific practice—the immediate strategy of formulating a methodology for everyday research, and the most general discussion of causes and phenomena in the natural world (the questions that will not go away, and that air continually from college bull sessions, to TV talk shows, to learned treatises on the nature of things). Darwin's residence at *both* poles of *immediate methodology* and *broadest theoretical generality* begins with his distinctive attitude towards the central importance of daily, palpable events in nature, and their power to account for all evolution by cumulation—hence my choice of an opening topic for this chapter (see Fig. 2-1).

Caesar voiced his suspicions of Cassius, fearing men who think too much (may all despots thus beware). But his grudging words of praise might well be invoked to epitomize the reasons for Darwin's unparalleled success: "He reads much; he is a great observer, and he looks quite through the deeds of men."



2-1. A repeat of Scilla's coral (Fig. 1-4) masquerading as the structure of Darwinian theory. See explanation in Chapter 1 for further details.

Darwin as a Historical Methodologist

ONE LONG ARGUMENT

An old quip, highlighting the intractability of philosophical dualism, proclaims: "what's matter? never mind; what's mind? doesn't matter." Predarwinian evolutionary systems embodied the same kind of Catch-22, this time in painful and practical terms, destined to ensnare any budding naturalist who hoped to study organisms by direct confrontation with testable hypotheses. Lamarck's system, for example, contrasted an intrinsic force of progress with a diversionary, and clearly secondary, force of adaptation to changing local environments. The secondary process worked in the immediate here and now, and might be engaged empirically by studies of adaptation and heredity. But the more important primary force, the source of natural order and the ultimate cause of human mentality, lurked in the background of time's immensity, and at the inaccessible interior of the very nature of matter. This characterization creates an intolerable dilemma for anyone who holds (as Darwin did) that science must be defined as testable doing, not just noble thinking. Recalling my opening quip, Lamarck's system virtually mocked the empirical approach to science, and forestalled any growing confidence in evolution: what is important cannot be seen; what can be seen is not important.

Darwin used a brilliant argument to cut through this dilemma, thus making the study of evolution a practical science. He acknowledged Lamarck's implied claim that small scale adaptation to local environment defines the tractable subject matter of evolution. But he refuted the disabling contention that adaptation in this mode only diverted the "real" force of evolution into side channels and dead ends. And he revised previous evolutionary thinking in the most radical way—by denying that Lamarck's "real" force existed at all, and by encompassing its supposed results as consequences of the "subsidiary" force accumulated to grandeur by the simple expedient of relentless action over sufficient time. Darwin established our profession not only by discovering a force—natural selection—that seems both powerful and true; he also, perhaps more importantly, made evolution accessible to science by granting to empiricists their most precious gifts of tractability and testability. The essence of Darwin's theory (specified in the next section) owes as much to his practical triumph at this immediate scale of daily work, as to his broadest perception that western views of nature had been seriously awry, and largely backwards.

Darwin, as we all know, began the last chapter of the *Origin* with a claim that "this whole volume is one long argument" (1859, p. 459). Fine, but an argument for what? For evolution itself? In part, of course, but such a general theme cannot mark the full intent of Darwin's statement, for the bulk of the *Origin* moves well beyond the basic arguments for evolution's factuality, as Darwin proceeds to craft a defense for natural selection and for the philosophy of nature so entailed. "One long argument" for natural selection, then? Again, in part; but we now confront the obverse of my last statement: too much of the *Origin* details basic evidence for evolution, independent of any particular mechanism of change. Instead, we must ask what deeper subject underlies both the defense of evolution as a fact and the proposal of a mechanism to explain its operation? How should we characterize the "one long argument" that pervades the entire book?

Ghiselin (1969) correctly identified the underlying theme as the construction, and defense by example, of a methodology—a mode of practice—for testing both the fact and mechanism of evolutionary change. But I cannot agree with Ghiselin that Darwin's consistent use of "hypothetico-deductive" reasoning constitutes his long argument (see Kitcher, 1985), for this style of scientific procedure, whatever its merits or problems, has been advocated as a general methodology for all scientific activity (see Hempel, 1965). Darwin, I

believe, sought to construct and defend a working method for the special subject matter of evolutionary inquiry—that is, for the *data of history.*

Inferences about history, so crucial to any evolutionary work, had been plagued by problems of confidence that seemed to bar any truly scientific inquiry into the past. Darwin knew that evolution would not win respect until methods of historical inference could be established and illustrated with all the confidence of Galileo viewing the moons of Jupiter. He therefore set out to formulate rules for inference in history. I view the *Origin* as one long illustration of these rules. Historical inference sets the more general theme underlying both the establishment of evolution as a fact, and the defense of natural selection as its mechanism. The "one long argument" of the *Origin* presents a comprehensive strategy and compendium of modes for historical inference (see fuller exposition of this view in Gould, 1986). We must grasp Darwin's practical campaign on this battlefield in order to understand his radical philosophy, and to identify the features of his theory that count as essential to any definition of "Darwinism."

THE PROBLEM OF HISTORY

Reading Darwin has been a persisting and central joy in my intellectual life. Lyell and Huxley may have been greater prose stylists, with more consistency in the ring and power of their words. Yet I give the nod to Darwin, and not only for the greater depth and power of his ideas. Darwin often wrote quite ordinary prose, page after page. But then, frequently enough to rivet the attention of any careful reader, his passion bursts through, and he makes a point with such insight and force (almost always by metaphor) that understanding breaks like sunrise. Every evolutionist can cite a list of favorite Darwinian passages, written on well-worn index cards for lectures (or, now, eternally embedded in Powerpoint files), posted on the office door or prominently displayed above the typewriter (now the computer terminal), or simply (and lovingly) committed to memory.

Several of my favorite passages celebrate the broadened understanding of nature that derives from recognizing organisms as products of history, rather than objects created in their present state. Darwin writes (1859, pp. 485–486):*

*I base this chapter on an exploration of the logic of argument in the first edition of the *Origin of Species* (1859). Provine (in lectures and personal communications) has argued that Darwinian historiography should focus on the definitive 6th edition of 1872, not only as Darwin's most considered and nuanced account, but primarily because this last edition has enjoyed such overwhelmingly greater influence through endless reprinting (continuing today) and translation into all major languages. The first edition had a print run of 1500 copies and sold out on the first day. I doubt that this original version ever reappeared in print before the facsimile edition edited by Mayr (1964), and this initial version remains rare relative to the ubiquitous sixth of almost every modern reprint. I agree with Provine's argument and, in fact, personally prefer the sixth edition for its subtleties on issues of macroevolution and adaptation. But I choose the first edition for this chapter as a necessary consequence of my idiosyncratic habits of historiographical work. I appreciate, and shame-

When we no longer look at an organic being as a savage looks at a ship, as at something wholly beyond his comprehension; when we regard every production of nature as one which has had a history; when we contemplate every complex structure and instinct as the summing up of many contrivances, each useful to the possessor, nearly in the same way as when we look at any great mechanical invention as the summing of the labor, the experience, the reason, and even the blunders of numerous workmen; when we thus view each organic being, how far more interesting, I speak from experience, will the study of natural history become!

By contrast, Darwin's chief quarrel with creationism resides not so much in its provable falseness, but in its bankrupt status as an intellectual argument—for a claim of creation teaches us nothing at all, but only states (in words that some people may consider exalted) that a particular creature or feature exists, a fact established well enough by a simple glance: "Nothing can be more hopeless than to attempt to explain the similarity of pattern in members of the same class, by utility or by the doctrine of final causes . . . On the ordinary view of the independent creation of each being, we can only say that so it is;—that it has so pleased the Creator to construct each animal and plant" (p. 435).

Moreover, and more negatively, creation marks the surrender of any attempt to understand connections and patterns. We express no causal insight whatever when we say that taxonomic order reflects the plan of a creator—for unless we can know the will of God, such a statement only stands as a redundant description of the order itself. (And God told us long ago, when he spoke to Job from the whirlwind, that we cannot know his will—"canst thou draw out leviathan with a hook?") Darwin, an ever genial man in the face of endless assaults upon his patience, directed several of his rare caustic comments against the ultimate idea-stopping claim that God so made it, praise his name. Darwin notes, for example, that horses are sometimes born with faint striping on their hides. A creationist can only assert that God made each equine species of zebras, horses, and asses alike, with such tendencies to vary and thereby to display, if only occasionally, the more comprehensive type.

lessly exploit, the historian's central concern for social context and the multifarious sources of intellectual arguments. But I am an internalist at heart, though wearing the sheep's clothing of my own Darwinian heritage with its emphasis on external adaptation, part by part. I love to follow the logic of argument, to treat a great text as Cuvier considered an organism—as an integrity, held together by sinews of logic (whatever the social or psychological origin of any particular item). I love to explore these connections, and to grasp the beauty of the totality. Thus, I prefer to practice the rather old-fashioned technique of *explication des textes* (see my longer rationale and attempt in Gould, 1987b, on Burnet, Hutton and Lyell). For this exercise, the first edition, despite its hurried composition as the scourge of Ternate breathed down Darwin's neck, represents the most coherent document, before all subsequent, externally-driven "adaptations" to critical commentary fixed the flaws and hedged the difficulties. Errors and inconsistencies build vital parts of integrity; I may share Cuvier's concern with necessary connections, but not his belief in optimal design. True integrity, in a messy world, implies rough edges, which not only have a beauty of their own, but also provide our best evidence for the logic of argument.

Evolution, on the other hand, supplies a true cause for an anomaly by positing community of descent with retention of ancestral states by heredity—something that might be tested in many ways, once we understand the mechanics of inheritance. (The following passage appears just before Darwin's summary to Chapter 5 on laws of variation.) Darwin lambastes the creationist alternative as causally meaningless: "To admit this view is, as it seems to me, to reject a real for an unreal, or at least for an unknown, cause. It makes the works of God a mere mockery and deception; I would almost as soon believe with the old and ignorant cosmogonists, that fossil shells had never lived, but had been created in stone so as to mock the shells now living on the sea-shore" (p. 167).

If we must locate our confidence about evolution in evidence for history—in part directly from the fossil record, but usually indirectly by inference from modern organisms—by what rules of reason, or canons of evidence, shall history then be established? Darwin's "long argument," in my view, can best be characterized as a complex solution to this question, illustrated with copious examples. We must first, however, specify the kinds of questions that *cannot* be answered. Many revealing statements in the *Origin* circumscribe the proper realm of historical inference by abjuring what cannot be known, or usefully comprehended under current limits. Darwin, for example, and following Hutton, Lyell and many other great thinkers, foreswore (as beyond the realm of science) all inquiry into the ultimate origins of things.* In the first paragraph of Chapter 7 on instincts, for example, Darwin writes (1859, p. 207): "I must premise, that I have nothing to do with the origin of the primary mental powers, any more than I have with that of life itself." Darwin invoked the same comparison in discussing the evolution of eyes, one of his greatest challenges (and firmest successes). He states that he will confine his attention to transitions in a structural sequence from simple to complex, and not engage the prior issue—answerable in principle, but beyond the range of knowledge in his day—of how sensitivity to light could arise within nervous tissue in the first place (1859, p. 187): "How a nerve comes to be sensitive to light, hardly concerns us more than how life itself first originated." Most crucially, and in a savvy argument that saved his entire system in the face of contemporary ignorance on a central issue, Darwin argues over and over again that we may bypass the vital question of how heredity works, and how variations arise—and only illustrate how evolution can occur, given the common-

*I have been both amused and infuriated that this issue still haunts us. I understand why American fundamentalists who call themselves "creation scientists," with their usual mixture of cynicism and ignorance, use the following argument for rhetorical advantage: (1) evolution treats the ultimate origin of life; (2) evolutionists can't resolve this issue; (3) the question is inherently religious; (4) therefore evolution is religion, and our brand deserves just as much time as theirs in science classrooms. We reply, although creationists do not choose to listen or understand, that we agree with points two and three, and therefore do not study the question of ultimate origins or view this issue as part of scientific inquiry at all (point one). I was surprised that Mr. Justice Scalia accepted this fundamentalist argument as the basis for his singularly inept dissent in the Louisiana creationism case, Edwards *v.* Aguillard (see Gould, 1991b).

place observation that sufficient variation *does* exist, and *is* inherited often enough:

> Whatever the cause may be of each slight difference in the offspring from their parents—and a cause for each must exist—it is the steady accumulation, through natural selection, of such differences, when beneficial to the individual, that gives rise to all the more important modifications of structure, by which the innumerable beings on the face of this earth are enabled to struggle with each other, and the best adapted to survive (p. 170—see also p. 131 for Darwin's argument that when we ascribe variation to "chance," we only mean to express our ignorance of causes).

Having established a domain of testability by exclusion, Darwin laid out his methodology for history—never explicitly to be sure, but with such accumulating force by example that the entire book becomes "one long argument" for the tractability of his new science. Those of us who practice the sciences of reconstructing specific events and unravelling temporal sequences have always fought a battle for appropriate status and respect, no less so today than in Darwin's time (see Gould, 1986), against those who would view such work as a "lesser" activity, or not part of science at all. History presents two special problems: (1) frequent absence of evidence, given imperfections of preservation; and (2) uniqueness of sequences, unrepeatable in their contingent complexity, and thereby distancing the data of history from such standard concepts as prediction, and experimentation.

We may epitomize the dilemma in the following way: many people define science as the study of causal processes. Past processes are, in principle, unobservable. We must therefore work by inference from results preserved in the historical record. We must study modern results produced by processes that can be directly observed and even manipulated by experiment—and we must then infer the causes of past results by their "sufficient similarity" (Steno's principle—see Gould, 1981c) with present results. This procedure requires, as Mill (1881) and other philosophers recognized long ago, a methodological assumption of temporal invariance for laws of nature. Historical study manifests its special character by placing primary emphasis upon comparison and degrees of similarity, rather than the canonical methods of simplification, manipulation, controlled experiment, and prediction.

Darwin had done some paleontological work, particularly in his treatises on barnacles (1851–1858), and his important discoveries of South American fossil vertebrates (formally named and described by Owen, at Darwin's invitation). But Darwin was not primarily a paleontologist, and he did not intend to base his argument for evolution on the evidence of fossils—especially since he viewed the stratigraphic record, with its vast preponderance of gaps over evidence, as more a hindrance than an aid to his theory (see chapters 9 and 10 of the *Origin*). Thus, of the two major sources for historical reconstruction—direct but imperfect information from fossils, and indirect but copious data from modern organisms—Darwin preferred the second as his wellspring of documentation. The *Origin* therefore focuses upon the establishment of a methodology for making inferences about history from features of modern organisms—and then using these multifarious inferences to prove both the fact of evolution and the probability of natural selection as a primary mechanism of change.

A FOURFOLD CONTINUUM OF METHODS FOR THE INFERENCE OF HISTORY

Darwin, as a subtle and brilliant thinker, must be read on several levels. Consider just three, at decreasing domains of overt display, but increasing realms of generality: On the surface—a lovely, and not a pejorative, location for any student of nature—each book treats a particular puzzle: different forms of flowers on the same plant (1877), modes of formation for coral atolls (1842), formation of soil by worms (1881), styles of movement in climbing plants (1880a), the fertilization of orchids by insects (1862). At an intermediary level, as Ghiselin (1969) showed in his innovative study of the entire Darwinian corpus, each book forms part of a comprehensive argument for evolution itself. But I believe that we must also recognize a third, even deeper and more comprehensive layer of coordinating generality—Darwin's struggle to construct and apply a workable method for historical inference: a series of procedures offering sufficient confidence to place the sciences of history on a par with the finest experimental work in physics and chemistry. I have come to regard each of Darwin's books as, all at the same time, a treatment of a particular puzzle (level one), an argument for an evolutionary worldview (level two), and a treatise on historical methodology (level three). But the methodological focus of level three has usually been overlooked because Darwin chose to work by practice rather than proclamation.

Darwin recognized that several methods of historical inference must be developed, each tailored to the nature and quality of available evidence. We may order his procedures by decreasing density of available information. I recognize four waystations in the continuum and argue that each finds a primary illustration in one of Darwin's books on a specific puzzle in natural history. The *Origin of Species,* as his comprehensive view of nature, uses all four methods, and may therefore be read as a summation of his seminal contribution to the methodology of historical science. I shall list, and then illustrate with examples from the *Origin,* these four principles ordered by decreasing density of information.

UNIFORMITY. Or working up by extrapolation from direct observations on rates and modes of change in modern organisms. Call this, if you will, the worm principle to honor Darwin's last book (1881), which explains the topsoil and topography of England by extrapolating the measured work of worms through all scales of time, from the weight of castings left daily on a patch of sod to the historical and geological realms of millennia to millions of years.

SEQUENCING. Or the definition and ordering of various configurations, previously regarded as unrelated and independent, into stages of a single historical process. Here we cannot observe the changes between configurations directly and we must therefore work by recognizing them as temporally ordered products of a single underlying process of change. Call this, if you will, the coral reef principle to honor Darwin's first book (1842) on a scientific subject. His successful theory proposes a single historical process for the formation of coral atolls by recognizing three configurations of reefs—fringing reefs, barrier reefs, and atolls—as sequential stages in the foundering of oceanic islands.

CONSILIENCE (CONCORDANCE OF SEVERAL). We now reach a break in types of information. Methods 1 and 2 permit the reconstruction of historical sequences, either by extrapolating up from the most palpable and testable of daily changes (method 1), or by ordering a series of configurations as temporal stages (method 2). In many cases, however, we cannot reconstruct sequences, and must infer history from the configuration of a single object or circumstance. Of the two major methods for inferring history from single configurations, consilience calls upon a greater range of evidence. This word, coined by William Whewell in 1840, means "jumping together." By this term, Whewell referred to proof by coordination of so many otherwise unrelated consequences under a single causal explanation that no other organization of data seems conceivable. In a sense, consilience defines the larger method underlying all Darwin's inference from historical records. In a more specific context, I use consilience (see Gould, 1986) for Darwin's principal tactic of bringing so many different points of evidence to bear on a single subject, that history wins assent as an explanation by overwhelming confirmation and unique coordination. Call this, if you will, the different flowers principle to honor the extraordinary range of evidence that Darwin gathered (1877) to forge a historical explanation for why some taxa bear different forms of flowers on the same plant.

DISCORDANCE (DISSONANCE OF ONE). Here we reach a rock bottom of minimalism—unfortunately all too common in a world of limited information. We observe a single object, but not enough relevant items to forge consilience about its status as the product of history. How can we work from unique objects? How shall we infer history from a giraffe? Darwin tells us to search for a particular form of discordance—some imperfection or failure of coordination between an organism and its current circumstances. If such a quirk, oddity, or imperfection—making no sense as an optimal and immutable design in a current context—wins explanation as a holdover or vestige from a past state in different circumstances, then historical change may be inferred. Call this, if you will, the orchid principle (though I have also designated it as the panda principle for my own favorite example, perforce unknown to Darwin, of the panda's false thumb, Gould, 1980d), to honor Darwin's argument (1862) for orchids as products of history. Their intricate adaptations to attract insects for fertilization cannot be read as wonders of optimal design, specially created for current utilities, for they represent contraptions, jury-rigged from the available parts of ordinary flowers.

The *Origin of Species* presents an ingenious compendium of all four methods.

UNIFORMITY. People who do not understand science in their bones, and who think that revolutionary treatises must be presented as ideological manifestos at broadest scale, often express surprise and disappointment in reading the *Origin*, especially at Darwin's opening chapter. They expect fanfare, and they get fantails—pigeons, that is. But Darwin ordered his book by conscious intent and strategy. He knew that he had to demonstrate evolution with data, not simply proclaim his new view of life by rhetoric. Uniformitarianism embodied his best method based on maximal information—so he started from the smallest scale, change in domestication, and worked up to the history of life. As a member of two London pigeon fancying clubs (which he had joined, not from an abiding affection for this scourge of cities, but to gain practical information about evolution in the small), Darwin led from his acquired strength.

What better starting point, under method 1, than indubitable proof of historical change in domesticated plants and animals. The logic of the *Origin* employs one long analogy between artificial and natural selection, with uniformity as the joining point. Darwin writes in his introduction (p. 4): "At the commencement of my observations it seemed to me probable that a careful study of domesticated animals and of cultivated plants would offer the best chance of making out this obscure problem. Nor have I been disappointed; in this and in all other perplexing cases I have invariably found that our knowledge, imperfect though it be, of variation under domestication, afforded the best and safest clue."

Darwin continually drives home this analogy and extrapolation: if by artificial selection at small scale (as we know for certain), why not by natural selection at larger scale: "If it profit a plant to have its seeds more and more widely disseminated by the wind, I can see no greater difficulty in this being effected through natural selection, than in the cotton-planter increasing and improving by selection the down in the pods on his cotton-trees" (p. 86).

But this argument by uniformitarian extrapolation presents a serious difficulty (exploited by Fleeming Jenkin, 1867, in the famous critique that Darwin ranked so highly, and took so seriously in revising the *Origin*): change surely occurs in domestication, but suppose that species function like glass spheres with a modal configuration at the center and unbridgeable limits to variation representing the surface. Artificial selection could then bring morphology from the center to the surface, but no further—and the key argument for smooth extrapolation to *all* change over any time would fail. Darwin therefore staked a verbal claim for no limit. "What limit can be put to this power, acting during long ages and rigidly scrutinizing the whole constitution, structure, and habits of each creature—favoring the good and rejecting the bad? I can see no limit to this power, in slowly and beautifully adapting each form to the most complex relations of life" (p. 469).

Darwin then applied the full sequence of extrapolation to the natural world, beginning with individual variants as the source of subspecies, then moving to subspecies as incipient species, and finally to species as potential ancestors for branches of life's tree—a full range of scales from variation within a population to the entire pageant of life: "I look at individual differences, though of small interest to the systematist, as of high importance for us, as being the first step towards such slight varieties as are barely thought worth recording in works of natural history. And as I look at varieties which are in any degree more distinct and permanent, as steps leading to more strongly marked and more permanent varieties; and at these latter, as leading to subspecies, and to species" (p. 51).

Darwin invoked this first method, a strong argument based on maximal information at smallest scale, as his favored choice when available. To cite just three instances as a sampler: (1) the paleontological panorama may be read as a story of gradual evolution because species in adjacent strata show minimal differences, but these differences increase gradually as stratigraphic distance expands (p. 335). (2) When we find hints of the feather patterns of rock pigeon in highly modified breeds, we do not hesitate to interpret these designs as vestiges of an ancestral stock; therefore, the faint stripes that we sometimes observe in coats of young horses point to a common origin for all species in the clade of horses, asses and zebras (pp. 166–167). (3) Marine molluscs often exhibit brighter colors in warmer waters. We note this pattern both among varieties of a single species living in cold and warm waters, and among related species. A creationist explanation requires uncomfortable special pleading: God sometimes makes a species with bright shells in warm climates, but he allows other species to vary naturally, in the same geographic pattern, within a single created kind. An evolutionist, using method one, will recognize these phenomena as two stages in a single sequence of extrapolation from smaller to larger scale (p. 133).

SEQUENCING. We can use a second style of inference about temporal order when we cannot obtain adequate data about the nature of immediate changes at smallest scale. Since historical processes begin at different times and proceed at varying rates, all stages of a sequence may exist simultaneously (for example, stage one in case A, which began very recently; stage two in case B, which began at the same time, but has proceeded at an uncommonly rapid rate; and stage three in case C, which began long ago). Thus, fringing reefs, barrier reefs and atolls all exist now. When we recognize these forms as sequential stages of a single process, we may infer the pathway of history.

Darwin epitomizes method two in writing (p. 51): "A series impresses the mind with the idea of an actual passage." Invoking his usual starting point, Darwin presents a first example from breeds of domesticated pigeons. The more adequate data of method one—observed steps of passage, accumulating to greater and greater difference in time—no longer exist, for the transitional populations have died, and only a set of morphological "islands," representing a set of established breeds, remains. But these islands can be ordered as a plausible sequence of change between ancestral rock pigeons and the most aberrant of artificially produced breeds: "Although an English carrier or short-faced tumbler differs immensely in certain characters from the rock pigeon, yet by comparing the several sub-breeds of these breeds, more especially those brought from distant countries, we can make an almost perfect series between the extremes of structure" (p. 27).

Darwin uses method two in a special and crucial way throughout the *Origin*. Several of the most telling critiques against Darwin's style of evolution by gradualistic continuity—best represented in Mivart's famous argument (1871) about inviability of "incipient stages of useful structures" (see Chapter 11 for full treatment)—held that insensibly graded passages between putative ancestors and descendants could not even be conceptualized, much less documented. Charges of inconceivability took several forms, each reducible to the claim that you can't get from here to there, however well the beginning and end points may function. Consider the two most prominent formulations: (1) Early stages (when rudimentary) could provide no adaptive advantage, however valuable the final product (2) Major functional changes cannot occur because intermediary stages would fall into a never-never land of inviability, with the original (and essential) function lost, and the new operation not yet established.

Darwin offered a twofold response to these arguments, both using this second historical method of sequencing. He first presented theoretical arguments for the conceivability, even the likelihood, of intermediary stages in supposed cases of impossibility. He argued that early stages, too small to work in their eventual manner, could have performed different functions at the outset, and been coopted later for another style of life. (Incipient wings, originally used in thermoregulation, became organs of flight when they evolved to sufficiently large size to provide "fortuitous" aerodynamic benefits—see Kingsolver and Koehl, 1985, for an experimental validation of this scenario, and Gould, 1991b, for general discussion). As the misleadingly named principle of "preadaptation," this concept of functional shift became an important principle in evolutionary theory (see Chapter 11). Darwin writes, using a verbal intensifier rarely found in his prose: "In considering transitions of organs, it is so important to bear in mind the probability of conversion from one function to another" (p. 191).

As a response to charges of inviability for intermediary stages, Darwin invoked the important principle of redundancy as a norm for organic structures and functions. Most important functions can be performed by more than one organ; and most organs work in more than one way. By coupling these two aspects of redundancy, transitions in single organs can easily be conceived. An organ doesn't mysteriously invent a new function, but usually intensifies and specializes a previously minor use, while shedding an old primary operation. This previously major function can then be lost because other organs continue to do the same necessary job.

Ironically, we now recognize Darwin's favorite example of such redundancy as not only incorrect, but truly backwards (Gould, 1989b)—the evolution of lungs from swimbladders. (In fact, swimbladders evolved from lungs, see Liem, 1988). Darwin ran his transition in the wrong way, but his argument for redundancy as the key to viability for intermediary steps remains correct and crucially important, for the logic works equally well in either direction. Ancestral fishes maintained two systems for breathing—gills and lungs (as do modern lungfish, taxonomically called Dipnoi, or "two breathing"). The original lung probably played a subsidiary role in buoyancy; this function could be enhanced, and the original use in breathing deleted, because gills could adopt the entire respiratory burden. Darwin wrote (pp. 204–205): "For instance, a swim-bladder has apparently been converted into an air-breathing lung. The same organ having performed simultaneously very different functions, and then having been specialized for one function; and two very distinct organs having performed at the same time the same function, the one having been perfected whilst aided by the other, must often have largely facilitated transitions."

As a second response, Darwin proceeded beyond conceivability and tried to document actual sequences for supposedly impossible transitions—as in the evolution of a light-sensitive spot into an "organ of extreme perfection" like the vertebrate eye. These sequences cannot represent true phylogenies (since they consist solely of living species), but they do constitute structural series illustrating the conceivability of transitions. After admitting, for example, that the gradual evolution of such a miracle of workmanship as the eye "seems, I freely confess, absurd in the highest possible degree" (p. 186), Darwin presents a structural series of disparate animals, including working configurations proclaimed impossible by opponents: "Yet reason tells me, that if numerous gradations from a perfect and complex eye to one very imperfect and simple, each grade being useful to its possessor, can be shown to exist . . . then the difficulty of believing that a perfect and complex eye could be formed by natural selection, though insuperable by our imagination, can hardly be considered real" (p. 186).

Darwin applies this principle to behavior and its products, as well as to form. For the exquisite mathematical regularity of the honeycomb, he writes (p. 225): "Let us look to the great principle of gradation, and see whether Nature does not reveal to us her method of work." (See also page 210 on complex instincts and their explanation by the establishment of structural series.)

CONSILIENCE (CONCORDANCE OF SEVERAL). Darwin took great pride in his formulation of natural selection as a theory for the mechanism of phyletic change. But he granted even more importance to his relentless presentation of dense documentation for the factuality of change—for only such a cascade of data would force the scientific world to take evolution seriously. (The contrast between the *Origin* as a compendium of facts, and Lamarck's *Philosophie zoologique* as a purely theoretical treatise, strikes me as an even more distinguishing difference than the disparate causal mechanisms proposed by the two authors.) Facts literally pour from almost every page of the *Origin*, a feature that became even more apparent following Darwin's forced change of plans, and his decision to compress his projected longer work into the "abstract" that we call the *Origin of Species*—a revised strategy that led him to omit almost every reference and footnote, and almost all discursive discussion between bits of information. In some parts, the *Origin* reaches an almost frenetic pace in its cascading of facts, one upon the other. Only Darwin's meticulous sense of order and logic of argument save the work from disabling elision and overload.

Whenever he introduces a major subject, Darwin fires a volley of disparate facts, all related to the argument at hand—usually the claim that a particular phenomenon originated as a product of history. This style of organization virtually guarantees that Whewell's "consilience of inductions" must become the standard method of the *Origin*. Darwin's greatest intellectual strength lay in his ability to forge connections and perceive webs of implication (that more conventional thinking in linear order might miss). When Darwin could not cite direct evidence for actual stages in an evolutionary sequence, he relied upon consilience—and sunk enough roots in enough directions to provide adequate support for a single sturdy trunk of explanation.

Again, Darwin starts with pigeons, unleashing a cannonade of disparate arguments, all pointing to the conclusion that modern breeds of pigeons derive from a single ancestral stock. None of these facts permits the construction of an actual temporal series (methods one and two); but all identify the features of a current configuration that point to history as the underlying cause. Darwin, as usual, proceeds by particular example, but I doubt that a better general description of consilience could be formulated:

> From these several reasons, namely, the improbability of man having formerly got seven or eight supposed species of pigeons to breed freely under domestication; these supposed species being quite unknown in a wild state, and their becoming nowhere feral; these species having very abnormal characters in certain respects, as compared with all other Columbidae, though so like in most other respects to the rock pigeon; the blue color and various marks occasionally appearing in all the breeds, both when kept pure and when crossed; the mongrel offspring being perfectly fertile;—from these several reasons, taken together, I can feel no doubt that all our domestic breeds have descended from the *Columba livia* with its geographical subspecies (pp. 26–27).

Every scholar could cite a favorite case of Darwinian consilience. For my part, I especially admire Darwin's uncharacteristically long discussion (pp. 388–406) on transport from continental sources and subsequent evolution to explain the biotas of oceanic islands. Consider the main items in Darwin's own order of presentation:

(1) The general paucity of endemic species on islands, contrasted with comparable areas of continents; why should God put fewer species on islands?

(2) The frequent displacement of endemic island biotas by continental species introduced by human transport. If God created species for islands, why should species designed for continents so often prove superior in competition: "He who admits the doctrine of the creation of each separate species, will have to admit, that a sufficient number of the best adapted plants and animals have not been created on oceanic islands; for man has unintentionally stocked them from various sources far more fully and perfectly than has nature" (p. 390).

(3) Taxonomic disparity of endemic species within groups records ease of access, not created fit to oceanic environments: "Thus in the Galapagos Islands nearly every land bird, but only two out of the eleven marine birds, are peculiar; and it is obvious that marine birds could arrive at these islands more easily than land birds" (pp. 390–391).

(4) Biotas of oceanic islands often lack the characteristic groups of similar habitats on continents. On these islands, endemic members of other groups often assume the ecological roles almost always occupied by more appropriate or more competitive taxa in the richer faunas of continents—for example, reptiles on the Galapagos, or wingless birds on New Zealand, acting as surrogates for mammals.

(5) In endemic island species, features operating as adaptations in related species on continents often lose utility when their island residences do not feature the same environment: "For instance, in certain islands not tenanted by mammals, some of the endemic plants have beautifully hooked seeds; yet few relations are more striking than the adaptation of hooked seeds for transportal by the wool and fur of quadrupeds. This case presents no difficulty on my view, for a hooked seed might be transported to an island by some other means; and the plant then becoming slightly modified, but still retaining its hooked seeds, would form an endemic species, having as useless an appendage as any rudimentary organ" (p. 392).

(6) Peculiar morphological consequences often ensue when creatures seize places usually inhabited by other forms that could not reach an island. Many plants, herbaceous in habit on continents, become arboraceous on islands otherwise devoid of trees.

(7) Suitable organisms frequently fail to gain access to islands. Why do so many oceanic islands lack frogs, toads, and newts that seem so admirably adapted for such an environment? "But why, on the theory of creation, they should not have been created there, it would be very difficult to explain" (p. 393).

(8) Correlation of biota with distance. Darwin could find no report of terrestrial mammals on islands more than 300 miles from a continent. He presents the obvious evolutionary explanation for a disturbing creationist conundrum:

> It cannot be said, on the ordinary view of creation, that there has not been time for the creation of mammals; many volcanic islands are sufficiently ancient, as shown by the stupendous degradation which they have suffered and by their tertiary strata: there has also been time for the production of endemic species belonging to other classes . . . why, it may be asked, has the supposed creative force produced bats and no other mammals on remote islands? On my view this question can easily be answered; for no terrestrial mammal can be transported across a wide space of sea, but bats can fly across (p. 394).

(9) Correlation with ease of access. Creatures often manage to cross shallow water barriers between a continent and island, but fail to negotiate deep-water gaps of the same distance.

(10) Taxonomic affinity of island endemics—perhaps the most obvious point of all: why are the closest relatives of island endemics nearly always found on the nearest continent or on other adjacent islands?

Any honorable creationist, after suffering such a combination of blows, all implicating a history of evolution as the only sensible coordinating explanation, should throw in the towel and, like a beaten prizefighter, acknowledge Darwin as the Muhammad Ali of biology.

DISCORDANCE (DISSONANCE OF ONE). Consilience works as a cumulative argument for inferring history from objects and phenomena, rather than directly from sequences. You develop a line of attack, list numerous points, and then close in for the kill. But the empirical world often fails to provide such a bounty of evidence. Often, scientists must reason from a single object or situation—just the thing itself, not a network of arguments suitable for a broad consilience. Can history be inferred from such minimal information?

Thinkers, like soldiers, often show their true mettle in greatest adversity. I am particularly attracted by Darwin's approach to method 4, and have often cited his arguments in these "worst cases" as my primary illustration of his genius (Gould, 1986)—for Darwin met his greatest difficulty, and then not only devised a resolution, but also developed an argument of power and range. In other words, he turned potential trouble into one of his greatest strengths.

To infer history from a single object, Darwin asserts, one must locate features (preferably several, so the argument may shade into method three) that make no sense, or at least present striking anomalies, in the current life of the organism. One must then show that these features did fit into a clearly inferable past environment. In such cases, history—as expressed by preservation of signs from the past—provides the only sensible explanation for modern quirks, imperfections, oddities, and anomalies.

Darwin structured the *Origin of Species* as a trilogy. The first four chapters lay out the basic argument for natural selection. The middle five treat difficulties with the theory, and ancillary subjects that must be incorporated or explained away (rules of variation, nature of geological evidence, instincts, hybridism, and general objections). The final five chapters present the grand consilience by summarizing evidence for evolution itself—not so much for natural selection as a mechanism—from a broad range of disparate fields: geology*, geographic variation, morphology, taxonomy, embryology, and so forth.

The last part of the trilogy features method four. One might almost say that chapters 10–14 constitute one long list of examples for inferring history

*This tripartite structure of the *Origin* is masked by our tendency to treat the two geological chapters (9–10) as a unity. (Darwin even summarizes them together at the end of Chapter 10.) But Chapter 9, as the title proclaims ("On the imperfection of the geological record"), belongs to the discussion of difficulties in part 2 of the *Origin*—while Chapter 10 ("On the geological succession of organic beings") initiates part three on documentation of evolution as a fact. (Even the consolidated summary of Chapter 10 makes a clear break between these two disparate parts of Darwin's geological argument.)

from the oddities and imperfections of modern objects. (This arrangement of the last part struck me with particular force, as I reread the *Origin* before writing this book, and realized that the introductory paragraph for almost every new subject—from geographic variation to rudimentary organs—explicitly restates the general argument for method four.) Of course, the rest of the *Origin* also abounds with cases of method four, beginning as usual with examples from domestication. (Darwin argues that the chicks of wildfowl hide in grass and bushes to give their mother an opportunity for escape by flight. Domesticated chickens retain this habit, which no longer makes sense "for the mother-hen has almost lost by disuse the power of flight"—p. 216.)

Of subjects treated in this final part of the *Origin*'s trilogy, rudimentary organs represent, almost by definition, the "holotype" of method four. Darwin's definition, in the first sentence of his discussion, emphasizes this theme—"organs or parts in this strange condition, bearing the stamp of inutility" (p. 450). Nature tries to give us a history lesson, Darwin argues in some frustration, but we resist the message as inconsistent with received wisdom about natural harmony: "On the view of each organic being and each separate organ having been specially created, how utterly inexplicable it is that parts, like the teeth in the embryonic calf or like the shrivelled wings under the soldered wing-covers of some beetles, should thus so frequently bear the plain stamp of inutility! Nature may be said to have taken pains to reveal, by rudimentary organs and by homologous structures, her scheme of modification, which it seems that we wilfully will not understand" (p. 480). What else but imprints of history can explain rudimentary organs? Darwin ridicules the special pleading of creationist accounts as fancy ways of saying nothing at all. "In works on natural history rudimentary organs are generally said to have been created 'for the sake of symmetry,' or in order 'to complete the scheme of nature;' but this seems to me no explanation, merely a restatement of the fact. Would it be thought sufficient to say that because planets revolve in elliptic courses round the sun, satellites follow the same course round the planets, for the sake of symmetry, and to complete the scheme of nature?" (p. 453). Always searching for analogies with a short-term human history that we cannot deny, Darwin compares rudimentary organs with silent letters, once sounded, in the orthography of words: "Rudimentary organs may be compared with the letters in a word, still retained in the spelling, but become useless in the pronunciation, but which serve as a clue in seeking for its derivation" (p. 455).

Darwin continues the same argument as an underpinning for all discussions on other aspects of organic form. He introduces morphology as "the most interesting department of natural history, [which] may be said to be its very soul" (p. 434) and continues immediately with an example of method four: "What can be more curious than that the hand of a man, formed for grasping, that of a mole for digging, the leg of the horse, the paddle of the porpoise, and the wing of the bat, should all be constructed on the same pattern, and should include the same bones, in the same relative positions" (p. 434).

Similarly, the section on embryology begins with an example of method four—the branchial circulation in young bird and mammalian embryos as indications of a "community of descent" with an aquatic past. This common condition in embryonic frogs, birds, and mammals cannot reflect design for *current* function: "We can not, for instance, suppose that in the embryos of the vertebrata the peculiar loop-like course of the arteries near the branchial slits are related to similar conditions,—in the young mammal which is nourished in the womb of his mother, in the egg of the bird which is hatched in a nest, and in the spawn of a frog under water" (p. 440).

The key argument of the section on taxonomy makes the same point in a different form: if animals had experienced no history of change, and were created in accord with current needs and functions, then why should similar anatomical designs include creatures of such widely divergent styles of life? Darwin writes, in the opening paragraph of his discussion on taxonomy: "The existence of groups would have been of simple signification, if one group had been exclusively fitted to inhabit the land, and another the water; one to feed on flesh, another on vegetable matter, and so on; but the case is widely different in nature; for it is notorious how commonly members of even the same subgroup have different habits" (p. 411).

These arguments strike us as most familiar when based on organic form, but fewer evolutionists recognize that method four also undergirds Darwin's two chapters on biogeography (11 and 12). Darwin uses dissonance between organism and dwelling place as the coordinating theme of these chapters: the geographic distributions of organisms do not primarily suit their *current* climates and topographies, but seem to record more closely a history of opportunities for movement. Again, Darwin presents the basic argument in his first paragraph (p. 346): "In considering the distribution of organic beings over the face of the globe, the first great fact which strikes us is, that neither the similarity nor the dissimilarity of the inhabitants of various regions can be accounted for by their climatal and other physical conditions."

Example tumbles upon example throughout these two chapters. Darwin notes that northern hemisphere organisms of subarctic and north temperate climes maintain far closer taxonomic similarity than the current geographic separation of their continents would imply. He therefore interprets these likenesses as vestiges of history—preserved expressions of the glacial age, when these climatic bands stood further to the north, near the arctic circle where all northern continents virtually touch (p. 370). He also finds too much organic similarity for the modern range of climatic differences along lines of longitude from north to south poles, and he again implicates the climax of glacial ages as a time of formation (with modern persistence as a vestige), when even a subarctic species might migrate in comfort, on a cold earth, across the equator from north to south along a single line of longitude. Invoking a complex and graphic metaphor for history, Darwin writes of disjunct distributions on opposite hemispheres, and of geographic refugia at high altitudes of lower latitudes between these endpoints:

> The living waters may be said to have flowed during one short period from the north and from the south, and to have crossed the equator; but

> to have flowed with greater force from the north so as to have freely inundated the south. As the tide leaves its drift in horizontal lines, . . . so have the living waters left their living drift on our mountain summits, in a line gently rising from the arctic lowlands to a great height under the equator. The various beings thus left stranded may be compared with savage races of man, driven up and surviving in the mountain fastnesses of almost every land, which serve as a record, full of interest to us, of the former inhabitants of the surrounding lowlands (p. 382).

Everyone cites the Galapagos in a virtual catechism about Darwin's evidence for evolution, but few biologists can state how he invokes these islands in the *Origin.* Most textbooks talk about a diversity of finches, each beautifully adapted to available resources on different islands, or of variation in tortoise carapaces from place to place. Both these stories exemplify both diversification and current adaptive value—but Darwin speaks not a word about either case in the *Origin!*

In fact, Darwin invokes the Galapagos primarily as an extended example of method four applied to biogeography: These islands house many endemic species, necessarily created *in situ* according to his opponents. But why then should all these endemics bear close relationship with species on the nearby American mainland? A creationist might say that God fits creatures to immediate circumstances, and that the Galapagos Islands, located so near America, must resemble America in environment, and therefore be best suited to house species of the same basic design. But now we grasp the beauty of the Galapagos as an almost uncannily decisive natural experiment for the influence of history. These islands do lie close to America, but could scarcely resemble the mainland *less* in climate, geology and topography—for the Galapagos are volcanic islands in the wake of a cool current that even permits access to the northernmost species of penguin! Therefore, if the Galapagos endemics resemble American species, they must be recording a history of accidental transport and subsequent evolutionary change—not similar creations for similar environments. Darwin's brilliant argument deserves citation *in extenso:*

> Here almost every product of the land and water bears the unmistakeable stamp of the American continent. There are 26 land birds, and 25 of these are ranked by Mr. Gould as distinct species, supposed to have been created here; yet the close affinity of most of these birds to American species in every character, in their habits, gestures, and tones of voice, was manifest. . . . why should this be so? Why should the species which are supposed to have been created in the Galapagos Archipelago, and nowhere else, bear so plain a stamp of affinity to those created in America? There is nothing in the conditions of life, in the geological nature of the islands, in their height or climate, or in the proportions in which the several classes are associated together, which resembles closely the conditions of the South American coast: in fact there is considerable dissimilarity in these respects. On the other hand, there is a considerable degree of resemblance in the volcanic nature of the soil, in climate, height, and size of islands, between the Galapagos and Cape de Verde Archipelagos: but what an entire and absolute difference in their inhabitants! The inhabitants of the Cape de Verde Islands are related to those of Africa, like those of the Galapagos to America. I believe this grand fact can receive no sort of explanation on the ordinary view of independent creation; whereas on the view here maintained, it is obvious that the Galapagos Islands would be likely to receive colonists . . . from America; and the Cape de Verde Islands from Africa; and that such colonists would be liable to modifications—the principle of inheritance still betraying their original birth place (pp. 397–399).

Finally, in rereading the *Origin,* I was struck by another, quite different, use of the argument from imperfection—one that had entirely escaped my notice before. Darwin showed little sympathy for our traditional and venerable attempts to read moral messages from nature. He almost delighted in noting that natural selection unleashes a reign of terror that would threaten our moral values if we tried—as we most emphatically should not—to find ethical guidelines for human life in the affairs of nature. But I hadn't realized that he sometimes presents the apparent cruelties of nature as imperfections pointing to evolution by natural selection—imperfections relative to an inappropriate argument about morality to be sure, but imperfections that trouble our souls nonetheless, and may therefore operate with special force as suggestive arguments for evolution:

> Nor ought we to marvel if all the contrivances in nature be not, as far as we can judge, absolutely perfect; and if some of them be abhorrent to our ideas of fitness. We need not marvel at the sting of the bee causing the bee's own death; at drones being produced in such vast numbers for one single act, and being then slaughtered by their sterile sisters; at the astonishing waste of pollen by our fir trees; at the instinctive hatred of the queen bee for her own fertile daughters; at ichneumonidae feeding within the live bodies of caterpillars; and at other such cases. The wonder indeed is, on the theory of natural selection, that more cases of the want of absolute perfection have not been observed (p. 472).

I may have burdened readers with too much detail about Darwin's arguments for inferring history, but method inheres in this extended madness. My general argument holds that the *Origin* should be understood as a book encompassing two opposite, but complementary, poles of science at its best and most revolutionary—first, as a methodological treatise proving by example that evolution can be tested and studied fruitfully; and second, as an intellectual manifesto for a new view of life and nature. As a methodological treatise, the *Origin* focuses upon the palpable and the small—arguing that uniformitarian extrapolation into geological scales can render all evolution. We may therefore avoid any appeal to "higher" forces that cannot be studied directly because they work only in the untestable immensity of deep time, or occur so rarely that we can entertain little hope for direct observation during the short span of human history. The disabling Lamarckian paradox—what is important can't be studied; and what can be studied isn't important—therefore disappears, and evolution becomes, under Darwin's system, a working science for the first time. These features of methodology potentiate Darwin's theoretical overview (as we shall see in the next section), and therefore contribute indispensably to what may legitimately be called the essence of Darwinism, the *sine quibus non* for a Darwinian view of nature. This book argues that we can define such a set of basic commitments, but then maintains that these commitments have become inadequate in our times.

Darwin as a Philosophical Revolutionary

THE CAUSES OF NATURE'S HARMONY

Darwin and William Paley

In November 1859, just a week before the official publication date of the *Origin,* Darwin wrote to his neighbor John Lubbock* "I do not think I hardly ever admired a book more than Paley's 'Natural Theology.' I could almost formerly have said it by heart" (in F. Darwin, 1887, volume 2, p. 219).

The Reverend James McCosh receives my vote for the most interesting among a largely forgotten group of late 19th century thinkers who played a vital role in their own time—liberal theologians friendly to evolution (though not usually to Darwin's philosophy), and who prove that if any warring camps can be designated in this realm, the combatants surely cannot be labeled as science *vs.* religion (see Gould, 1999b), but rather as expressions of a much deeper struggle between tradition and reform, or dogmatics and openness to change. McCosh doesn't even merit a line in the *Encyclopedia Britannica,* though he did serve as president of Princeton University, where he had a major influence on the career of Henry Fairfield Osborn and other important American evolutionists.

In 1851, McCosh published an article entitled "Typical Forms" in the *North British Review.* Hugh Miller, the self-taught Scottish geologist and general thinker, called this article "at once the most suggestive and ingenious which we have almost ever perused," and urged McCosh to expand his argument to an entire volume. McCosh accepted this advice and, in collaboration with George Dickie, published *Typical Forms and Species Ends in Creation* in 1869. The Greek inscription on the title page—*typos kai telos* (type and purpose)—epitomizes the argument. McCosh holds that God's order and benevolence may be inferred from two almost contradictory properties that reside in tension within all natural objects—"the principle of order" and "the principle of special adaptation." (These two principles persist in Darwin's formulation under the names "Unity of Type" and "Conditions of Existence"—1859, p. 206, for example (see my extensive treatment of this passage on pp. 251–260), where their fundamental character merits upper case designations from Darwin.) McCosh defines his first principle as "a general plan, pattern, or type, to which every given object is made to conform"; and his second as a "particular end, by which each object, while constructed after a general model is, at the same time, accommodated to the situation which it has to occupy, and a purpose which it is intended to serve" (1869, p. 1). (If we call these two principles "anatomical ground plan" and "adaptation" we will be able to make the appropriate evolutionary translation without difficulty.)

*Later Lord Avebury and an author of many fine evolutionary works himself. But Lubbock's greatest contribution to human thought was probably indirect, a result of neighborly fellowship—for he sold to Darwin a corner of property that became the famous "sandwalk" where Darwin, perambulating and kicking aside a flint cobble for each circumnavigation, solved several riddles of life and human existence. Darwin graded the difficulty of his problems by the number of circuits required for solution—two-flint problems, five-flint problems, etc. I suspect that macroevolutionary theory must present us with at least a fifty-flint problem!

McCosh argues that God's existence and benevolence can be inferred from either principle—from the first by the order of taxonomy, and the abstract beauty of bodily symmetry and structure; and from the second, by "adaptation,"* or the exquisite fit of form to function. McCosh also notes that the second, or functional, argument constitutes the "national signature" of British thought: "The arguments and illustrations adduced by British writers for the last age or two in behalf of the Divine existence, have been taken almost exclusively from the indications in nature of special adaptation of parts" (1869, p. 6).

The main lineage of this national tradition for "natural theology" based on the "argument from design" runs from Robert Boyle's *Disquisition About the Final Causes of Natural Things* (1688) and John Ray's *Wisdom of God Manifested in the Works of the Creation* (1691) in Newton's generation that promulgated what historians call "*the* scientific revolution"; to a grand culmination in William Paley's *Natural Theology* (1802), one of the most influential books of the 19th century; to an anticlimax, during the 1830's, in the eight "Bridgewater Treatises" (including volumes by Buckland and Whewell), established by a legacy from the deceased Earl of Bridgewater for a series of volumes "on the power, wisdom, and goodness of God, as manifested in the creation." Critics in Darwin's circle generally referred to this series as the "bilgewater treatises."

Revolutions usually begin as replacements for older certainties, and not as pristine discoveries in uncharted terrain. In understanding the second pole of Darwin's genius as the uncompromising radicalism of his new philosophy for life and history, we must first characterize the comfortable orthodoxy up-

*The word adaptation did not enter biology with the advent of evolutionary theory. The *Oxford English Dictionary* traces this term to the early 17th century in a variety of meanings, all designating the design or suitability of an object for a particular function, the fit of one thing to another. The British school of natural theology used "adaptation" as a standard word for illustrating God's wisdom by the exquisite fit of form to immediate function. Darwin, in borrowing this term, followed an established definition while radically revising the cause of the phenomenon.

rooted by the theory of natural selection. Darwin's essential argument begins with a definition of the dominant philosophy for natural history in his day—natural theology in the Paleyan mode.

At the outset of Chapter 4, I will say more about Paley and the alternative vision of continental natural theology (adaptationism vs. laws of form). For now, a simple statement of the two chief precepts of Paleyan biology will suffice:

NATURAL THEOLOGY IN GENERAL. The rational and harmonious construction of nature displays the character and benevolence of a creating God. In the last four chapters of his book, Paley tells us what we may infer about God from the works of creation. God's existence, of course, shines forth in his works, but this we know from many other sources. More specifically (and with a Paleyan chapter for each), nature instructs us about God's personality, his natural attributes, his unity, and (above all) his goodness.

PALEY'S PARTICULAR VERSION OF NATURAL THEOLOGY. Natural theology has been expressed in two basic modes (see Chapter 4), one primarily continental (laws of form), the other mainly British (adaptationism). Paley held that God manifests his creating power in the exquisite design of organisms for their immediate function. We all know Paley's famous opening metaphor: if I find a watch lying abandoned on an open field, I can conclude from the complex set of parts, all shaped to a common purpose and all well designed for a specific end, that some higher intelligence constructed the watch both directly and for a particular use. Since organisms show even more complexity and even more exquisite design, they must have been fashioned by an even greater intelligence. But fewer biologists know Paley's more specific argument *against* the alternative version of natural theology (laws of form), as presented in his chapter 15 on "relations." The parts of organisms exist in concert not because laws of form or symmetry demand one feature to balance another, but "from the relation which the parts bear to one another in the prosecution of a common purpose" (1803 edition, p. 296)—that is, to secure an optimal adaptation of the whole.

At the very outset of the *Origin,* Darwin tells us that his explanation of evolution will stress the Paleyan problem of exquisite adaptation. He writes, in the Introduction, that we could obtain sufficient confidence about evolution by "reflecting on the mutual affinities of organic beings, on their embryological relations, their geographical distribution, geological succession, and other such facts" (1859, p. 3). "Nevertheless," he continues, "such a conclusion, even if well founded, would be unsatisfactory, until it could be shown how the innumerable species inhabiting this world have been modified, so as to acquire that perfection of structure and coadaptation which most justly excites our admiration" (1859, p. 3). The explanation of adaptation therefore stands forth as the primary problem of evolution. Many lines of evidence prove *that* evolution occurred. But if we wish to learn *how* evolution works, we must study adaptation.

This basic Darwinian argument operates as a close copy of Paley's defense, recast in evolutionary language, for the English alternative in natural theology. We can infer, Paley often states, *that* God exists from innumerable aspects of nature. But if we wish to know any more about the creator—his nature, his attributes, his intentions—we must study the excellence of adaptation via the "argument from design." Paley writes (1803, p. 60): "When we are enquiring simply after the *existence* of an intelligent Creator, imperfection, inaccuracy, liability to disorder, occasional irregularities, may subsist, in a considerable degree, without inducing any doubt into the question."

On the other hand, adaptation in the fashioning of contrivances for definite ends reveals God's nature. Paley invokes this theme as a litany in developing his initial parable of the watch and watchmaker. He cites other possible explanations for the origin of the watch, and then intones, after each: "Contrivance is still unaccounted for. We still want a contriver" ("want," that is, in the old sense of "lack," not the modern "desire"—p. 13). "Contrivance must have had a contriver, design, a designer" (p. 14). Later, he tells us explicitly that nature can testify to God's character and goodness only by the phenomenon of adaptation (pp. 42–43): "It is only by the display of contrivance, that the existence, the agency, the wisdom of the Deity, *could* be testified to his rational creatures. This is the scale by which we ascend to all the knowledge of our Creator which we possess, so far as it depends upon the phenomena, or the works of nature . . . It is in the construction of instruments, in the choice and adaptation of means, that a creative intelligence is seen. It is this which constitutes the order and the beauty of the universe."

I had never read *Natural Theology* straight through before pursuing my research for this book. In so doing, I was struck by the correspondences between Paley's and Darwin's structure of argument (though Darwin, of course, inverts the explanation). Darwin did not exaggerate when stating to Lubbock that he had virtually committed Paley to memory. The style of Darwin's arguments, his choice of examples, even his rhythms and words, must often reflect (perhaps unconsciously) his memory of Paley. Consider just a few examples of this crucial linkage:

1. Paley, like Darwin, relies upon comparison and extrapolation from artificial to natural. Darwin moves from artificial to natural selection, Paley from human to animal machines. Both rely on the central argument that a common mechanism works much more powerfully in nature. Paley's words recall Darwin's argument that natural selection, working on all parts for so much time, must trump artificial selection, which only affects the few features we choose to emphasize in the short duration of human history. "For every indication of contrivance, every manifestation of design, which existed in the watch, exists in the works of nature; with the difference, on the side of nature, of being greater and more, and that in a degree which exceeds all computation" (1803, p. 19).

2. Both men invoke the same examples. Paley compares the eye and telescope; Darwin lauds the eye as the finest example of complex natural design, and then presents an evolutionary explanation. Paley cites the swimbladder as an independent device created for life in water; Darwin illustrates homology with the tetrapod lung and proposes an evolutionary passage.

3. Darwin often uses Paley's logic, sometimes against his predecessor. Paley, for example, dismisses arguments about "tendencies to order" or "principles of design" as empty verbiage, explaining nothing; a true cause must be identified, namely God himself. Darwin makes the same point, but cites evolution as the true cause, while branding statements about creation *ex nihilo* as empty verbiage. Paley writes (p. 76): "A principle of order is the word: but what is meant by a principle of order, as different from an intelligent Creator, has not been explained either by definition or example: and, without such explanation, it should seem to be a mere substitution of words for reasons, names for causes."

4. Paley discusses many themes of later and central importance to Darwin. He criticizes the major evolutionary conjectures of his day, including Buffon on "interior molds," and the idea of use and disuse. (Since I doubt that he had read Lamarck's earliest evolutionary work by 1802, Paley probably derived this aspect of Lamarck's theory from its status as folk wisdom in general culture.) Paley also states the following crisp epitome of the very argument from Malthus that so struck Darwin. (I am not claiming that this passage provided a covert source for Darwin's central insight. Darwin, after all, had also read Malthus.) "The order of generation proceeds by something like a geometrical progression. The increase of provision, under circumstances even the most advantageous, can only assume the form on an arithmetic series. Whence it follows, that the population will always overtake the provision, will pass beyond the line of plenty, and will continue to increase till checked by the difficulty of procuring subsistence" (p. 540).

This influence, and this desire to overturn Paley, persisted throughout Darwin's career. Ghiselin (1969), for example, regards Darwin's orchid book as a conscious satire on Paley's terminology and argument. Darwin called this work (1862), his next book after the *Origin of Species,* "On the various contrivances by which British and foreign orchids are fertilized by insects." Paley used the word "contrivance," as my previous quotations show, to designate an organic design obviously well-made by an intelligent designer. But Darwin argues that orchids must be explained as contraptions, not contrivances. Their vaunted adaptations are jury-rigged from ordinary parts of flowers, and must have evolved from such an ancestral source; the major adaptive features of orchids have not been expressly and uniquely designed for their current functions.

Now suppose, as a problem in abstract perversity, that one made a pledge to subvert Paley in the most radical way possible. What would one claim? I can imagine two basic refutations. One might label Paley's primary observation as simply wrong—by arguing that exquisite adaptation is relatively rare, and that the world is replete with error, imperfection, misery and caprice. If God made such a world, then we might want to reassess our decision to worship him. An upsetting argument indeed, but Darwin chose an even more radical alternative.

With even more perversity, one might judge Paley's observation as undoubtedly correct. Nature features exquisite adaptation at overwhelming relative frequency. But the unkindest cut of all then holds that this order, the very basis of Paley's inference about the nature of God, arises not directly from omnipotent benevolence, but only as a side-consequence of a causal principle of entirely opposite import—namely, as the incidental effect of organisms struggling for their own benefit, expressed as reproductive success. Could any argument be more subversive? One accepts the conventional observation, but then offers an explanation that not only inverts orthodoxy, but seems to mock the standard interpretation in a manner that could almost be called cruel. This more radical version lies at the core of Darwin's argument for natural selection. (Darwin actually employed both versions of the radical argument against Paley, but for different aspects of his full case. He invoked oddities and imperfections as his major evidence for the factuality of evolution (see pp. 111–116). But he used the more radical version—exquisite adaptation exists in abundance, but its cause inverts Paley's world—to construct his mechanism for evolutionary change, the theory of natural selection.)

We all understand, of course, that the force of Darwin's radicalism extends well beyond the inversion of an explanatory order; he also undercut a primary source of human comfort and solace. This book cannot address such a vital issue at any depth, but I must record the point—for this wrenching became so salient in subsequent human history. If the natural footprints of Paley's God—the source of our confidence in his character, his goodness and, incidentally, the only hint from nature that we should accept other revealed doctrines, in particular the idea of bodily resurrection (1803, pp. 580–581)—must be reconceived as epiphenomena of a struggle for personal success, then what becomes of nature's beauty, instruction and solace? What a bitter cup Darwin offers us, compared with Paley's sweet promise (1803, pp. 578–579): "The hinges in the wings of an earwig, and the joints of its antennae, are as highly wrought, as if the Creator had had nothing else to finish. We see no signs of diminution of care by multiplication of objects, or of distraction of thought by variety. We have no reason to fear, therefore, our being forgotten, or overlooked, or neglected."

But then, the man who served as the primary focus of Paley's veneration had also promised that the truth would make us free; and Darwin justly argued that nature cannot provide the source of morality or comfort in any case.

Darwin and Adam Smith

Many scientists fail to recognize that all mental activity must occur in social contexts, and that a variety of cultural influences must therefore impact all scientific work. Those who do note the necessary link usually view cultural embeddedness as an invariably negative component of inquiry—a set of biases that can only distort scientific conclusions, and that should be identified for combat. But cultural influences can also facilitate scientific change, for incidental reasons to be sure, but with crucially positive results nonetheless—the exaptive principle that evolutionists, above all, should grasp and honor!

The origin of Darwin's concept of natural selection provides my favorite example of cultural context as a promoter.

The link of Darwin to Malthus has been recognized and accorded proper importance from the start, if only because Darwin himself had explicitly noted and honored this impetus. But if Darwin required Malthus to grasp the central role of continuous and severe struggle for existence, then he needed the related school of Scottish economists—the *laissez-faire* theorists, centered on Adam Smith and the *Wealth of Nations* (first published in the auspicious revolutionary year of 1776)—to formulate the even more fundamental principle of natural selection itself. But the impact of Adam Smith's economics did not strike Darwin with the force of eureka; the concepts crept upon him in the conventional fashion of most influences upon our lives. How many of us can specify a definite parental admonition, or a particular taunt of our peers, as central to the construction of our deepest convictions?

Silvan S. Schweber (1977), a physicist and historian of science, has traced the chain of influence upon Darwin from Adam Smith's school of Scottish economists—beginning in the early 1830's, and culminating in Darwin's intense study of these ideas as he tried to fathom the role of individual action during the weeks just preceding his "Malthusian" insight of September 1838. I believe that Schweber has found the key to the logic of natural selection and its appeal for Darwin in the dual role of portraying everyday and palpable events as the stuff of all evolution (the methodological pole), and in overturning Paley's comfortable world by invoking the most radical of possible arguments (the philosophical pole).

In fact, I would advance the even stronger claim that the theory of natural selection is, in essence, Adam Smith's economics transferred to nature. We must also note the delicious (and almost malicious) irony residing in such an assertion. Human beings are moral agents and we cannot abide the hecatomb*—the death through competition of nearly all participants—incurred by allowing individual competition to work in the untrammeled manner of pure *laissez-faire*. Thus, Adam Smith's economics doesn't work in economics. But nature need not operate by the norms of human morality. If the adaptation of one requires the deaths of thousands in amoral nature, then so be it. The process may be messy and wasteful, but nature enjoys time in abundance, and maximal efficiency need not mark her ways. (In one of his most famous letters, Darwin wrote to Joseph Hooker in 1856: "What a book a devil's chaplain might write on the clumsy, wasteful, blundering, low, and horribly cruel works of nature!") The analog of pure *laissez-faire* can and does operate in nature—and Adam Smith's mechanism therefore enjoys its finest, perhaps its only, full application in this analogous realm, not in the domain that elicited the original theory itself.

*"Hecatomb," an unfamiliar word in English, should enter the vocabulary of all evolutionists as a wonderfully appropriate description for this key aspect of Darwinism. A hecatomb is, literally, an offering of a hundred oxen in sacrifice. Yet, even in Homer, the word had come to designate any large number of deaths incurred as a sacrifice for some intended benefit—a good description of natural selection. And hecatomb trips so much more lightly off the tongue than "substitutional load."

The primary argument of *laissez-faire* rests upon a paradox. One might suppose that the best path to a maximally ordered economy would emerge from an analysis conducted by the greatest experts all assembled, and given full power to execute their recommendations (the closest human analog to Paley's lone Deity), followed by the passage of laws to implement these rationally-derived, higher-level decisions. Yet Adam Smith argued that a society should follow the opposite path as a best approach to this desired end: law makers and regulators should step aside and allow each individual to struggle for personal profit in an untrammeled way—a procedure that would seem to guarantee the opposite result of chaos and disorder. In allowing the mechanism of personal struggle to run freely, good performers eliminate the less efficient and strike a dynamic balance among themselves. The "fallout," for society, yields a maximally ordered and prosperous economy (plus a hecatomb of dead businesses). The mechanism works by unbridled struggle for personal reward among individuals.

Schweber documents numerous sources in Darwin's wide readings for this central theme of political economy. In May 1840, for example, Darwin encountered the following passages in J. R. McCulloch's *Principles of Political Economy* (2nd edition of 1830—see Schweber, 1980, p. 268):

> Every individual is constantly exerting himself to find out the most advantageous methods of employing his capital and labor. It is true, that it is his own advantage, and not that of society, which he has in view; but a society being nothing more than a collection of individuals, it is plain that each, in steadily pursuing his own aggrandisement, is following that precise line of conduct which is most for the public advantage (p. 149). The true line of policy is to leave individuals to pursue their own interests in their own way, and never to lose sight of the maxim *pas trop gouverner* [not to govern too much]. It is by this spontaneous and unconstrained . . . effort of individuals to improve their conditions . . . and by them only, that nations become rich and powerful (p. 537).

The theory of natural selection lifts this entire explanatory structure, *virgo intacta,* and then applies the same causal scheme to nature—a tough customer who can bear the hecatomb of deaths required to produce the best polity as an epiphenomenon. Individual organisms engaged in the "struggle for existence" act as the analog of firms in competition. Reproductive success becomes the analog of profit—for, even more than in human economies, you truly cannot take it with you in nature.

Finally, continuing the analogy, Paley's dethronement follows the most radical path of supreme irony. For, in the ideal *laissez-faire* economy, all firms (purified in the unforgiving fires of competition) become sleek and well-designed, while the entire polity achieves optimal balance and coordination. But no laws explicitly operate to impose good design or overall balance by fiat—none at all. The struggle among firms represents the only causal process at work. Moreover, this cause operates at a lower level, and solely for the benefit of individual firms. Only as an incidental result, a side-consequence, does good design and overall balance emerge. Adam Smith, in coining one of the most memorable metaphors in our language, ascribed this process to the action of an "invisible hand." In the modern terms of hierarchy theory, we might say that overall order arises as an effect of upward causation from individual struggle. We may thus gain some clarity in definition, but we can't match the original prose. In his most famous words, Smith wrote in the *Wealth of Nations* (Book 4, Chapter 2): "He intends only his own gain, and he is in this, as in many other cases, led by an invisible hand to promote an end which was no part of his intention . . . I have never known much good done by those who affected to trade for the public good."

But Paley had assured us, in 500 closely-argued pages, that the analogous features of the natural world—good design of organisms and harmony of ecosystems—not only prove the existence of God, but also illustrate his nature, his personality, and his benevolence. In Darwin's importation of Adam Smith's argument, these features of nature become epiphenomena only, with no direct cause at all. The very observations that Paley had revered as the most glorious handiwork of God, the unquestionable proof of his benevolent concern, "just happen" as a consequence of causes operating at a lower level among struggling individuals. And, as the cruellest twist of all, this lower-level cause of pattern seems to suggest a moral reading exactly opposite to Paley's lofty hopes for the meaning of comprehensive order—for nature's individuals struggle for their own personal benefit, *and nothing else!* Paley's observations could not be faulted—organisms are well designed and ecosystems are harmonious. But his interpretations could not have been more askew—for these features do not arise as direct products of divine benevolence, but only as epiphenomena of an opposite process both in level of action and intent of outcome: individuals struggling for themselves alone.

I write this chapter with two aims in mind: first, to explicate the major sources and content of Darwin's argument; and second, to identify the truly essential claims of Darwinism, in order to separate them from a larger set of more peripheral assertions and misunderstandings—so that we can rank and evaluate the role of modern proposals and debates by the depth of their challenge to the central logic of our profession's orthodoxy. To fulfill this second goal, I try to identify a set of minimal commitments required of those who would call themselves "Darwinians." I argue that this minimal account features a set of three broad claims and their (quite extensive) corollaries. I then use this framework to organize the rest of this book, for I devote the historical chapters of this first part to pre- and post-Darwinian discussions of the three claims. Then, following a chapter on the construction of the Modern Synthesis as a Darwinian orthodoxy for the twentieth century, I revisit the three claims in the second part, this time by examining modern challenges to their exclusive sway.

By interpreting Darwin's radical theory as a response to Paley (actually an inversion), based on an importation of the central argument from Adam

Smith's *laissez-faire* economics, I believe that we achieve our best insight into the essential claims of Darwinism and natural selection. First, and foremost, we grasp the theoretical centrality of Darwin's conclusion that natural selection works through a struggle among *individual organisms* for reproductive success. Darwin's choice of levels, and his attempted restriction of causality to one level alone, then becomes neither capricious nor idiosyncratic, but, rather, central to the logic of an argument that renders the former "proof" of God's direct benevolence as an epiphenomenon of causal processes acting for apparently contrary reasons at a lower level. Second, we recognize the focal role of adaptation as the chief phenomenon requiring causal explanation—for good design had also set the central problem for English traditions in natural theology, the worldview that Darwin overturned by deriving the same result with an opposite mechanism.

These two principles—the operation of selection on struggling organisms as active agents, and the creativity of selection in constructing adaptive change—suffice to validate the theory in observational and microevolutionary expression. But Darwin nurtured far more ambitious goals (as the foregoing discussion of his methodology illustrates, see pages 97–116): he wished to promote natural selection, by extrapolation, as the preeminent source of evolutionary change at all scales and levels, from the origin of phyla to the ebb and flow of diversity through geological time. Thus, the third focal claim in the Darwinian tripod of essential postulates—the extrapolationist premise—holds that natural selection, working step by step at the organismic level, can construct the entire panoply of vast evolutionary change by cumulating its small increments through the fullness of geological time. With this third premise of extrapolation, Darwin transfers to biology the uniformitarian commitments that set the worldview of his guru, the geologist Charles Lyell.

THE FIRST THEME: THE ORGANISM AS THE AGENT OF SELECTION

Once the syllogistic core,* the "bare bones" mechanism of natural selection, has been elucidated, two major questions—the foci of the next two sections

*By the "syllogistic core" of natural selection ("the bare-bones argument"), I refer to the standard pedagogical presentation of the abstract mechanism of the theory as a set of three undeniable factual statements followed by the inference of natural selection (the fourth statement) as a logical entailment of the three facts, *viz:*

1. Superfecundity: all organisms produce more offspring than can possibly survive.
2. Variation: all organisms vary from other conspecifics, so that each individual bears distinguishing features.
3. Heredity: at least some of this variation will be inherited by offspring (whatever the mechanism of hereditary transition—a mystery to Darwin, but the argument only requires *that* heredity exist, not that its mode of action be known).
4. Natural selection: if we accept these foregoing three statements as factual (2 and 3 ranked as "folk wisdom" in Darwin's time and could scarcely be doubted; while Darwin took great pains to validate 1 in early chapters of the *Origin,* showing, for example, that even the most slowly reproducing of all animals, the African elephant, would soon fill the

of this chapter—must be resolved before we can understand the theory's basic operation: the issues of *agency* and *efficacy.* The basic historical context of selection—its discovery and utilization by Darwin as a refutation of Paleyan natural theology through the imported causal structure of Adam Smith's invisible hand—grants primacy to the issue of *agency* (therefore treated here in the first of two sections on fundamental attributes). The rebuttal of the former centerpiece of natural history—the belief that organic designs record the intentions of an omnipotent creative power—rests upon the radical demotion of agency to a much lower level, devoid of any prospect for conscious intent, or any "view" beyond the immediate and personal. So Darwin reduced the locus of agency to the lowest level that the science of his day could treat in a testable and operational way—*the organism* (for ignorance of the mechanism of heredity precluded any possibility of still further reduction to cellular or genic levels). The purely abstract statement of natural selection (the syllogistic core) leaves the key question of agency entirely unanswered. Selection may be in control, but on what does selection act? On the subcellular components of heredity? on organisms? on populations? on species? or on all these levels simultaneously?

Darwin grasped with great clarity what most of his contemporaries never understood at all—that the question of agency, or levels of selection, lies at the heart of evolutionary causation. And he provided, from the depth of his personal convictions, the roots of his central premises, and the logic of his complete argument, a forthright answer that overturned a conceptual world—natural selection works on *organisms* engaged in a struggle for personal success, as assessed by the differential production of surviving offspring.

We all know that Darwin emphasized selection at the organismal level, but many evolutionists do not appreciate the centrality of this claim within his theory; nor do they recognize how actively he pursued its defense and illustra-

continent if all offspring survived and reproduced), then the principle of natural selection follows by syllogistic logic. If only some offspring can survive (statement 1), then, on average (as a statistical phenomenon, not a guarantee for any particular organism), survivors will be those individuals that, by their fortuity of varying in directions most suited for adaptation to changing local environments, will leave more surviving offspring than other members of the population (statement 2). Since these offspring will inherit those favorable traits (statement 3), the average composition of the population will change in the direction of phenotypes favored in the altered local environment.

As Darwin did himself in the *Introduction* to the *Origin,* nearly all textbooks and college courses present the "bare bones" of natural selection in this fashion (I have done so in more than 30 years of teaching). The device works well, but does not permit a teacher to go beyond the simplest elucidation of selection as a genuine force that can produce adaptive change in a population. In other words, the syllogistic core only guarantees that selection can work. By itself, the core says nothing about the locus, the agency, the efficacy, or the range of selection in a domain—the sciences of natural history—where all assessments of meaning rest upon such claims about mode, strength, and relative frequency, once the prior judgment of mere existence has been validated. Thus, an elucidation of this "syllogistic core" can only rebut charges of hokum or incoherence at the foundation. An analysis of the three key issues of the Darwinian essence, the subject of the rest of this chapter, then engages the guts of natural history.

tion. To explicate this issue, we must reemphasize the roles of William Paley and Adam Smith in the genesis of Darwin's system—using Smith to overturn Paley.

Adaptation and the "creativity of natural selection," as discussed in the next section, represent Darwin's evolutionary translation of Paley's chief concern with excellence in organic design. But the substitution of natural selection for God as creative agent, while disruptive enough to Western traditions, does not express the primary feature of Darwin's radicalism. To find this root, we must pursue a different inquiry about the locus of selection. After all, selection might operate at the highest level of species, even communities of species, for the direct production of order and harmony. We would then, to be sure, need to abandon God's role as an immediate creator, but what a gentle dispensation compared with Darwin's actual proposal: for if the agency of selection stood so high, God could be reconceptualized as the loving instigator of the rules. And the rules, by working directly for organic harmony, would then embody all that Paley sought to illustrate about God's nature.

Darwin's inversion of Paley therefore required a primary postulate about the locus of selection. Selection operates *on organisms,* not on any higher collectivity. Selection works directly for the benefit of organisms only, and not for any larger harmony that might embody God's benevolent intent. Ironically, through the action of Adam Smith's invisible hand, such "higher harmony" may arise as an epiphenomenal result of a process with apparently opposite import—the struggle of individuals for personal success. Darwin's revolution demands that features of higher-level phenomenology be explained as effects of lower-level causality—in particular, that the struggle among organisms yield order and harmony in the polity of nature.

Darwin's theory therefore presents, as the primary underpinning for its radical import in philosophy, a "reductionist" account of broadest-scale phenomena to a single causal locus at a low level accessible to direct observation and experimental manipulation: the struggle for existence among organisms. Moreover, this claim for organismal agency expresses Darwin's chief desideratum at each focus of his theory—at the methodological pole for tractability, and at the theoretical pole for reversal of received wisdom. Darwinians have often acknowledged the *descriptively* hierarchical character of nature—and some commentators have been misled to view Darwinism, for this reason, as hierarchical in mechanism of causal action as well. But Darwinism tries to explain all these levels by *one locus of causality*—selection among organisms. Strict Darwinism is a one-level causal theory for rendering nature's hierarchical richness. The major critique of our times, in advocating hierarchical levels of *causality,* therefore poses a fundamental challenge to an essential postulate of Darwin's system.

Consider four aspects and demonstrations of Darwin's conviction about the exclusivity of selection on organisms:

EXPLICIT STATEMENTS. Darwin did not passively "back in" to a claim for the organismic level as a nearly exclusive locus. He knew exactly what he had asserted and why—and he said so over and over again. Statements that selection works "for the good of individuals" recur, almost in catechistic form, throughout the *Origin:* "Natural selection will never produce in a being anything injurious to itself, for natural selection acts solely by and for the good of each (p. 201) . . . Natural selection acts only by the accumulation of slight modifications of structure or instinct, each profitable to the individual under its conditions of life" (p. 233). Even if higher-level order arises as a result, the causal locus must be recognized as individual benefit: "In social animals [natural selection] will adapt the structure of each individual for the benefit of the community; if each in consequence profits by the selected change" (p. 87).

Several other statements illustrate Darwin's emphasis on struggle among organisms, and his desire to avoid all implication that members of a species might amalgamate to collectivities functioning as units of selection in themselves. He continually stresses, for example, that competition tends to be more intense among members of a single species than between individuals of different species—thus emphasizing the difficulty of forming such collectivities. Moreover, Darwin's development of the theory of sexual selection, and his increasing reliance on this mechanism as his views matured, also forestalls any temptation to advocate group selection—as no form of intraspecific competition can be more intense than struggle among similar individuals for personal success in mating.

RESPONSE TO CHALLENGES IN THE *ORIGIN*. The primary commitments of a theory lie best revealed, not so much in the initial exposition of their logic, but in their later employment to resolve difficulties and paradoxes. Darwin devotes much more of the *Origin* than most readers have generally realized to defending his single-level theory of selection on organisms.

Darwin structured the *Origin* as a trilogy—a first part (4 chapters) on the exposition of natural selection, a last section (5 chapters) on the evidence for evolution, and a middle series of 5 chapters on difficulties and responses. Two chapters of this middle section treat a broad range of potential challenges to the creativity of selection and its sequelae—chapter 9 on the geological record (to defend gradualism in the face of apparently contradictory evidence), and chapter 5 on laws of variation (to assert the isotropy of variation—see pp. 144–146). A third (chapter 6) treats general "Difficulties on Theory," mostly centered on gradualism.

Darwin therefore devotes only two of these five chapters, 7 on "Instinct" and 8 on "Hybridism," to specific difficulties—that is, to issues of sufficient import in his mind to merit such extensive and exclusive treatment. Readers have not always discerned the common thread between these two chapters—Darwin's defense of struggle among organisms as the locus of selection. The chapter on hybridism presents, as its central theme, an argument against species selection as the cause of sterility in interspecific crosses. The chapter on instinct treats the more general subject of selection's application to behavior as well as to form, but Darwin devotes more than half of this chapter to social insects, and he presents his primary examples of differentiation among castes and sterility of workers as threats to the principle of selection on organisms.

Darwin raises two separate challenges to natural selection for the case of sterile castes in the Hymenoptera. How, first of all, can sterile castes evolve adaptive differences from queens (and from each other), when individuals of these castes cannot reproduce? If non-reproductive organisms can evolve adaptations, mustn't selection then be working at the higher level of colonies as wholes? Darwin answers, by analogy to domesticated animals once again, that differential survival of non-reproductives may still record selection on fertile members of the population. After all, a breeder can improve the distinct form of castrated animals (raised for food or labor), by mating only those fertile individuals that sire non-reproductives with the most advantageous traits (as recognized by the correlation of selectable features in parents with different traits in their castrated offspring):

> I have such faith in the powers of selection, that I do not doubt that a breed of cattle, always yielding oxen with extraordinarily long horns, could be slowly formed by carefully watching which individual bulls and cows, when matched, produced oxen with the longest horns; and yet no one ox could ever have propagated its kind. Thus I believe it has been with social insects: a slight modification of structure, or instinct, correlated with the sterile condition of certain members of the community, has been advantageous to the community: consequently the fertile males and females of the same community flourished, and transmitted to their fertile offspring a tendency to produce sterile members having the same modification. And I believe that this process has been repeated, until that prodigious amount of difference between the fertile and sterile females of the same species has been produced, which we see in many social insects (p. 238).

(This quotation illustrates a common source of misunderstanding. Darwin does often use such phrases as "advantageous to the community." By our later linguistic conventions, such a statement might seem to signify a leaning to group selectionist arguments. But these conventions did not exist in Darwin's generation. Note how he uses this phrase only as a description of a result. Darwin identifies the causal process yielding this result, in this case and almost every other time he invokes such language, as selection on organisms, with benefit to communities as an epiphenomenal effect.)

The second challenge, the origin of sterility itself, seems more serious—for how could selection, especially in its necessarily gradualistic mode, promote the diminution of reproductive power in individuals? Clearly, the increasingly sterile workers cannot be promoting their own fitness; but their labor may aid their entire nest or hive. Must not the evolution of sterility therefore provide *prima facie* evidence for group selection, and for the failure of Darwin's argument about the exclusivity of selection on organisms?

Darwin does indeed refer to sterility as "one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory" (p. 236). He then offers an explanation, based exclusively on organismal selection and similar to his argument about differences in form between workers and reproductives (p. 236): "How the workers have been rendered sterile is a difficulty; but not much greater than that of any other striking modification of structure; for it can be shown that some insects and other articulate animals in a state of nature occasionally become sterile; and if such insects had been social, and it had been profitable to the community that a number should have been annually born capable of work, but incapable of procreation, I can see no very great difficulty in this being effected by natural selection."

The phrase "profitable to the community" seems to imply group selection but, as argued above, this modern interpretation need not reflect Darwin's intent. He did not, after all, know about haplodiploidy, different degrees of relatedness, or parent-offspring conflict. He does not argue here at the *locus classicus* for modern theories of group selection—altruism defined as the rendering of aid (at personal peril or expense) to non-relatives. Rather, he views the hive as a group of cooperating bodies, all tightly related and all generated by the queen. Anything beneficial to the hive fosters the reproductive success of the queen in ordinary natural selection upon her as an individual. The sterility of a worker does not differ in principle from the horns of an ox—a trait not found in parents, but produced by selection *on* parents. A queen that can generate more sterile workers might be favored by selection just as a breeder picks cows that yield castrated oxen with longer horns.

At most, one might hold that Darwin treats the entire hive as an entity—a statement about higher-level selection on the "superorganism" model (see D. S. Wilson and Sober, 1989, and Sober and Wilson, 1998). But here we meet an issue that must be regarded as more linguistic than substantive. Just as Janzen (1977) wishes to identify a clone as a single EI (for "evolutionary individual"), and to treat single bodies of rotifers or aphids as parts, so too might Darwin view the bodies in a hive as iterated organs of the whole. Nonetheless, selection acts on the queen as an individual reproducer. The determinants of her success undoubtedly include the form and function of her sterile offspring. Natural selection can "get at" a beaver through the form of its dam, or at a bird through the shape of its nest—and we do not talk about selection on the higher-level entity of organism plus product. Why should selection not "get at" the queen ant or bee through the conformation of the hive and the function of its members? (See Ruse, 1980, for a parallel argument, in agreement with mine, on Darwin's explanation of hymenopteran castes by organismic selection.)

Darwin takes up a different challenge to the exclusivity of organismic selection in the next chapter on "Hybridism." Crosses between varieties of a species are usually fertile, but crosses between species are generally sterile, or at least greatly impaired in fecundity. Under the guiding precepts of gradualism and uniformitarian methodology, we must view species as former varieties promoted by selection to the greater difference of true distinctness. But natural selection could not have built sterility in gradual degrees from an original fertility between parent and offspring—for sterility cannot benefit the hybrid individual: "On the theory of natural selection the case is especially important, inasmuch as the sterility of hybrids could not possibly be of any advantage to them, and therefore could not have been acquired by the continued preservation of successive profitable degrees of sterility. I hope, however, to be able to show that sterility is not a specially acquired or endowed quality but is incidental on other acquired differences" (p. 245).

Darwin considers two possible explanations. He constructs his entire chapter on hybridism as a defense of natural selection in its ordinary, organismal mode through the rejection of one explanation based on species selection and the advocacy of another rooted in selection on organisms with an interesting twist. Darwin admits that species selection, at first glance, seems to provide a simple and attractive solution: interspecific sterility must originate as an adaptation of species, built and promoted to preserve integrity by preventing introgression and subsequent dissolution. (A. R. Wallace strongly promoted this view. Darwin's firm rejection led to a protracted argument that strongly colored their relationship—see Kottler, 1985; Ruse, 1980.)

But Darwin rejected this explanation because he could not conceive how a species might act as an entity in this manner. Nonetheless, he could not possibly argue in response that hybrid sterility arose by direct selection for the trait itself. He therefore proposed a subtle argument, almost surely correct in our current judgment, for the origin of hybrid sterility as an incidental consequence of other differences established by organismal selection. A. R. Wallace, in striking contrast, remained so committed to viewing every natural phenomenon as a direct adaptation that he willingly roamed up and down among levels of selection (quite unaware of the logical difficulties thus entailed) until he found a locus that could support a direct adaptive explanation.

Darwin argued that any population, in diverging far enough from an ancestor to rank as a separate species, must undergo a series of changes (usually extensive), mediated by natural selection and leading to a set of unique features. Any two species will therefore come to differ in a series of traits directly built by natural selection. These disparities will probably render the two species sufficiently unlike, particularly in rates and modes of reproduction and development, that any hybrids between them will probably be stunted or infertile—not because selection acted directly for sterility, but only as an incidental effect of differences evolved by natural selection for other reasons. Although interspecific sterility cannot be *built* directly by selection for its advantages to organisms, this feature can and will originate *as a consequence* of ordinary selection on organisms. Darwin contrasts his proposal with Wallace's alternative based on direct adaptation *via* species selection:

> Now do these complex and singular rules indicate that species have been endowed with sterility simply to prevent their becoming confounded in nature? I think not. For why should the sterility be so extremely different in degree, when various species are crossed, all of which we must suppose it would be equally important to keep from blending together? . . . The foregoing rules and facts, on the other hand, appear to me clearly to indicate that the sterility both of first crosses and of hybrids is simply in-

cidental or dependent on unknown differences, chiefly in the reproductive systems, of the species which are crossed (p. 260).

In what I regard as Darwin's most brilliant use of his favorite device—argument by analogy—he then compares hybrid sterility with incompatibility in hybrid grafts (whereas grafts between varieties of the same species usually "take"). I find this comparison particularly compelling because we would not be tempted to construct an argument about species selection to explain the incompatibility of grafts—as no advantage for the integrity of species accrues thereby, especially since the "experiment" of grafting between two species almost never occurs in nature. Yet the logical structures of these two arguments about grafting and sterility, as well as the attendant results, share an identical logic—joining within species, and maintenance of separation between species, based upon incidental effects wrought by increasing degrees of difference evolved for other reasons:

> It will be advisable to explain a little more fully by an example what I mean by sterility being incidental on other differences, and not a specially endowed quality. As the capacity of one plant to be grafted or budded on another is so entirely unimportant for its welfare in a state of nature, I presume that no one will suppose that this capacity is a *specially* endowed quality, but will admit that it is incidental on differences in the laws of growth of the two plants . . . The facts by no means seem to me to indicate that the greater or lesser difficulty of either grafting or crossing together various species has been a special endowment; although in the case of crossing, the difficulty is as important for the endurance and stability of specific forms, as in the case of grafting it is unimportant for their welfare (pp. 261–263).

Darwin then drives the point home with a lovely prose flourish (and a memorable visual image!) in explicitly rejecting an appeal to supraorganismal selection. Nature knows no explicit principle of higher-level order. "There is no more reason to think that species have been specially endowed with various degrees of sterility to prevent them crossing and blending in nature, than to think that trees have been specially endowed with various and somewhat analogous degrees of difficulty in being grafted together in order to prevent them becoming inarched in our forests" (p. 276).

THE DEVELOPMENT OF DARWIN'S VIEWS ON ORGANISMIC SELECTION. If the first edition of the *Origin* only marked a waystation in fluctuation or degree of commitment, then Darwin's stand on organismic selection, however strongly expressed in this initiating volume, might not be deemed so central to his worldview. But Ruse (1980) has documented Darwin's continuing and increasing attention to this issue—particularly as he argued with Wallace (see also Kottler, 1985) about the principle of incidental effects to explain hybrid sterility as a side consequence of natural selection rather than a direct product of species selection. Ruse writes (1980, p. 620): "By the end of the decade [the 1860's] with respect to the animal and plant worlds, there was nothing implicit about Darwin's commitment to individual selection. He had looked long and hard at group selection and rejected it."

HOW DARWIN STRUGGLES WITH, AND "WALLS OFF," EXCEPTIONS. The exegetical literature on Darwin usually states that he allowed only two exceptions, in the entire corpus of his writing, to the exclusivity of natural selection on organisms—first, in permitting some form of group selection for the neuter castes of social insects, and second, for the origin of human moral behavior. I agree with Ruse (see point 2 just above) that Darwin did not stray from his orthodoxy for social insects, though some of his terminological choices invite misinterpretation today. For human morality, on the other hand, Darwin did throw in the towel after long struggle—for he could not render altruism towards non-relatives by organismal selection. Nonetheless, a theory often becomes sharpened (not destroyed or even much compromised in a world of relative frequencies) by specifying a domain of exceptions—provided that the exceptions be rare in occurrence, and peculiar in form. As humans, we surely have a legitimate personal interest in our moral behavior, but we cannot enshrine this property as occupying more than a tiny corner of nature (whatever its eventual impact upon our planet, and whatever our parochial concern for its uniqueness).

In the *Descent of Man,* Darwin presents his most interesting and extensive discussion of supraorganismal selection. As an example of his clarity on the issue of levels of selection, consider the following passage on why natural selection could not foster altruistic behavior within a tribe—with an explicit final statement that differential success among distinct tribes should not be called natural selection:

> But it may be asked, how within the limits of the same tribe did a large number of members first become endowed with these social and moral qualities, and how was the standard of excellence raised? It is extremely doubtful whether the offspring of the more sympathetic and benevolent parents, or of those who were the most faithful to their comrades, would be reared in greater number than the children of selfish and treacherous parents of the same tribe. He who was ready to sacrifice his life, as many a savage has been, rather than betray his comrades, would often leave no offspring to inherit his noble nature . . . Therefore it seems scarcely possible (bearing in mind that we are not here speaking of one tribe being victorious over another) that the number of men gifted with such virtues, or that the standard of their excellence, would be increased through natural selection, that is, by the survival of the fittest (1871, vol. 1, p. 163).

In the light of this conundrum, and as part of his resolution, Darwin does allow for selection at the tribal level defined as differential success of groups with more altruists: "It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an advancement in the standard of morality, and an increase in the number of well-endowed men will certainly give an immense advantage to one tribe over another" (1871, p. 166).

This passage has often been quoted, but without its surrounding context of contrary alternatives and restrictive caveats, as a clean example of Darwin's move to a higher level of selection when required. But such an interpretation seriously misrepresents Darwin's motives and logic. He did make the move, but only as one factor in a surrounding context of mitigation. I regard these mitigations and restrictions to hold the line of organismal selection (expressed in three distinct arguments, discussed below) as far more interesting than the move itself, for Darwin's extreme reluctance to address selection at any level other than the organismic lies so well exposed in the totality.

1. The *Descent,* as a whole, rests upon the strongest mode of argument for organismal selection. Darwin did not write a separate book on human evolution; his ideas (mostly speculative) on this subject occupy the first, and shorter, part of a two volume treatise entitled, in full: *The Descent of Man, and Selection in Relation to Sex.* In other words, Darwin wrote the *Descent* as an introduction to his general exposition of sexual selection. We might regard the two parts as oddly juxtaposed until we realize that many of Darwin's major arguments about human evolution—in the establishment of secondary sexual characters, and in differentiation among races, for example—invoke sexual selection by intraspecific competition, rather than ordinary natural selection as adaptation to external environments. As Ruse (1980) notes, Darwin viewed sexual selection as the strongest general argument against group selection, for its theme of relentless struggle in mating among members of a population guarantees that individualism must reign, largely by precluding the formation of alliances that higher-level selection could exploit. (Modern notions of sexual selection do envision the formation of such alliances, so the argument may strike us as incorrect today—but Darwin conceived sexual selection as a hyperindividual mode.)

2. Darwin does not present his argument for tribal selection as a happy solution to the problem of morality, but only as one potential factor among others. He also devises an argument based on organismal selection—in the form that would be called "reciprocal altruism" today: "As the reasoning powers and foresight of the members became improved, each man would soon learn from experience that if he aided his fellow-men, he would commonly receive aid in return. From this low motive he might acquire the habit of aiding his fellows" (1871, p. 163).

3. Darwin presents tribal selection as a peculiarity based on the uniqueness of human consciousness, and thus as a strictly circumscribed exception to the generality of organismal selection throughout living nature. As conscious beings, we become especially sensitive to the "praise and blame" of our fellows. If altruistic behavior gains a status as virtuous, then we might be persuaded—against our deeper biological drive for seeking personal advantage—to engage in such behaviors in order to foster praise or avoid calumny. In other words, a form of "cultural evolution," rooted in our unique level of consciousness, could overcome the behaviors driven by organismal selection, and could establish a preference for altruistic acts that might then serve as a basis for tribal selection. But such an argument cannot enjoy wide application in nature, as all other species lack this special mental mechanism for spreading abstract ideas against the thrust of natural selection:

> We may therefore conclude that primeval man, at a very remote period, would have been influenced by the praise and blame of his fellows. It is obvious, that the members of the same tribe would approve of conduct which appeared to them to be for the general good, and would reprobate that which appeared evil . . . A man who was not impelled by any deep, instinctive feeling, to sacrifice his life for the good of others, yet was roused to such actions by a sense of glory, would by his example excite the same wish for glory in other men, and would strengthen by exercise the noble feeling of admiration. He might thus do far more good to his tribe than by begetting offspring with a tendency to inherit his own high character (1871, p. 165).

Note also how Darwin, in this passage, explicitly limits within tribal boundaries the extent of such spread against organismal selection. If some form of group selection had to be acknowledged for a special case, Darwin sought to confine its operation to the smallest aggregation within the species—and then to let these small collectivities struggle with others in a minimal context of groupiness.

Thus, in permitting a true exception to organismal selection, Darwin's primary attitude exudes extreme reluctance—restriction to minimal groupiness, provision of other explanations in the ordinary organismal mode, limitation to a unique circumstance in a single species (human consciousness for the spread of an idea against the force of organismal selection), and placement within a more general argument for sexual selection, the strongest form of the orthodox mode.

In my researches for this book, I made a discovery that strongly supports this view of Darwin's attitude towards supraorganismal selection. I found that the traditional sources (Ruse, Kottler and others) did not identify Darwin's major, explicit struggle to contain an apparent need for higher-level selection, and to assert exclusivity for the organismal mode. He fought a far more important battle with himself on an issue well beyond particular problems raised by single taxa (sterility of worker castes or human morality): the explanation of the principle that he ranked second only to natural selection itself as a component of evolutionary theory—the "principle of divergence." (Evolutionists have not recognized this important component of Darwin's developing ideas about selection because he excised this discussion as he abstracted his longer work to compose the *Origin.* But the full version exists in the uncompleted manuscript of his intended larger work—edited and published by Stauffer, 1975, but not widely read by practicing biologists.) Moreover, in his long version, Darwin wrestles not with the lowest interdemic level of tribal selection, but with species selection itself. I will present a full exposition in Chapter 3 (pp. 224–250), but should mention for now that Darwin's tactic closely follows his argument about human morality, and therefore emphasizes his extreme reluctance to embrace supraorganismal selection, and his almost desperate effort to confine explanation to the organismal mode. The recognition that Darwin, despite such strong reluctance, could not avoid some role for species selection, builds a strong historical argument for the ineluctability of a hierarchical theory of selection. (I shall show in Chapter 3 that none of the few 19th century scientists who truly grasped the full range and subtlety of selectionist theory could avoid important roles for levels other than the organismic.)

As with the next topic of creativity for natural selection (pp. 137–159), the issue of levels in selection has resounded through the entire history of evolutionary theory, and continues to set a major part of the agenda for modern debate—as it must, for the subject lies (with only a few others) at the very heart of Darwinian logic. Wallace never comprehended the question of levels at all, as he searched for adaptation wherever he could find it, oblivious to any problems raised by the locus of its action; Kropotkin, in asserting mutual aid, never grasped the problem either; Weismann shared Darwin's insight about the problem's fundamental nature, but also came to understand, after a long and explicit intellectual struggle with his own strong reluctance, that exclusivity must yield to hierarchy (pp. 197–224).

In our generation, Wynne-Edwards (1962) riled an entire profession by defending the classical form of group selection as a generality, while Williams (1966) penned a powerful rebuttal, urging us all to toe the Darwinian line (see Chapter 7 for a full account). The classical ethologists invoked various forms of group selection (often by default); the sociobiologists proclaimed a revolution by reaction and return to the pure Darwinism of individual advantage. Dawkins (1976) attempted an even stronger reduction to exclusivity for genic selection, but his false argument rests on a confusion of bookkeeping with causality, and his own later work (1982) negates his original claim, though Dawkins seems unaware of his own contradictions (see Chapter 8). Supporters of hierarchy theory—I am one, and this is a partisan book—are revising Darwinism into a multilevel theory of selection.

This issue will not go away, and must excite both interest and passion. Nothing else lies so close to the raw nerve of Darwin's radicalism. The exclusivity of organismal selection, after all, provides the punch line that allowed the vision of Adam Smith to destroy the explicit beauty and harmony of William Paley's world.

Viewed in this light, the *Origin*'s very few statements about solace become particularly revealing. Darwin had just overturned a system that provided the philosophical basis of human comfort for millennia. What could he supply in return, as we continue to yearn for solace in this vale of tears? One might be tempted to read the few Darwinian statements about solace as peculiar, exceptional, even "soft" or illogical. But we should note another feature of these statements as well: they yield no ground whatever on the key issue of organismal struggle. Solace must be found in other guises; the linchpin of selection as struggle among organisms cannot be compromised.

Darwin offers two sources for solace. First, the struggle, however fierce, usually brings no pain or distress to organisms (humans, with their intrusive consciousness, have introduced a tragic exception into nature). "When we reflect on this struggle, we may console ourselves with the full belief, that the war of nature is not incessant, that no fear is felt, that death is generally prompt, and that the vigorous, the healthy, and the happy survive and multiply" (p. 79).

Second, this struggle does lead to general improvement, if only as an epiphenomenon, and whatever the cost: "As natural selection works solely by and for the good of each being, all corporeal and mental endowments will tend to progress towards perfection" (p. 489). Darwin could never compromise his central logic; for even this "softest" of all his statements explicitly asserts that selection can only work on organisms—"for the good of each being." And why not? The logic of organismal struggle includes both fierce beauty and empirical adequacy—whatever the psychic costs. And, since roses by other names smell just as sweet, then beauty, even as an epiphenomenon, becomes no less pleasing, and no less a balm for the soul.

THE SECOND THEME: NATURAL SELECTION AS A CREATIVE FORCE

The following kind of incident has occurred over and over again, ever since Darwin. An evolutionist, browsing through some pre-Darwinian tome in natural history, comes upon a description of natural selection. Aha, he says; I have found something important, a proof that Darwin wasn't original. Perhaps I have even discovered a source of direct and nefarious pilfering by Darwin! In the most notorious of these claims, the great anthropologist and writer Loren Eiseley thought that he had detected such an anticipation in the writings of Edward Blyth. Eiseley laboriously worked through the evidence that Darwin had read (and used) Blyth's work and, making a crucial etymological mistake along the way (Gould, 1987c), finally charged that Darwin may have pinched the central idea for his theory from Blyth. He published his case in a long article (Eiseley, 1959), later expanded by his executors into a posthumous volume entitled "Darwin and the Mysterious Mr. X" (1979).

Yes, Blyth had discussed natural selection, but Eiseley didn't realize—thus committing the usual and fateful error in this common line of argument—that all good biologists did so in the generations before Darwin. Natural selection ranked as a standard item in biological discourse—but with a crucial difference from Darwin's version: the usual interpretation invoked natural selection as part of a larger argument for created permanency.* Natural selection,

*Only two exceptions have been noted to this generality—both in the domain of anomalies that prove the rule. The Scottish fruit grower Patrick Matthew (in 1831) and the Scottish-American physician William Charles Wells (in 1813, published in 1818) spoke of natural selection as a positive force for evolutionary change, but neither recognized the significance of his speculation. Matthew buried his views in the appendix to a work entitled "Naval Timber and Arboriculture"; Wells published his conjecture in a concluding section, treating the origin of human races, to a paper on the medical case of a piebald woman. He presented this paper to the Royal Society in 1813, but only published it as he lay dying in 1818—as a subsidiary to his two famous essays on the origin of dew, and on why we see but one image with two eyes.

Matthew, still alive and vigorously kicking when Darwin published the *Origin,* wrote to express his frustration at Darwin's non-citation. Darwin offered some diplomatic palliation in the historical introduction added to later editions of the *Origin,* while professing, with ample justice, that he had meant no malice, but had simply never encountered Matthew's totally forgotten and inauspiciously located speculation. He responded to Matthew's ire in the *Gardener's Chronicle* for April 21, 1860: "I freely acknowledge that Mr. Matthew has anticipated by many years the explanation which I have offered of the origin of species, under the name of natural selection. I think that no one will feel surprised that neither I, nor apparently any other naturalist, has heard of Mr. Matthew's views, considering how briefly they are given, and that they appeared in the Appendix to a work on Naval Timber and Arboriculture."

Wells' article is particularly intriguing, if only for an antiquarian footnote, in the context of this book's focus on supraorganismal levels of selection. Although Wells has often been cited as a precursor, very few citationists have read his paper, and have therefore simply assumed that he spoke of natural selection by Darwin's route of advantages to individuals within populations. In fact, as I discovered (Gould, 1983a), Wells attributes racial differentiation in skin color to group selection among populations.

I do not wish to make overly much of this point, as "precursoritis" is the bane of historiography; yet I am tickled by the ironic tidbit, in the light of later orthodoxy, that the first formulation of natural selection went forward in the supraorganismic mode. The point should not be overstressed, if only because Wells reached this alternative by the fallacious argument that favorable variants could not spread within populations. Echoing Jenkins' later criticism of Darwin, Wells held that blending inheritance prevents the transformation of populations from within because advantageous variants "quickly disappear from the intermarriages of different families. Thus, if a very tall man be produced, he very commonly marries a woman much less than himself, and their progeny scarcely differs in size from their countrymen" (1818, pp. 434–435).

Populations must therefore be transformed by fortuitous spread and propagation within small and isolated groups: "In districts, however, of very small extent, and having little intercourse with other countries, an accidental difference in the appearance of the inhabitants will often descend to their late posterity" (p. 435). Change may then occur within an entire species by group selection among these differentiated populations:

> Of the accidental varieties of man, which would occur among the first few and scattered inhabitants of the middle regions of Africa, some would be better fitted than the others to bear the diseases of the country. This race would consequently multiply, while the others would decrease, not only from their inability to sustain the attacks of disease, but from their incapacity of contending with their more vigorous neighbors. The color of this vigorous race I take for granted . . . would be dark. But the same disposition to form varieties still existing, a darker and a darker race would in the course of time occur, and as the darkest would be the best fitted for the climate, this would at length become the most prevalent, if not the only race, in the particular country in which it had originated (pp. 435–436).

Note Wells' unquestioned assumption that our original color must have been white, and that dark skin could only arise as a modification of the type. As a final interesting footnote, Wells denied (probably wrongly) that dark skin could be adaptive in itself, and argued for its establishment in Africa as a result of noncausal correlation with unknown physiological mechanisms for protection against tropical disease. Thus, Wells presents an "internalist" explanation based on what Darwin would later call "correlation of growth." With this argument about channels, and his basic claim for group selection, Wells' departure from Darwin's later preferences lie very much in the spirit of modern critiques, though for reasons that we would now reject (as if our anachronistic judgment mattered).

in this negative formulation, acted only to preserve the type, constant and inviolate, by eliminating extreme variants and unfit individuals who threatened to degrade the essence of created form. Paley himself presents the following variant of this argument, doing so to refute (in later pages) a claim that modern species preserve the good designs winnowed from a much broader range of initial creations after natural selection had eliminated the less viable forms: "The hypothesis teaches, that every possible variety of being hath, at one time or other, found its way into existence (by what cause or in what manner is not said), and that those which were badly formed, perished" (Paley, 1803, pp. 70–71).

Darwin's theory therefore cannot be equated with the simple claim that natural selection operates. Nearly all his colleagues and predecessors accepted this postulate. Darwin, in his characteristic and radical way, grasped that this standard mechanism for preserving the type could be inverted, and then converted into the primary cause of evolutionary *change.* Natural selection obviously lies at the center of Darwin's theory, but we must recognize, as Darwin's second key postulate, the claim that natural selection acts as *the creative force* of evolutionary *change.* The essence of Darwinism cannot reside in the mere observation that natural selection operates—for everyone had long accepted a *negative* role for natural selection in eliminating the unfit and preserving the type.

We have lost this context and distinction today, and our current perspective often hampers an understanding of the late 19th century literature and its preoccupations. Anyone who has read deeply in this literature knows that no argument inspired more discussion, while no Darwinian claim seemed more vulnerable to critics, than the proposition that natural selection should be viewed as a *positive* force, and therefore as the primary cause of evolutionary change. The "creativity of natural selection"—the phrase generally used in Darwin's time as a shorthand description of the problem—set the cardinal subject for debate about evolutionary mechanisms during Darwin's lifetime and throughout the late 19th century.

Non-Darwinian evolutionists did not deny the reality, or the operationality, of natural selection as a genuine cause stated in the most basic or abstract manner—in the form that I called the "syllogistic core" on page 125 (still used as the standard pedagogical device for teaching the "bare bones" logic of Darwinism in general and introductory college courses). They held, rather, that natural selection, as a headsman or executioner, could only eliminate the unfit, while some other cause must play the positive role of constructing the fit.

For example, Charles Lyell—whom Darwin convinced about the factuality of evolution but who never (much to Darwin's sadness and frustration) accepted the mechanism of natural selection—admitted that he had become stymied on the issue of creativity. He could understand, he wrote in his fifth journal on the "species question" in March, 1860, how natural selection might act like two members of the "Hindoo Triad"—like Vishnu the preserver and Siva the destroyer, but he simply could not grasp how such a force could also work like Brahma, the creator (in Wilson, 1970, p. 369).

E. D. Cope, chief American critic and exponent of neo-Lamarckism, chose a sardonic title to highlight Darwin's supposedly fatal weakness in claiming a creative role for natural selection. He called his book *The Origin of the Fittest* (1887)—a parody on Darwin's "survival of the fittest," and a motto for what natural selection could *not* accomplish. Cope wrote: "The doctrines of 'selection' and 'survival' plainly do not reach the kernel of evolution, which is, as I have long since pointed out, the question of 'the origin of the fittest.' This omission of this problem from the discussion of evolution is to leave Hamlet out of the play to which he has given the name. The law by which structures originate is one thing; those by which they are restricted, directed, or destroyed, is another thing" (1887, p. 226).

We can understand the trouble that Darwin's contemporaries experienced in comprehending how selection could work as a creative force when we confront the central paradox of Darwin's crucial argument: natural selection makes nothing; it can only choose among variants originating by other means. How then can selection possibly be conceived as a "progressive," or "creative," or "positive" force?

In resolving this paradox, Darwin recognized his logical need, within the basic structure of his argument, to explicate the three main requirements and implications of an argument for selection's creativity: (1) the nature of variation; (2) the rate and continuity of change; (3) the meaning of adaptation. This interrelated set of assertions promotes natural selection from mere existence as a genuine, but secondary and negative, mechanism to domination as the primary cause of evolutionary change and pattern. This set of defenses for selection's creativity therefore ranks as the second of three essential postulates, or "minimal commitments" of Darwinian logic.

As the epitome of his own solution, Darwin admitted that his favored mechanism "made" nothing, but held that natural selection must be deemed "creative" (in any acceptable vernacular sense of the term) if its focal action of differential preservation and death could be construed as the primary cause for imparting direction to the process of evolutionary change. Darwin reasoned that natural selection can only play such a role if evolution obeys two crucial conditions: (1) if nothing about the provision of raw materials—that is, the sources of variation—imparts direction to evolutionary change; and (2) if change occurs by a long and insensible series of intermediary steps, each superintended by natural selection—so that "creativity" or "direction" can arise by the summation of increments.

Under these provisos, variation becomes raw material only—an isotropic sphere of potential about the modal form of a species. Natural selection, by superintending the differential preservation of a biassed region from this sphere in each generation, and by summing up (over countless repetitions) the tiny changes thus produced in each episode, can manufacture substantial, directional change. What else but natural selection could be called "creative," or direction-giving, in such a process? As long as variation only supplies raw material; as long as change accretes in an insensibly gradual manner; and as long as the reproductive advantages of certain individuals provide the statistical source of change; then natural selection must be construed as the directional cause of evolutionary modification.

These conditions are stringent; and they cannot be construed as vague, unconstraining, or too far in the distance to matter. In fact, I would argue that the single most brilliant (and daring) stroke in Darwin's entire theory lay in his willingness to assert a set of precise and stringent requirements for variation—all in complete ignorance of the actual mechanics of heredity. Darwin understood that if any of these claims failed, natural selection could not be a creative force, and the theory of natural selection would collapse. We pay our highest tribute to the power of natural selection in recognizing how Darwin used the theory to deduce a set of necessary properties for variation, well before science understood the mechanism of heredity—and in noting that these properties then turned out to be both basically correct and also entailed by the causes later discovered!

The requirements for variation

In order to act as raw material only, variation must walk a tightrope between two unacceptable alternatives. First and foremost, variation must exist in sufficient amounts, for natural selection can make nothing, and must rely upon the bounty thus provided; but variation must not be too florid or showy either, lest it become the creative agent of change all by itself. Variation, in short, must be copious, small in extent, and undirected. A full taxonomy of non-Darwinian evolutionary theories may be elaborated by their denials of one or more of these central assumptions.

COPIOUS. Since natural selection makes nothing and can only work with raw material presented to its stringent review, variation must be generated in copious and dependable amounts (especially given the hecatomb of selective deaths accompanying the establishment of each favorable feature). Darwin's scenario for selective modification always includes the postulate, usually stated explicitly, that all structures vary, and can therefore evolve. He argues, for example, that if a short beak were favored on a full-grown pigeon "for the bird's own advantage" (p. 87), then selection would also work within the egg for sufficient beak strength to break the shell despite diminution in overall size of the beak—unless evolution followed an alternate route of selection for thinner shells, "the thickness of the shell being known to vary like any other structure" (p. 87).

Darwin's faith in the copiousness of variation can be gauged most clearly by his response to the two most serious potential challenges of his time. First, he acknowledges the folk wisdom that some domestic species (dogs, for example) have developed great variety, while others (cats, for example) differ far less among populations. If these universally recognized distinctions arise as consequences of differences in the intrinsic capacity of species to vary, then Darwin's key postulate of copiousness would be compromised—for failure of sufficient raw material would then be setting a primary limit upon the rate and style of evolutionary change, and selection would not occupy the driver's seat.

Darwin responds by denying this interpretation, and arguing that differing intensities of selection, rather than intrinsically distinct capacities for variation, generally cause the greater or lesser differentiation observed among domestic species. I regard this argument as among the most forced and uncomfortable in the *Origin*—a rare example of Darwinian special pleading. But Darwin realizes the centrality of copiousness to his argument for the creativity of natural selection, and he must therefore face the issue directly:

> Although I do not doubt that some domestic animals vary less than others, yet the rarity or absence of distinct breeds of the cat, the donkey, peacock, goose, etc., may be attributed in main part to selection not having been brought into play: in cats, from the difficulty in pairing them; in donkeys, from only a few being kept by poor people and little attention paid to their breeding; in peacocks, from not being very easily reared and a large stock not kept; in geese, from being valuable only for two purposes, food and feathers, and more especially from no pleasure having been felt in the display of distinct breeds (p. 42).

Second, copiousness must also be asserted in the face of a powerful argument about limits to variation following modal departure from "type." To use Fleeming Jenkin's (1867) famous analogy: a species may be compared to a rigid sphere, with modal morphology of individuals at the center, and limits to variation defined by the surface. So long as individuals lie near the center, variation will be copious in all directions. But if selection brings the mode to the surface, then further variation in the same direction will cease—and evolution will be stymied by an intrinsic limitation upon raw material, even when selection would favor further movement. Evolution, in other words, might consume its own fuel and bring itself to an eventual halt thereby. This potential refutation stood out as especially serious—not only for threatening the creativity of natural selection, but also for challenging the validity of uniformitarian extrapolation as a methodology of research. Darwin responded, as required by logical necessity, that such limits do not exist, and that new spheres of equal radius can be reconstituted around new modes: "No case is on record of a variable being ceasing to be variable under cultivation. Our oldest cultivated plants, such as wheat, still often yield new varieties: our oldest domesticated animals are still capable of rapid improvement or modification" (p. 8).

I cannot here provide a full history for the subsequent odysseys of these key Darwinian precepts. But a few cursory comments indicate how these claims have remained central and contentious throughout the history of post-Darwinian thought, and how they continue to underlie important debates within Darwinism today.

The argument about copiousness, particularly as expressed in the claim for limits to further variability after intense selection, dogged the 19th century literature and emerged as a key issue in the biometrician *vs.* Mendelian debates early in our century (see Provine, 1971). Castle (1916, 1919) pursued his famous experiments on selection in hooded rats in order to test the hypothesis of limits imposed by variability upon continued change. One of the most appealing features of Mendelism—and a strong reason for acceptance following its "rediscovery" in 1900—lay in the argument that mutation could restore variation "used up" by selection. Nor has the issue abated today. In another form, copiousness underlay the great debate between Dobzhansky and Muller (see Lewontin, 1974)—the classical *vs.* the balance view in Dobzhansky's terminology. Kimura's (1963, 1983) modern theory of neutralism may be invoked to acknowledge the fact of copiousness while avoiding the pitfalls of genetic load—and therefore becomes "neoclassical" in Lewontin's terminology.

SMALL IN EXTENT. If the variations that yielded evolutionary change were large—producing new major features, or even new taxa in a single step—then natural selection would not disappear as an evolutionary force. Selection would still function in an auxiliary and negative role as headsman—to heap up the hecatomb of the unfit, permit the new saltation to spread among organisms in subsequent generations, and eventually to take over the population. But Darwinism, as a theory of evolutionary change, would perish—for selection would become both subsidiary and negative, and variation itself would emerge as the primary, and truly creative, force of evolution, the source of occasionally lucky saltation. For this reason, and quite properly, saltationist (or macromutational) theories have always been viewed as anti-Darwinian—despite the protestations of de Vries (see Chapter 5), who tried to retain the Darwinian label for his continued support of selection as a negative force. The unthinking, knee-jerk response of many orthodox Darwinians whenever they hear the word "rapid" or the name "Goldschmidt," testifies to the conceptual power of saltation as a cardinal danger to an entire theoretical edifice.

Darwin held firmly to the credo of small-scale variability as raw material because both poles of his great accomplishment required this proviso. At the methodological pole of using the present and palpable as a basis, by extrapolation, for all evolution, Darwin longed to locate the source of all change in the most ordinary and pervasive phenomenon of small-scale variation among members of a population—Lyell's fundamental uniformitarian principle, recast for biology, that all scales of history must be explained by currently observable causes acting within their current ranges of magnitude and intensity. "I believe mere individual differences suffice for the work," Darwin writes (p. 102). At the theoretical pole, natural selection can only operate in a creative manner if its cumulating force builds adaptation step by step from an isotropic pool of small-scale variability. If the primary source of evolutionary innovation must be sought in the occasional luck of fortuitous saltations, then internal forces of variation become the creative agents of change, and natural selection can only help to eliminate the unfit after the fit arise by some other process. Darwin, again using domestication as an analog, passionately defends the central role of variation so small as to pass beneath nearly everyone's notice (p. 32):

> If selection consisted merely in separating some very distinct variety, and breeding from it, the principle would be so obvious as hardly to be worth notice; but its importance consists in the great effect produced by the accumulation in one direction, during successive generations, of differences absolutely inappreciable by an uneducated eye—differences which I for one have vainly attempted to appreciate. Not one man in a thousand has accuracy of eye and judgment sufficient to become an eminent breeder. If gifted with these qualities, and he studies his subject for years, and devotes his lifetime to it with indomitable perseverance, he will succeed, and may make great improvements; if he wants [that is, lacks] any of these qualities, he will assuredly fail.

Saltational variation has always served as a rallying point for non-Darwinian evolutionary argument (see Chapters 4 and 5 for a full discussion). T. H. Huxley centered his own doubts about natural selection firmly upon Darwin's preference for change by insensible steps. Bateson (1894), in developing the concept of homeosis, and D'Arcy Thompson (1917), in his ideas on noncontinuity in certain geometrical transformations, advanced saltation as an explicitly anti-Darwinian argument. The early mutationists read Mendel as a warrant for discontinuous change, and a disproof of strict Darwinism as espoused by the "biometricians." Goldschmidt (1940; see Gould, 1982a) joined some interesting views on developmental discontinuity to an untenable genetic theory, all the better to espouse a saltationist view that made him the chief whipping boy of the Modern Synthesis.

Reciprocally, Darwinians countered with strong and explicit support. R. A. Fisher began his great book (1930) by rooting a defense of Darwin in a linkage of copiousness with small-scale variation—specifically, by arguing for an inverse correlation of frequency and effect, and then claiming that variations of large effect therefore become too rare to serve as evolution's raw material.

UNDIRECTED. Textbooks of evolution still often refer to variation as "random." We all recognize this designation as a misnomer, but continue to use the phrase by force of habit. Darwinians have never argued for "random" mutation in the restricted and technical sense of "equally likely in all directions," as in tossing a die. But our sloppy use of "random" (see Eble, 1999) does capture, at least in a vernacular sense, the essence of the important claim that we do wish to convey—namely, that variation must be *unrelated to the direction of evolutionary change;* or, more strongly, that nothing about the process of creating raw material biases the pathway of subsequent change in adaptive directions. This fundamental postulate gives Darwinism its "two step" character, the "chance" and "necessity" of Monod's famous formulation—the separation of a source of raw material (mutation, recombination, etc.) from a force of change (natural selection).

In a sense, the specter of directed variability threatens Darwinism even more seriously than any putative failure of the other two postulates. Insufficient variation stalls natural selection; saltation deprives selection of a creative role but still calls upon Darwin's mechanism as a negative force. With directed variation, however, natural selection can be bypassed entirely. If adaptive pressures automatically trigger heritable variation in favored directions, then trends can proceed under regimes of random mortality; natural selection, acting as a negative force, can, at most, accelerate the change.

Lamarckism (defined in the modern sense of "soft" heredity) represents the quintessential theory of directed variability. Variation arises with intrinsic bias in adaptive directions either because organisms respond creatively to "felt needs" and pass acquired features directly to their offspring, or because environments induce heritable variation along favored pathways. Other directional theories differ in viewing intrinsic variation as unrelated to adaptation, but still capable of overwhelming any counteracting selection, and therefore setting the path of evolutionary change. Historically important theories in this mode include various notions of orthogenesis that postulate the inevitable origin of hypertrophied and inadaptive structures; and theories of "racial life cycles" that envision an ineluctably aging protoplasm doomed to extinction despite any effort at "rejuvenation" by natural selection. (I shall discuss such ideas in Chapter 5.)

Darwin clearly understood the threat of directed variability to his cardinal postulate of creativity for natural selection. He explicitly restricted the sources of variation to auxiliary roles as providers of raw material, and granted all power over the direction of evolutionary change to natural selection. Drawing his customary analogy to artificial selection, Darwin writes (p. 30): "The key is man's power of accumulative selection: nature gives successive variations; man adds them up in certain directions useful to him. In this sense he may be said to make for himself useful breeds."

Darwin also understood that variation could not be construed as truly random in the mathematical sense—and that history did not imply or require this strict form of randomness. He recognized biased tendencies to certain states of variation, particularly reversions toward ancestral features. But he viewed such tendencies as weak and easily overcome by selection. Thus, by the proper criterion of relative power and frequency, selection controls the direction of change: "When under nature the conditions of life do change, variations and reversions of character probably do occur; but natural selection, as will hereafter be explained, will determine how far the new characters thus arising shall be preserved" (p. 15).

We may summarize Darwin's third requirement for variation under the rubric of *isotropy,* a common term in mineralogy (and other sciences) for the concept of a structure or system that exhibits no preferred pathway as a consequence of construction with equal properties in all directions. Darwinian variation must be *copious in amount, small in extent, and effectively isotropic.* (Think again of a dynamic sphere, with all radii accessible. The modal form lies at the center and may move by selection along any radius. At any new location, a sphere of comparable size may be reconstituted about the altered modal form.) Only under these stringent conditions can natural selection—a force that makes nothing directly, and must rely upon variation for all raw material—be legitimately regarded as creative.

Gradualism

Darwinism, like most comprehensive and complex concepts, defies easy definition. Darwinism cannot be analogized to an object, like the Parthenon, with a clear criterion of membership for each potential slab (whether now resident in the British Museum or in Athens). Moreover, the various propositions of Darwinism cannot be regarded as either independent or of equal force. Darwinism cannot be construed as a deductive system, with some defining axioms and a set of logical entailments tied together like a classical proof in plane geometry. But neither can Darwinism be viewed as a set of separate stones, all of similar size, and each ejectable from a bag without great disturbance to the others.

As discussed at length in Chapter 1 (pp. 12–24), I view the conceptual structure of Darwinism much like the metaphor that Darwin himself first used (see Barrett *et al.*, 1987) for depicting evolution (in the "B Notebook" on transmutation kept during the 1830's)—the "coral of life" (later superseded, in Chapter 4 of the *Origin*, and in other writings, by the tree of life). The central trunk (the theory of natural selection) cannot be severed, or the creature dies (see Fig. 1-4, p. 18). The first-order branches are also so fundamental that any severing of a complete branch converts the theory into something essentially different that must be newly named. (I have suggested that the theory of natural selection includes three major branches, discussed in sections B-D of this subchapter.) Each major branch then divides into smaller sub-branches. (In the present section C, I argue that the second major branch, the claim for "creativity of natural selection," divides into three important sub-branches of "requirements for variation," "gradualism," and "the adaptationist program.")

As further argued in Chapter 1, this model allows us to address the important question of dispensability. At some level above the base, we may excise a sub-branch, deny its premises, and still consider ourselves Darwinians. I envision the central trunk and first-order branches as indispensable. Along the continuum from necessary to avoidable, we may begin to make selective negations at the level of sub-branches, but not without severe stress to the entire structure. Thus, T. H. Huxley could oppose gradualism and still consider himself a supporter of natural selection (though his approbation remained ambiguous and indifferent at best, and his role as "Darwin's bulldog" rested upon his defense of evolution itself, not his explication of natural selection). And a modern developmental saltationist might call himself a Darwinian, though not without an array of "buts" and qualifications.

One other feature of the model requires explicit commentary. I have chosen a coral in preference to the more conventional tree, because the branches of many corals form a network by lateral anastomoses (while each limb of a tree stands free, and may be chopped off without necessarily affecting the others).

The premises of Darwin's theory (the branches and sub-branches of the coral model) are organically connected. One might be able to excise a single branch without killing the others, but some pain and readjustment will certainly be felt throughout the entire structure. The three sub-branches of the "creativity" limb, for example, are strongly conjoined in this manner. If variation forms an isotropic sphere (the expectation of sub-branch one), then change by natural selection can only occur a short step at a time (as predicted by the gradualism of sub-branch two). And if variation imposes no constraint upon the direction of change (an inference from isotropy), then natural selection works freely and adaptation prevails (as required by sub-branch three).

Finally, as so often emphasized throughout this book, we must recognize and embrace natural history as a science of relative frequencies. None of these basic Darwinian premises operates without exception throughout nature. Darwin insisted*—explicitly and vociferously—that natural selection only enjoyed a predominant relative frequency, not exclusivity: "the main but not exclusive means of modification," as he writes at the close of the introduction (p. 6). Darwin then extended his claim for a predominant relative frequency, but not for exclusivity, to all other sub-branches of his essential argument as well. Failure of raw material might occasionally explain a puzzling absence of evolutionary modification—but lack of selective pressure for change surely represents the more likely explanation for stasis by far. Substantial change might occur as a very rare event, but *most* alteration must be insensible, even on geological scales: "We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages" (p. 84).

Understanding Darwin's mode of justification by relative frequency be-

*Charles Darwin surely ranks as the most genial of history's geniuses—possessing none of those bristling quirks and arrogances that usually mark the type. Yet, one subject invariably aroused his closest approach to fury—the straw-man claim, so often advanced by his adversaries, that he regarded natural selection as an exclusive mode of change in evolution. Darwin, who understood so well that natural history works by relative frequency, explicitly denied exclusivity and argued only for dominance. So frustrated did he become at the almost willful misunderstanding of a point so clearly made, that he added this rueful line to the 6th edition of the *Origin* (1872b, p. 395): "As my conclusions have lately been much misrepresented, and it has been stated that I attribute the modification of species exclusively to natural selection, I may be permitted to remark that in the first edition of this work, and subsequently, I placed in a most conspicuous position—namely at the close of the Introduction—the following words: 'I am convinced that natural selection has been the main, but not the exclusive means of modification.' This has been of no avail. Great is the power of steady misinterpretation."

Darwin's good friend G. J. Romanes, author of a famous essay on Darwin's pluralism vs. the panselectionism of Wallace and Weismann, wrote of this statement (1900, p. 5): "In the whole range of Darwin's writings there cannot be found a passage so strongly worded as this: it presents the only note of bitterness in all the thousands of pages which he has published." But Darwin wrote other bristling statements on the same sensitive subject. In 1880, for example, he castigated Sir Wyville Thomson for caricaturing him as a panselectionist: "This is a standard of criticism not uncommonly reached by theologians and metaphysicians when they write on scientific subjects, but is something new as coming from a naturalist . . . Can Sir Wyville Thomson name any one who has said that the evolution of species depends only on natural selection?" (1880b, p. 32).

comes vitally important because selective quotation represents the most common error made by evolutionists in interpreting his work and theory. The *Origin*, as a volume of single authorship, maintains a stronger plot line and features fewer inconsistencies than the Bible; but Darwin and the Good Lord do share the common trait of saying something about nearly everything. Wrenched from context and divorced from a crucial assessment by relative frequency, a Darwinian statement can be found to support almost any position, even the most un-Darwinian.

Since Darwin prevails as the patron saint of our profession, and since everyone wants such a preeminent authority on his side, a lamentable tradition has arisen for appropriating single Darwinian statements as defenses for particular views that either bear no relation to Darwin's own concerns, or that even confute the general tenor of his work. Thus, for example, Darwin wrote extensively about variational constraint, and he maintained great interest in this topic (see Chapter 4). But the logic of his work entails adaptive control of evolutionary change and isotropy of variation as generally prevalent—and Darwin ultimately comes down (as he must) on the side of these necessary underpinnings for natural selection. Proper textual analysis requires that general tenor, not selective statement, be presented. Two basic procedural modes, each with distinctive criteria, set the framework for such textual analysis. The empirical mode makes its judgments of importance by relative frequency and interconnectedness of statements. Meanwhile, and simultaneously, the logical mode employs theoretical consistency as an arbiter for judging the validity and power of the structure of argument. We revere Darwin because he unfailingly manifested the two key traits of brilliance and honesty. He knew where his arguments led, and he followed them relentlessly, however unpleasant the consequences. We do him the greatest possible disservice when we approach his work as a superficial grazer, searching for some particular item of personal sustenance, while ignoring the beauty and power of *general tenor and logical entailment*.

I raise this point here because abuse of selective quotation has been particularly notable in discussions of Darwin's views on gradualism. Of course Darwin acknowledged great variation in rates of change, and even episodes of rapidity that might be labelled catastrophic (at least on a local scale); for how could such an excellent naturalist deny nature's multifariousness on such a key issue as *the* character of change itself? But these occasional statements do not make Darwin the godfather of punctuated equilibrium, or a cryptic supporter of saltation (as de Vries actually claimed, thus earning a unique and official rebuke from the organizers of the Darwinian centenary celebration at Cambridge—see p. 416).

Gradualism may represent the most central conviction residing both within and behind all Darwin's thought. Gradualism far antedates natural selection among his guiding concerns, and casts a far wider net over his choice of subjects for study. Gradualism sets the explanatory framework for his first substantive book on coral reefs (1842) and for his last on the formation of topography and topsoil by earthworms (1881)—two works largely devoid of reference to natural selection. Gradualism had been equated with rationality itself by Darwin's chief guru, Charles Lyell (see Chapter 6). All scholars have noted the centrality of gradualism, both in the ontogeny (Gruber and Barrett, 1974) and logic (Mayr, 1991) of Darwin's thought.

I will not play "duelling quotations" with "citation grazers," though a full tabulation of relative frequencies could easily bury their claims under a mountain of statements. For the present assessment of branch two ("creativity of natural selection") on the coral of essential Darwinian logic, the necessity of gradualism will suffice. Selection becomes creative only if it can impart direction to evolution by superintending the slow and steady accumulation of favored subsets from an isotropic pool of variation. If gradualism does not accompany this process of change, selection must relinquish this creative role and Darwinism then fails as a creative source of evolutionary novelty. If important new features, or entire new taxa, arise as large and discontinuous variations, then creativity lies in production of the variation itself. Natural selection no longer causes evolution, and can only act as a headsman for the unfit, thus promoting changes that originated in other ways. Gradualism therefore becomes a logical consequence of the operation of natural selection in Darwin's creative mode. Gradualism also pervades the methodological pole of Darwin's greatness because the uniformitarian argument of extrapolation will not work unless change at the grandest scale arises by the summation through time of small, immediate, and palpable variations.

Gradualism, for Darwin, represents a complex doctrine with several layers of meaning, all interconnected, while remaining independent in some important senses. I shall consider three increasing levels of specificity, arguing, on the Goldilocks model, that one meaning is too nebulous, another overly wrought, but the third (in the middle) "just right" as the crucial validator of natural selection (whereas the other two meanings play equally crucial roles for other aspects of Darwin's view of life).

HISTORICAL CONTINUITY OF STUFF AND INFORMATION. At the broadest level, gradualism merely asserts unbroken historical connectedness between putative ancestor and descendant, without characterizing the mode or rate of transition. If new species originate as creations *ex nihilo* by a divine power, then connectivity fails. The assertion of gradualism in this broadest meaning encapsulates the chief defense for the factuality of evolution. Such a contention could not be more vital to Darwin's revolution of course, but this sense of gradualism only asserts *that* evolution occurred, while telling us nothing about *how* evolution happens; the logical tie of gradualism to natural selection cannot reside here.* Thus, this first, or "too big," sense of gradual-

*Some modern evolutionists have made the error of assuming that contemporary debates about gradualism engage this now obvious and entirely uncontroversial meaning. Thus Gingerich (1984a), abandoning his earlier and properly empirical approach to gradualism (sense iii of p. 152) vs. punctuation (1976), argues that gradualism must be true *a priori*, as equivalent to "empiricism" in paleontology. He then provides a curious definition of stasis as "gradualism at zero rate"—an oxymoron with respect to the definition of gradualism that punctuated equilibrium opposes with a prediction of stasis. I was, at first, deeply ism validates evolution itself (*vs.* creationism), but not Darwin's, or anyone else's, proposed mechanism of evolutionary change.

INSENSIBILITY OF INTERMEDIACY. We now come to the heart of what natural selection requires. This second, "just right," statement does not advance a claim about how much time a transition must take, or how variable a rate of change might be. The second meaning simply asserts that, in going from A to a substantially different B, evolution must pass through a long and insensible sequence of intermediary steps—in other words, that ancestor and descendant must be linked by a series of changes, each within the range of what natural selection might construct from ordinary variability. Without gradualism in this form, large variations of discontinuous morphological import—rather than natural selection—might provide the creative force of evolutionary change. But if the tiny increment of each step remains inconsequential in itself, then creativity must reside in the summation of these steps into something substantial—and natural selection, in Darwin's theory, acts as the agent of accumulation.

This meaning of gradualism underlies Darwin's frequent invocation of the old Leibnizian and Linnaean aphorism, *Natura non facit saltum* (nature does not proceed by leaps). Darwin's commitment to this postulate can only strike us as fierce and, by modern standards, overly drawn. Thus, Darwin writes (p. 189): "If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down." And lest we doubt that "my theory" refers specifically to the mechanism of natural selection (and not simply to the assertion of evolution), Darwin often draws an explicit link between selection as a creative force and gradualism as an implied necessity: "Undoubtedly nothing can be effected through Natural Selection except by the addition of infinitesimally small changes; and if it could be shown that . . . transitional states were impossible, the theory would be overthrown" (in *Natural Selection*—see Stauffer, 1975, p. 250). And in the concluding chapter of the *Origin:* "As natural selection acts solely by accumulating slight, successive, favorable variations, it can produce no great or sudden modification; it can act only by very short and slow steps. Hence the canon of 'Natura non facit saltum' . . . is on this theory simply intelligible" (p. 471).

But would the theory of natural selection "absolutely break down" if even a single organ—not to mention an entire organism—could arise by large and discontinuous changes? Does Darwinism truly require the following extreme formulation: "Natural selection can only act by the preservation and accumulation of infinitesimally small inherited modifications" (p. 95). At some level of discontinuity, of course, Darwin's strong statement must prevail. If the altered morphology of new species often arose in single steps by fortuitous macromutation, then selection would lose its creative role and could act only as a secondary and auxiliary force to spread the sudden blessing through a population. But can we justify Darwin's application of the same claim to single organs? Suppose (as must often happen) that developmental heterochrony produces a major shift in form and function by two or three steps without intermediary stages. The size of these steps may lie outside the "normal" variation of most populations at most moments, but not beyond the potential of an inherited developmental program. (Incidentally, these types of changes represent the concept that Goldschmidt embodied in the legitimate meaning of "hopeful monster," before he made his unfortunate decision to tie this interesting concept to his fallacious genetics of "systemic mutation"—see Chapter 5 and Gould, 1982a.)

puzzled by Gingerich's definition until I realized the source of his confusion. He had switched definitions from the empirical issue of rates (meaning iii of this discussion)—a lively and testable argument opposing stasis to gradualism defined as a rate of *change*—to the completely settled question of historical continuity. Does anyone seriously think that supporters of punctuated equilibrium, or any scientist for that matter, would deny historical continuity? His argument therefore dissolves into the empty linguistic effort of trying to win a debate by shifting a definition. The question of punctuated equilibrium will be resolved by empirical testing under the third definition of gradualism. (See Chapter 9 for a full discussion of this issue.)

Would natural selection perish if change in this mode were common? I don't think so. Darwinian theory would require some adjustments and compromises—particularly a toning down of assertions about the isotropy of variation, and a more vigorous study of internal constraint in genetics and development (see Chapter 10 for advocacy of this theoretical shift)—but natural selection would still enjoy a status far higher than that of a mere executioner. A new organ does not make a new species; and a new morphology must be brought into functional integration—a process that requires secondary adaptation and fine tuning, presumably by natural selection, whatever the extent of the initial step.

I believe, therefore, that Darwin's strong, even pugnacious, defense of strict gradualism reflects a much more pervasive commitment, extending far beyond the simple recognition of a logical entailment implied by natural selection—and that this stronger conviction must record such general influences as Darwin's attraction to Lyell's conflation of gradualism with rationality itself, and the cultural appeal of gradualism during Britain's greatest age of industrial expansion and imperial conquest (Gould, 1984a). Huxley's savvy assessment of the *Origin* still rings true, for while he offered, in his famous letter to Darwin, written just as the *Origin* rolled off the presses, to "go to the stake" for Darwin's view, he also stated his major criticism: "You have loaded yourself with an unnecessary difficulty in adopting *Natura non facit saltum* so unreservedly" (in L. Huxley, 1901, p. 189).

Darwin persevered nonetheless. We often fail to recognize how much of the *Origin* presents an exposition of gradualism, rather than a defense of natural selection. As a striking example, the famous (and virtually only) statement about human evolution asserts the pedagogical value of gradualism—not natural selection—in our Socratic quest to know ourselves: "Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation. Light will be thrown on the origin of man and his history" (p. 488).

Chapter 9 on geological evidence, where the uninitiated might expect to find a strong defense for evolution from the most direct source of evidence in the fossil record, reads instead as a long (and legitimate) apologia for a threatening discordance between data and logical entailment—a fossil record dominated by gaps and discontinuities when read literally *vs.* the insensible transitions required by natural selection as a creative agent. Darwin, with his characteristic honesty, states the dilemma baldly in succinct deference to his methodological need for equating temporal steps of change with differences noted among varieties of contemporary species: "By the theory of natural selection all living species have been connected with the parent-species of each genus, by differences not greater than we see between the varieties of the same species at the present day" (p. 281).

Darwin, as we all know, resolved this discordance by branding the fossil record as so imperfect—like a book with few pages present and only a few letters preserved on each page—that truly insensible continuity becomes degraded to a series of abrupt leaps in surviving evidence:

> Why then is not every geological formation and every stratum full of such intermediate links? Geology assuredly does not reveal any such finely graduated organic chain; and this, perhaps, is the most obvious and gravest objection which can be urged against my theory. This explanation lies, as I believe, in the extreme imperfection of the geological record (p. 280).
>
> He who rejects these views on the nature of the geological record, will rightly reject my whole theory (p. 342).

SLOWNESS AND SMOOTHNESS (BUT NOT CONSTANCY) OF RATE. Darwin also championed the most stringent version of gradualism—not mere continuity of information, and not just insensibility of innumerable transitional steps; but also the additional claim that change must be insensibly gradual even at the broadest temporal scale of geological durations, and that continuous flux (at variable rates to be sure) represents the usual state of nature.

This broadest version of gradualism does not hold strong logical ties to natural selection as an evolutionary mechanism. Change might be episodic and abrupt in geological perspective, but still proceed by insensible intermediacy at a generational perspective—given the crucial scaling principle that thousands of generations make a geological moment. For this reason, Eldredge and I have never viewed punctuated equilibrium, which does refute Darwinian gradualism in this third sense, as an attack on the creativity of natural selection itself (Eldredge and Gould, 1972; Gould and Eldredge, 1977, 1993). The challenge of punctuated equilibrium to natural selection rests upon two entirely different issues of support provided by punctuational geometry for the explanation of cladal trends by differential species success and not by extrapolated anagenesis, and for the high relative frequency of species selection, as opposed to the exclusivity of Darwinian selection on organisms (see Chapters 8 and 9).

Some *fidei defensores* of the Darwinian citadel have sensed the weakness of this third version of gradualism, and have either pointed out that the creativity of natural selection cannot be compromised thereby (quite correct, but then no one ever raised such a challenge, at least within the legitimate debate on punctuated equilibrium); or have argued either that Darwin meant no such thing, or that, if he really did, the claim has no importance (see Dawkins, 1986). This last effort in apologetics provides a striking illustration of the retrospective fallacy in historiography. Whatever the current status of this third formulation within modern Darwinism, this broadest style of gradualism was vitally important to Darwin; for belief in slow change in geological perspective lies at the heart of his more inclusive view about nature and science, an issue even larger than the mechanics of natural selection.

Darwin often states his convictions about extreme slowness and continuous flux in geological time—as something quite apart from gradualism's second meaning of insensible intermediacy in microevolutionary perspective. Evolutionary change, Darwin asserts, usually occurs so slowly that even the immense length of an *average* geological formation may not reach the mean time of transformation between species. Thus, apparent stasis may actually represent change at average rates, but to an imperceptible degree even through such an extensive stretch of geological time! "Although each formation may mark a very long lapse of years, each perhaps is short compared with the period requisite to change one species into another" (p. 293).

Change not only occurs with geological slowness on this largest scale; but most transformations also proceed in sufficient continuity and limited variation in rate that elapsed time may be roughly measured by degree of accumulated difference: "The amount of organic change in the fossils of consecutive formations probably serves as a fair measure of the lapse of actual time" (p. 488).

Darwin presents his credo in crisp epitome: "Nature acts uniformly and slowly during vast periods of time on the whole organization, in any way which may be for each creature's own good" (p. 269). Note how Darwin concentrates so many of his central beliefs into so few words: gradualism, adaptationism, locus of selection on organisms.

But the most striking testimony to Darwin's conviction about gradualism in this third sense of slow and continuous flux lies in several errors prominently highlighted in the *Origin*—all based on convictions about steady rate (gradualism in the third sense), not on the insensible intermediacy genuinely demanded by natural selection (gradualism in the second sense), or on the simple continuity of historical information required to validate the factuality of evolution itself (gradualism in the first sense). For example, Darwin makes a famous calculation (dropped from later editions) on the "denudation of the Weald"—the erosion of the anticlinal valley located between the North and South Chalk Downs of southern England (pp. 285–287). He tries to determine an average value for yearly erosion of seacliffs today, and then extrapolates his figure as a constant rate into the past. His date of some 300 million years for the denudation of the Weald overestimated the true duration by five times or more. (The deposition of the Chalk, an Upper Cretaceous formation, persisted nearly to the period's end 65 million years ago.)

Moving to a biological example that underscores Darwin's hostility to episodes of "explosive" evolutionary diversification (he used his usual argument about the imperfection of the fossil record to deny their literal appearance and to spread them out in time), Darwin predicted that the Cambrian explosion would be exposed as an artifact, and that complex multicellular creatures must have thrived for vast Precambrian durations, gradually reaching the complexity of basal Cambrian forms. (When Darwin published in 1859, the Cambrian had not yet been recognized, and his text therefore speaks of the base of the Silurian, meaning lower Cambrian in modern terminology): "If my theory be true, it is indisputable that before the lowest Silurian stratum was deposited, long periods elapsed, as long as, or probably far longer than, the whole interval from the Silurian age to the present day; and that during these vast, yet quite unknown periods of time, the world swarmed with living creatures" (p. 307).

Paleontologists have now established a good record of Precambrian life. The world did swarm indeed, but only with single-celled forms and multicellular algae, until the latest Precambrian fauna of the Ediacara beds (beginning about 600 million years ago). The explosion of multicellular life now seems as abrupt as ever—even more so since the argument now rests on copious documentation of Precambrian life, rather than a paucity of evidence that could be attributed to imperfections of the geological record (see Chapter 10, pp. 1155–1161). Darwin on the other hand, predicted that complex, multicellular creatures must extend far into the Precambrian. He wrote: "I cannot doubt that all the Silurian [= Cambrian] trilobites have descended from some one crustacean, which must have lived long before the Silurian [= Cambrian] age" (p. 306). Darwin also conjectured, again incorrectly, that the ancestral verterbrate, an animal with an adult phenotype resembling the common embryological *Bauplan* of all modern verterbates, must have lived long before the dawn of Cambrian times: "It would be vain to look for [adult] animals having the common embryological character of the Vertebrata, until beds far beneath the lowest Silurian strata are discovered" (p. 338).

Darwin struggled for clarity and consistency. He did not always succeed. (How can an honest person so prevail in our complex and confusing world? I shall, for example, examine Darwin's ambivalences on progress in Chapter 6.) Darwin did not always keep the different senses of gradualism distinct. He frequently conflated meanings, arguing (for example) that the validity of natural selection (sense 2) required an acceptance of slow and continuous flux (sense 3). Consider once again the following familiar passage: "It may be said that natural selection is daily and hourly scrutinizing, throughout the world, every variation, even the slightest . . . We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages" (p. 84).

This conflation came easily (and probably unconsciously) to Darwin, in large part because gradualism stood prior to natural selection in the core of his beliefs about the nature of things. Natural selection exemplified gradualism, not vice versa—and the various forms of gradualism converged to a single, coordinated view of life that extended its compass far beyond natural selection and even evolution itself. This situation inspired Huxley's frustration as he remonstrated with Darwin (see the famous quote on p. 151): you will have enough trouble convincing people about natural selection; why do you insist upon uniting this theory with an unnecessary and, by the way, false claim for gradualism?

We can best sense this overarching Darwinian conviction in a lovely passage that conflates all three senses of gradualism—the rationalist argument against creationism, the validation of natural selection by insensible intermediacy, and the slow pace of change at geological scales—all in the context of Darwin's homage to his guru Lyell, and his aesthetic and ethical convictions about the superiority of these "noble views" about natural causation and the nature of change:

> I am well aware that this doctrine of natural selection . . . is open to the same objections which were at first urged against Sir Charles Lyell's noble views on "the modern changes of the earth, as illustrative of geology;" but we now very seldom hear the action, for instance, of the coast-waves, called a trifling and insignificant cause, when applied to the excavation of gigantic valleys or to the formation of the longest lines of inland cliffs. Natural selection can act only by the preservation and accumulation of infinitesimally small inherited modifications, each profitable to the preserved being; and as modern geology has almost banished such views as the excavation of a great valley by a single diluvial wave, so will natural selection, if it be a true principle, banish the belief in the continued creation of new organic beings, or of any great and sudden modification in their structure (pp. 95–96).

The adaptationist program

Darwin's three constraints on the nature of variation form a single conceptual thrust: variation only serves as a prerequisite, a source of raw material incapable of imparting direction or generating evolutionary change by itself. Gradualism, in the second meaning of insensible intermediacy, then guarantees that the positive force of modification proceeds step by tiny step. Therefore, the explanation of evolution must reside in specifying the causes of change under two conditions that logically entail a primary focus on adaptation as a canonical result: we know the general nature of change (gradualism), and we have eliminated an internal source from variation itself (the argument for isotropy). Change must therefore arise by interaction between external conditions (both biotic and abiotic) and the equipotential raw material of variation. Such gradual adjustment of one to the other must yield adaptation as a primary outcome.

Adaptational results flow logically from the mechanisms defining all other subbranches on the limb of Darwinism designated here as the "creativity of natural selection." But Darwin constructed this limb in reverse order in the psychological development of his theory. For he had long viewed an explanation of adaptation as the chief requirement of evolutionary theory. He sought the causes of evolution within his patrimony—the English tradition in natural theology—and he attempted to subvert this patrimony from within by accepting its chief empirical postulate of good design and then providing an inverted theoretical explanation (see p. 125).

When Darwin permits himself to make one of his rare forays into lyrical prose, we can grasp more fully (and dramatically) the extent of his feelings and the depth of his conviction. Consider the following passage on why the basic results of evolution and variation teach us so little about the origin of species, and why an understanding of mechanism requires an explanation of adaptation:

> But the mere existence of individual variability and of some few well-marked varieties, though necessary as the foundation for the work, helps us but little in understanding how species arise in nature. How have all those exquisite adaptations of one part of the organization to another part, and to the conditions of life, and of one distinct organic being to another being, been perfected? We see these beautiful co-adaptations most plainly in the woodpecker and missletoe; and only a little less plainly in the humblest parasite which clings to the hairs of a quadruped or feathers of a bird; in the structure of the beetle which dives through the water; in the plumed seed which is wafted by the gentlest breeze; in short, we see beautiful adaptations everywhere and in every part of the organic world (pp. 60–61).

Pursuing the theme of rare Darwinian lyricism as a guide to what he viewed as essential, consider his convictions about the overwhelming power of natural selection—a point that he usually conveyed by comparison with the limitations of artificial selection in breeding and agriculture:

> Man can act only on external and visible characters: nature cares nothing for appearances, except in so far as they may be useful to any being. She can act on every internal organ, on every shade of constitutional difference, on the whole machinery of life. Man selects only for his own good; Nature only for that of the being which she tends. Every selected character is fully exercised by her; and the being is placed under well-suited conditions of life. Man keeps the natives of many climates in the same country; he seldom exercises each selected character in some peculiar and fitting manner; he feeds a long and a short beaked pigeon on the same food; he does not exercise a long-backed or long-legged quadruped in any peculiar manner; he exposes sheep with long and short wool to the same climate. He does not allow the most vigorous males to struggle for the females. He does not rigidly destroy all inferior animals, but protects during each varying season, as far as lies in his power, all his productions . . . Under nature, the slightest difference of structure or constitution may well turn the nicely-balanced scale in the struggle for life and so be preserved. How fleeting are the wishes and efforts of man! how short his time! and consequently how poor will his products be, compared with those accumulated by nature during whole geological periods. Can we wonder, then, that nature's productions should be far "truer" in character than man's productions; that they should be infinitely better adapted to the most complex conditions of life, and should plainly bear the stamp of far higher workmanship? (pp. 83–84).

But Darwin's world also differs strongly from Paley's, and the outcome of natural selection, however great the power of Darwin's mechanism, cannot be perfection, but only improvement to a point of competitive superiority in local circumstances. Natural selection operates as a principle of "better than," not as a doctrine of perfection: "Natural selection tends only to make each organic being as perfect as, or slightly more perfect than, the other inhabitants of the same country with which it has to struggle for existence" (p. 201). Thus, the signs of history will not be erased; creatures will retain signatures of their past as quirks, oddities and imperfections (see pp. 111–116 on methodology). Natural selection will fashion the organic world, while leaving enough signs of her previous handiwork to reveal a forming presence.

I have called this section "the adaptationist program," rather than, simply, "adaptation" because Darwin presents a protocol for actual research, not just an abstract conceptual structure. The relevant arguments may be ordered in various ways, but consider this sequence:

- Adaptation is the central phenomenon of evolution, and the key to any understanding of mechanisms.
- Natural selection crafts adaptation.
- Natural selection maintains an overwhelmingly predominant relative frequency as a cause of adaptation. Variation only provides raw material, and cannot do the work unaided.

Adaptation may be viewed as a problem of transforming environmental (external) information into internal changes of form, physiology and behavior. Two forces other than natural selection might play such a role—the creative response of organisms to felt needs with inheritance of acquired characters (Lamarck's system), or direct impress of environments upon organisms, also with inheritance of traits thus acquired (a system often associated with Geoffroy Saint-Hilaire). Darwin regards both alternatives as true causes, and he explicitly contrasts them with natural selection in several passages within the *Origin*. But, in these statements and elsewhere, he always grants natural selection the cardinal role by virtue of relative frequency—"by far the predominant Power," he writes on page 43, in upper case for emphasis. "Over all other causes of change, I am convinced that Natural Selection is paramount" (in *Natural Selection*, 1975 edition, p. 223).

In this light, how should evolutionists proceed if they wish to discover the mechanisms of change? Should they study the causes of variation (a vitally important issue, but unresolvable in Darwin's time, and not the cause of change in any case)? Or should they examine the large-scale phenomena of taxonomic order or geographic distribution (issues of great import again, but lying too far from immediate causation)? Instead, the best strategy, Darwin asserts, lies in the study of adaptation, for adaptation is the direct and primary result of natural selection; and the relative frequency of selection stands so high that almost any adaptation will record its forming power.

Adaptation therefore becomes, for Darwin, the primary subject for practical study of evolutionary mechanisms. Recall the basic methodological problem of a science of history (see p. 102): science aims, above all, to understand causal processes; past processes cannot be observed in principle; we must therefore learn about past causes by making inferences from preserved results. Adaptation is the common and coordinating result of nearly any episode of non-trivial evolutionary change. Adaptation not only pervades nature with an overwhelming relative frequency, but also embodies the immediate action of the primary cause of change—natural selection. The adaptations of organisms therefore constitute the bread and butter objects of study in evolutionary biology. Our first order approach to change must pose the following question in any particular case: what adaptive value can we assign; how did natural selection work in this instance? In a revealing statement, Darwin rolls all exceptions, all ifs and buts, into a set of subsidiaries to adaptation forged by natural selection—as either consequences of adaptation, inherited marks of older adaptations, or rare products of other processes: "Hence every detail of structure in every living creature (making some little allowance for the direct action of physical conditions) may be viewed, either as having been of special use to some ancestral form, or as being now of special use to the descendants of this form—either directly, or indirectly through the complex laws of growth" (p. 200).

The primary anti-Darwinian argument of late 19th century biology proceeded by denying a creative role to natural selection—but Darwin countered with a strong riposte. If adaptation pervades nature and must be constructed by natural selection, and if the steps of evolutionary sequences are generally so tiny that we may seek their source in palpable events subject to our direct view and manipulation, then we not only gain a theoretical explanation for evolutionary change. We also obtain the practical gift of a workable research program rooted in the observable and the resolvable.

But nothing so precious comes without a price, or without consequences. Darwin's argument works; no logical holes remain. But the research program thus entailed must embody attitudes and assumptions not necessarily true—or at least not necessarily valid at sufficiently high relative frequency to make the world exclusively, or even primarily, Darwinian. To accept Darwin's full argument about the creativity of natural selection, one must buy into an entire conceptual world—a world where externalities direct, and internalities supply raw material but impose no serious constraint upon change; a world where the functional impetus for change comes first and the structural alteration of form can only follow. *The creativity of natural selection makes adaptation central, isotropy of variation necessary, and gradualism pervasive.*

But suppose these precepts do not govern a commanding relative frequency of cases? What if adaptation does not always record the primacy of natural selection, but often arises as secondary fine tuning of structures arising in other ways? What if variation imposes strong constraints and supplies powerful channels of preferred direction for change? What if the nature of variation (particularly as expressed in development) often produces change without insensible intermediacy?

All these arguments merge into a structuralist critique that seriously challenges the predominant functionalism of classical Darwinism. As a common thread, these challenges deny exclusivity to natural selection as the agent of creativity, and claim a high relative frequency of control by internal factors. McCosh was right in establishing his pre-evolutionary contrast of a "principle of order" and a "principle of special adaptation" (see p. 116). Darwin was right in translating this distinction into evolutionary terms as "Unity of Type" and "Conditions of Existence," though he was probably wrong in his fateful decision—the basis of Darwinian functionalism—to yoke the two categories together under a common cause by defining unity of type as the historical legacy of previous adaptation, thus asserting the domination of natural selection (1859, p. 206—see extensive commentary in chapter 4). And E. S. Russell (1916) was also right in contrasting the "formal or transcendental" with the "functional or synthetic" approach to morphology.

We are children of Darwin, and an English school of adaptation and functionalism far older than evolutionary theory. Darwin's key claim for the creativity of natural selection—and the resulting sequelae of gradualism, adaptationism, and the isotropy of variation—builds the main line of defense for this powerful and venerable attitude towards nature and change. For many of us, these claims lie too close to the core of our deeply assimilated and now largely unconscious beliefs to be challenged, or even overtly recognized as something potentially disputable. Yet a coherent alternative has been proposed, and now provides one of the three most trenchant modern critiques of strict Darwinism. I believe that these critiques, taken together, will reorient evolutionary theory into a richer structure with a Darwinian core. But we cannot appreciate the alternatives until we grasp the basis of orthodoxy as an argument of compelling brilliance and power. Important critiques can only operate against great orthodoxies.

THE THIRD THEME: THE UNIFORMITARIAN NEED TO EXTRAPOLATE; ENVIRONMENT AS ENABLER OF CHANGE

The first two themes—causal focus on organisms as agents of selection and creativity of selection in crafting adaptation—establish the biological core of Darwinian theory. That is, they perform the *biological* "work" needed to assure the third and last essential component of a Darwinian worldview: the uniformitarian argument for full application in extrapolation to all scales and times in the history of life. Mere operation in the microevolutionary here and now cannot suffice. Natural selection must also assert a vigorous claim for preeminence throughout the 3.5 billion years of phylogeny, lest the theory be reduced to an ornamental device, imposing only a fillip of immediate adaptive detail upon a grand pageant generated by other causes and forces.

Darwin, who fledged professionally as a geologist (the subject of his first three scientific books in the 1840's, on coral reefs, volcanic islands, and the geology of South America), and who regarded Charles Lyell as his intellectual hero, while embracing his mentor's doctrine of uniformitarianism as the core of his own philosophy as well, fully understood that his revolution would succeed only if he could show how natural selection might act as architect for the *full panoply* of life's history throughout geological time. The "methodological pole," one of the two foci of Darwin's revolution (see Section II of this chapter), brilliantly develops a set of procedures for defending extrapolation in various contexts of limited evidence.

The link of the first two themes (agency and efficacy) to this third theme of extended scope or capacity—thus forming in their threefold ensemble a minimally complete statement of revolution—received succinct expression in Ernst Mayr's (1963, p. 586) epitome of Darwinism as preached by the Modern Synthesis: "All evolution is due to the accumulation of small genetic changes, guided by natural selection [the first two themes of agency and efficacy], and that transpecific evolution [the third theme of scope, or uniformitarian extension] is nothing but an extrapolation and magnification of the events that take place within populations and species."

In this book, my explicit discussion for this third theme of extrapolation (Chapters 6 and 12) shall be shorter than my treatment of the first theme of agency (Chapters 3 and 8–9), leading from Darwin's nearly exclusive focus on the organismal level to the modern revision of hierarchical selection theory, and the second theme of efficacy (Chapters 4–5 and 10–11) on older and modern critiques of panadaptationism, with an emphasis on structural principles and constraints. I allocate my attention in this unequal manner because the first two themes already include, within themselves, the *biological* arguments for extrapolation, as embodied in Darwin's uniformitarian beliefs and practices. For my explicit and separate treatment of the crucial extrapolationist theme in this work, I therefore follow a different strategy, if only to avoid redundancy in a book that we all undoubtedly regard, author and readers alike, as quite long enough already! I will not rehearse Darwin's biological arguments for extrapolation, but will rather, as a "place holder" of sorts, concentrate upon the nature of the geological stage that must welcome Darwin's biological play.

I proceed in this way for a principled reason, and not merely as a convenience. All major evolutionary theories before Darwin, and nearly all important versions that followed his enunciation of natural selection as well, retained fealty to an ancient Western tradition, dating to Plato and other classical authors, by presenting a fundamentally "internalist" account, based upon intrinsic and predictable patterns set by the nature of living systems, for development or "unfolding" through time. (Ironically, such internalist theories follow the literal meaning of "evolution" (unfolding) far better than the Darwinian system that eventually absorbed the term. Darwin understood this

etymological point perfectly well, and he initially declined to use the word "evolution"—preferring "descent with modification"—probably because he recognized the difference between the literal meaning of "evolution" and his own concept of life's history and change by natural selection—see Gould, 2000a.)

Darwin's theory, in strong and revolutionary contrast, presents a first "externalist" account of evolution, in which contingent change (the summation of unpredictable local adaptations rather than a deterministic unfolding of inherent potential under internal, biological principles) proceeds by an interaction between organic raw material (undirected variation) and environmental guidance (natural selection). Darwin overturned all previous traditions by thus granting the external environment a causal and controlling role in the direction of evolutionary change (with "environment" construed as the ensemble of biotic and abiotic factors of course, but still external to the organism, however intrinsically locked to, and even largely defined by, the presence of the organism itself). Thus, and finally, in considering the validity of extrapolation to complete the roster of essential Darwinian claims, the role of the geological stage becomes an appropriate focus as a surrogate for more overtly biological discussion.

If the uniqueness of Darwinism, and its revolutionary character as well, inheres largely in the formulation of natural selection as a theory of interaction between biological insides and environmental outsides—and not as a theory of *evolutio*, or intrinsic unfolding—then "outsides" must receive explicit discussion as well, a need best fulfilled within this treatment of extrapolation. Under internalist theories of *evolution*, environment, at most, holds power to derail the process by not behaving properly—drying up, as on Mars, or freezing over, as nearly occurred on Earth more than once during our planet's geological history. Under Darwinian functionalism, however, environment becomes an active partner in both the modes and directions of evolutionary change.

As the Utopian tradition recognizes, we can often devise lovely and optimal systems in abstract principle, but then be utterly unable to apply them in practice because an imperfect world precludes their operation. The central logic of Darwinism faces an issue of this kind. The two essential biological postulates of natural selection—its operation at the organismal level, and its creativity in crafting adaptations—build a sufficient theoretical apparatus to fuel the system. The play of evolution can run with such a minimal cast, but we do not know whether the drama can actually unfold on our planet until we also examine and specify the character of the theater—the geological and environmental stage for the play of natural selection. The geological stage therefore becomes a major actor in the drama set on its own premises.

Moreover, and reinforcing my argument that Darwin's strength lies in his brave specificity, Darwin places a great burden on geology and environment by devising such stringent conditions for the nature of this external setting. Again, we encounter the Goldilocks problem—environment cannot impose too much or provide too little, but must be "just right" in the middle.

Environment, as an active Darwinian agent, cannot underperform. In particular, an absence of environmental change would probably bring evolution to an eventual halt, as selective pressures for adaptive alteration diminished (see Stenseth and Maynard Smith, 1984). Purely biotic interaction might drive evolution for some time following a cessation of environmental change, but probably not indefinitely.

The possibility of too little change has rarely been viewed as a threat to Darwinism, largely because the geological record seems so clearly to emphasize potential dangers in the other direction (though see pp. 492–502 on Lord Kelvin). The specter of "too much" change, on the other hand, has haunted Darwinism from the start. In particular, if the theory of geological catastrophism were generally true, or even just sufficiently important in relative frequency, then Darwinism would be compromised as the primary agent of pattern in the history of life.

By catastrophism, I mean to designate the classical theory of global paroxysm as a primary agent of geological change—in particular, the idea that mass extinctions thus engendered might lie largely outside the domain of traditional Darwinism. Of course, mass extinctions cannot be construed as "undarwinian" *per se*. If environment changes so rapidly that organisms cannot adapt fast enough by natural selection, then many species will die. But, in a conceptual world of relative frequency, where Darwinism must not only operate, but also dominate as the creator of change, such formative power for mass extinction constitutes a serious challenge. If we survey the entire history of life, and find that catastrophic mass extinction, with non-Darwinian fortuity in causes of change (on either the "random" or the "different rules" model—see Chapter 12, and Gould, 1985a, 1993c), establishes more features of overall pattern than the ordinary interplay of taxa during normal times (between such episodes of coordinated death) can build and maintain, then Darwin's view of life lacks the generality once accorded. In particular, the key uniformitarian argument will then fail. The adaptive struggles of immediate moments will not extrapolate to explain the patterns of life's history. Moreover, if these undarwinian components of fortuity in extinction, and success for reasons unrelated to the original adaptive basis of traits, also maintain strong influence at lesser scales of smaller mass extinctions (Raup and Sepkoski, 1984), and even, in a fractal manner, for some ordinary extinctions in normal times (Raup, 1991), then the challenge may become truly pervasive.

These characterizations of Darwinian requirements cannot be dismissed or downgraded as conjectures or reconstructions, only inferentially based on deductions from premises stated by Darwin for different reasons. Darwin devoted an entire chapter of the *Origin*, number 10 "on the geological succession of organic beings," to an exploration of the geological stage and its requirements for natural selection. He argues that biotic competition, gradualistically expressed through time as coordinated waxing and waning of interacting clades, marks the overall pattern of life—and that the apparent fossil evidence for more rapid change, set by physical environments and leading to mass extinctions, must generally be read as artifacts of an imperfect record (see Chapter 12 for detailed exegesis of Darwin's arguments on this subject).

This issue exposes another essential Darwinian theme not yet discussed (but receiving full treatment in Chapter 6)—the nature of competition; the prevalence of biotic over abiotic effects; the metaphor of the wedge; and the fundamental role of Darwinian ecology as a validator of progress (in the absence of any available defense from the bare-bones mechanism of natural selection itself). Thus, the argument for uniformitarian change in geology undergirds a central conviction of the Darwinian corpus.

We cannot overestimate the depth of Darwin's debt to his intellectual hero, Charles Lyell. The uniformitarianism of his mentor not only provided, by transfer into biology, a theory of evolutionary change. The doctrine of uniformity also supplied, on its original geological turf, a world that could grant enough slow and continuous environmental change to fuel natural selection—but not so much, or so quickly, that selection would be overcome, and the rein of pattern seized by environment in its own right. In natural selection, environment proposes and organisms dispose; this subtle balance of inside and outside must be maintained. But in a world of too much environmental change, the external component does not only propose, but can also dispose of organisms and species without much backtalk. Darwinism does not run well on such a one-way street.

Judgments of Importance

In the difficult genre of comprehensive historical reviews, a few special books stand out as so fair in their judgments and so lucid in their characterizations that they set the conceptual boundaries of disciplines for generations. In morphology, E. S. Russell's *Form and Function* (1916) occupies this role for the brilliance and justice of its characterizations, even though Russell, as an avowed Lamarckian, made no secret about his own preferences (and made the wrong choice by modern standards). In evolutionary biology, similar plaudits may be granted to Vernon L. Kellogg's *Darwinism Today* (1907). Kellogg, a great educator and entomologist from Stanford, had collaborated with David Starr Jordan on the best textbooks of his generation. He also played an ironic role in the history of evolution by serving a term (while America maintained her early neutrality) as chief agent for Belgian relief, posted to the German General Staff in Berlin during World War I. There, he listened in horror to German leaders perverting Darwinism as a justification for war and conquest—and he exposed these distortions in his fascinating volume, *Headquarters Nights* (1917). William Jennings Bryan read this book and, understanding the abuse but blaming the victims of misinterpretation rather than the perpetrators, launched his campaign to ban the teaching of evolution as a result (see Gould, 1991b).

As the Darwinian centennial of 1909 neared, Kellogg decided to write a volume providing a fair hearing for all varieties of Darwinism, and all alternative views in a decade of maximal agnosticism and diversity in evolutionary theories. Kellogg's book adopts the same premise as this treatise—that

Darwinism embodies a meaningful central logic, or "essence," and that other proposals about evolutionary mechanisms can be classified with reference to their consonance or dissonance with these basic Darwinian commitments.

I was particularly pleased to learn that Kellogg's categories, though differently named and parsed, are identical with those recognized here. He divides the plethora of proposals under discussion in his time into those "auxiliary to" and those "alternative to" natural selection. Among auxiliaries that aid, expand, improve, or lie within the spirit of Darwinism, Kellogg highlights two principal themes: studies of Wagner, Jordan, and Gulick on the role of isolation in the formation of species; and hierarchical models of selection as espoused by Roux and Weismann (discussed in detail in Chapter 3). I noted with special gratification that Kellogg recognized hierarchy as an auxiliary, not a confutation, to Darwinism, for this same contention sets a principal theme of this book.

In his second category of confutations, Kellogg identified "three general theories, or groups of theories, which are offered more as alternative and substitionary theories for natural selection than as auxiliary or supporting theories" (1907, p. 262): Lamarckism (inheritance of acquired characters in the form advocated by late 19th century neo-Lamarckians), orthogenesis, and heterogenesis (Kellogg's designation for saltationism).

Kellogg's taxonomy works particularly well in evaluating the central principles of Darwinism. His "auxiliaries" aid selection (by addition of other principles that do not challenge or diminish selection, or by expansion of selection to other levels); but his "alternatives" confute particular maxims of the minimal commitments for Darwinian logic. The Kelloggian "alternatives" all deny the fundamental postulate of creativity for selection by designating other causes as originators of evolutionary novelties, and by relegating selection to a diminished status as a negative force. Each alternative rejects a necessary Darwinian postulate about the nature of variation (see pp. 141–146): Lamarckism and orthogenesis deny the principle of undirected variability; saltationism refutes the claim that variation must be small in extent.

I warmly endorse Kellogg's approach. As practicing scientists, we often do not pay enough respect to the logical structure of an argument—to its rigors and its entailments. We tend to assume that conclusions flow unambiguously from data, and that if we observe nature closely enough, and experiment with sufficient care and cleverness, the right ideas will somehow coalesce or flow into place by themselves. But scholars should know, from the bones and guts of their practice, that all great theories originate by intense and explicit mental struggle as well. We should not castigate such efforts as "speculation" or "armchair theorizing"—for mental struggle deserves this designation only when the thinker opposes or disparages our shared conviction that, ultimately, empirical work or testing must accompany and validate such exercises in thought (and then all scientists would agree to let the calumny fall). Great theories emerge by titration of this basically lonely mental struggle with the more public, empirical acts of fieldwork and benchwork.

One need look no further than Charles Darwin for proper inspiration. He rooted his theory in practical testability, and he continually devised and performed clever experiments, despite limited resources (of available equipment and personnel at Down, not of funds; for Darwin was a wealthy man and did not need to spend his time seeking patronage, his generation's equivalent of modern grant swinging). But natural selection did not flow from the external world into a *tabula rasa* of Darwin's mind. He carried out with himself, as recorded in his copious notebooks (Barrett *et al.*, 1987), one of the great mental struggles of human history—proposing and rejecting numerous theories along his slow and almost painful journey by inches, accompanied by lateral feints and backward plunges, towards the theory of natural selection. That theory, when fully formulated in the 1850's, emerged as an intricately devised amalgam of logically connected parts, each with a necessary function—and not as a simple message from nature. We must treat this theory, as Kellogg does, with respect for its integrity.

With the coalescence and hardening of the Modern Synthesis (Gould, 1983b), culminating in the Darwinian celebrations of 1959, an orthodoxy descended over evolutionary theory, and a generation of unprecedented agreement ensued (often for reasons of complacency or authority). However, the press of new concepts and discoveries has since fractured this shaky consensus, and we now face a range of options and alternatives fully as broad as those available in the contentious decade of Kellogg's review. In this renewed context, I recommend Kellogg's procedure as both intellectually admirable and maximally useful—namely, *to arrange and evaluate various views and challenges by classification according to their attitudes towards the minimal commitments of Darwinism.* I say "admirable" because such an approach pays proper respect to the intellectual power of Darwin's synthesis, and "useful" because a taxonomy by minimal commitments of an essential logic allows us to rank, assess, and interconnect an otherwise confusing array of proposals and counterproposals. And just as the widespread debate of Kellogg's time led to the Modern Synthesis of the next generation, I believe that the renewed arguments of our day will pay dividends in the form of a richer and more adequate consensus for our new millennium. Kellogg's characterization of his own era therefore becomes relevant to our current situation:

> The present time is one of unprecedented activity and fertility both in the discovery of facts and in attempts to perceive their significance in relation to the great problems of bionomics. Both destructive criticism of old, and synthesis of new hypotheses and theories, are being so energetically carried forward that the scientific layman and educated reader, if he stand but ever so little outside of the actual working ranks of biology, is likely to lose his orientation as to the trends of evolutionary advance. Precisely at the present moment is this modification of the general point of view and attitude of philosophical biologists unusually important and far-reaching in its relation to certain long-held general conceptions of biology and evolution (1907, p. ii).

I have therefore followed Kellogg's lead and attempted, in this introductory chapter, to characterize the central logic and minimal commitments of Darwinism—an essence, if you will, to invoke a good word and concept that has become taboo in our profession. I will then use this characterization as a foundation for classifying various challenges and controversies—just as Kellogg did—according to their stance towards the essential concepts of Darwinism. The most interesting and far-reaching challenges directly engage these essential concepts, either as alternatives to refute them in part, or as auxiliaries to expand and reinterpret them in fundamental ways. *This book presents, as its primary thesis, the notion that (i) Darwinism may be viewed as a platform with a tripod of essential support; (ii) each leg of the tripod now faces a serious reforming critique acting more as an auxiliary than an alternative formulation; and (iii) the three critiques hold strong elements in common, and may lead to a fundamentally revised evolutionary theory with a retained Darwinian core.*

We must rank challenges by their degree of engagement with the Darwinian core; we cannot follow a strategy of mindless "raw empiricism" towards the *Origin* and simply compile a list of Darwin's mistakes. All great works are bursting with error; how else could true creativity be achieved? Could anyone possibly reformulate a universe of thought and get every detail right the first time? We should not simply count Darwin's errors, but rather assess their importance relative to his essential postulates. (Consider, for example, the standard rhetorical, and deeply anti-intellectual, ploy of politically motivated and destructive critics, American creationists in particular. They just list the mistakes, envelop each in a cloud of verbal mockery, and pretend that the whole system has drowned in this tiny puddle of inconsequential error.)

I suggest that we use the list of minimal commitments to gauge the status of Darwin's errors. Very few faults of simple fact can, as individual items, be of much consequence unless they confute a core commitment. Darwin argued, for example, that swimbladders evolved into lungs (see p. 107) though exactly the opposite occurred—but no premise of the general theory suffers any injury by this mistake, however embarrassing. What about more important theoretical claims like Darwin's hypothesis of "pangenesis" as a mechanism of heredity (Darwin, 1868)? Again, Darwin's view of life would have been easier to vindicate if the theory had been affirmed, but none of his three essential postulates about the nature of variation fell with the disproof of pangenesis, and the core commitments remained intact, if unproven. What about the impact of major claims that turn out to be basically true, Mendelism for example? We must make our judgment by assessing their engagement with the core commitments. In the first decade of the 20th century, most evolutionists invoked Mendelism as a saltational theory of macromutation against the Darwinian core commitment to small-scale variation (see Chapter 5). Later, largely through R. A. Fisher's analysis and the resolution of the Mendelian *vs.* biometrician debate, macromutations were rejected, "ordinary" small-scale variation granted a Mendelian basis, and Mendelism comfortably reinterpreted as support for the same core commitment. Again, challenges and new proposals must be judged and ranked by their engagement with the essence of a reigning theory. Darwinism embodies a definable set of minimal commitments; all great theories do and must.

We should use this perspective of engagement with the core commitments to assess the relative theoretical importance of issues now commanding attention among evolutionists. For example, Kimura's theory of neutralism (1983) ranks as fundamental and reformative for proposing a new domain of causation at high relative frequency. I regard as unfair, and disrespectful of Darwin's clear commitments, the common rhetorical strategy of arguing, as Stebbins and Ayala did for example (1981), that selection and neutralism should be judged as competing paradigms comfortably embraced within the Modern Synthesis. The Synthesis, as an intellectual structure, has always been understood as Darwinism strengthened by modern knowledge about genetics and heredity. The Synthesis must therefore assert a dominant relative frequency for selection. Of course such a theory allows for neutrality—one could scarcely deny either the mathematics or the conditions of potential operation—but only at a low relative frequency, so that the preeminence of selection will remain unchallenged.

Kimura's claim for high, even dominant, relative frequency of neutral *change* at the nucleotide level introduces a world different from Darwin's. At most, one can say that this world, largely invisible at the organismic level, does not subvert Darwin's proposal that selection dominates the phenotypic realm of overt form, function, and physiology of organisms. But in so saying, we must admit that a large part of reality, though unaddressed by Darwin himself, cannot be explained on Darwinian principles if Kimura's theory holds. Darwinism does not fall thereby, but a new and distinct domain, primarily regulated by a different style of causality, has been added to evolutionary explanation. How can one deny that evolutionary theory becomes substantially reformulated and enriched thereby? Why would one want to issue such a denial, unless psychic health depends upon the continued assertion of comfortable orthodoxy, whatever the required twist of logic?

My own expertise lies in paleontology, and this book shall emphasize critiques from the attendant domain of macroevolution, descriptively defined as patterns and causes of evolution at and above the species level. (I acknowledge, of course, the fascination and transforming power of work at the molecular level. I also recognize that macroevolution must shake hands with molecular genetics in order to forge the new consensus. If this book slights the molecular side, my own ignorance stands as the only cause, and this work necessarily suffers thereby.)

Basically, I shall defend the view that each leg of Darwin's essential tripod, as explicated in this chapter, now faces a serious critique from the domain of macroevolutionary change. These critiques rank as *auxiliaries* to Darwinism in Kellogg's sense; for they either expand or add to the core commitments. But the expansions are large and the additions substantial—so the resulting revision can no longer be called ordinary Darwinism in any conventional meaning. I am convinced that the three critiques intertwine in a potentially unified way. But consensus is premature and we can only see the resulting shape of the revised and unified theory through a glass darkly—though in the future, no doubt, face to face.

Proceeding in reverse order through critiques of Darwinism's three core claims, catastrophic mass extinction, and more general views about fortuity in abiotically driven extinction at all levels, challenge Darwin's essential notion of a dominant relative frequency for biotic struggle in a crowded world—the third leg of the tripod, as represented by the geological stage required for an evolutionary play based entirely on extrapolation of microevolutionary principles (Chapters 6 and 12). The general idea of constraint—more in the positive sense of internally biased channels for change, rather than the negative meaning of limited variation for potentially useful alterations (see Gould, 1989a)—rejects the key Darwinian notion of isotropy in raw material, and consequent control of evolutionary direction by natural selection. Constraint therefore challenges the second leg of the tripod—the "creativity of natural selection"—not by confuting the proposition that natural selection acts as a creative force, but by insisting on diminished relative frequency and a sharing of control. Moreover, by reasserting the structuralist side of the old dichotomy between structure and function in biology—an issue far predating evolution, and inherent in the struggle between continental vs. Paleyan approaches to natural theology—the idea of constraint reengages one of the deepest issues in all the life sciences (Chapters 4–5 and 10–11).

Most importantly, and as the best integrator of all three critiques, the hierarchical theory of natural selection, by asserting both the existence and relative importance of selection at all levels from genes to species, challenges the first leg of the tripod—the insistence, so crucial to Darwin's radical overthrow of Paley via Adam Smith, that selection works almost exclusively on organisms (Chapters 3 and 8–9). I believe that this hierarchical theory provides the most fundamental, and potentially unifying, of all critiques—for I suspect that many constraints will be explained as effects of lower level selection indirectly expressed in phenotypes; while the contribution of mass extinction to repatterning life's history will include a crucial component of selection at levels above the organismic. Moreover, the attendant need to reconceptualize trends and stabilities not as optimalities of selection upon organisms alone, but as outcomes of interactions among numerous levels of selection, implies an evolutionary world sufficiently at variance from Darwin's own conception that the resulting theory, although still "selectionist" at its core, must be recognized as substantially different from current orthodoxy—and not just as a dash of spice on an underflavored dish. I therefore devote the largest section of this book's second half (Chapters 8 and 9) to defining and defending this hierarchical theory of selection.

If the next generation of evolutionists follows and extends this protocol at the outset of our new millennium, as presaged by the tentative work and exploration of so many scientists at the close of the last millennium, then we shall honor, all the more, the vitality of the tight definitions and firm commitments proposed by Darwin himself at the foundation of our discipline. Few theories hold the range of power, and the intricacy of logic, necessary to generate an intellectual structure of such continuing fascination and relevance. We do not pay our proper respect to Darwin by bowing before the icons of

his central propositions, but by engaging these focal precepts as living presences, ripe for reformulation, almost 150 years after their initial presentation. In Darwin's own world of continuous flux, anything that lasts so long becomes a many-splendored thing. In a revised world of structuralism, we might say that Darwin first located and embellished one of the few brilliant and coherent positions in an intellectual universe with few nucleating places. Either formulation engenders the same result of abiding respect for Darwin's view of life—leading to proper thanks owed by all of us for the good fortune of such an interesting founder. What greater pleasure can we know than to engage Darwin in dialogue—as we can and must do, because his theory rests upon a powerful and defining essence. Darwin, in short, is the extraordinary man who, all by himself, embodied the only three beings proclaimed worthy of respect by Baudelaire—for he pulled down an old order, and came to know a large part of the new world that he created. *Il n'existe que trois êtres respectables: le prêtre, le guerrier, le poète. Savoir, tuer, et créer.* There exist only three beings worthy of our respect: the priest, the warrior, and the poet. Know, kill, and create.