trends within a clade. Change must therefore be concentrated in events of branching speciation, and trends must arise by the differential sorting of species with favored attributes. If new species generally arise in geological moments, as the theory of punctuated equilibrium holds, then trends owe their explanation even more clearly to higher-level sorting among species-individuals acting as discrete entities with momentary births and stable durations in geological time.

Organismic selection may trump species selection in principle when both processes operate at maximal efficiency, but if change associated with speciation operates as “the only game in town,” then a weak force prevails while a potentially stronger force lies dormant. Nuclear bombs certainly make conventional firearms look risible as instruments of war, but if we choose not to employ the nukes, then bullets can be devastatingly effective. The empirical pattern of punctuated equilibrium therefore becomes the factual “weapon” that overcomes Fisher’s strong theoretical objection to the efficacy of species selection.

(This argument provides a second example for the importance of punctuated equilibrium in validating the independence of macroevolutionary theory by failure of pure extrapolationism from microevolutionary dynamics. We saw previously (pp. 604–608) that punctuated equilibrium strongly fosters the argument for species as evolutionary individuals capable of operating as units of selection. We now note that punctuated equilibrium also affirms the potential strength of species selection against a cogent theoretical claim for its impotence.)

In summary, three of four classical arguments against higher-level selection do not apply to species, while the fourth loses its force in a world dominated by punctuated equilibrium. I see no barrier to the cardinal importance of species selection in the history of life.

**EMERGENCE AND THE PROPER CRITERION FOR SPECIES SELECTION**

_Differential proliferation or downward effect?_ This subject and its literature, as I have noted throughout the chapter, have been plagued to an unusual degree by conceptual confusions and disputes about basic definitions and terminology. As an important example, and as many participants have noted (see especially Damuth and Heisler, 1988; and Brandon, 1988, 1990), two quite different criteria for the definition of higher-level selection have circulated through the literature. (In most cases, they yield the same conclusion, so this situation has not produced anarchy; but in a few cases, some crucial, they may lead to different assertions, so the situation has fostered confusion.)

In the first approach, one chooses a focal level of analysis (conventionally one of the two lower levels of organism or gene), and then considers the effect of membership in a higher-level group upon fitness values of the chosen lower-level unit. If, for an identical organism, life in one kind of deme yields a fitness different from life in another kind of deme, then selection includes a group effect from the deme level. (We invoke this formulation, for example, if we argue for group selection by showing that organisms in a deme with altruists do better than identical organisms in a group lacking altruists.)

In the second approach, strongly favored here, we hold firm to the classical bare-bones Darwinian definition, but recognize that selection can work on evolutionary individuals at many hierarchical levels. Selection has traditionally been defined as the differential reproductive success of evolutionary individuals based on the fitnesses of their traits in interaction with the environment. Thus, we recognize higher-level selection by the differential proliferation of some higher-level individuals (demes, species, clades) over others—just as we define conventional natural selection by the differential reproductive success of some organisms based on phenotypic traits that confer fitness.

These two approaches often yield concordant results for the obvious reason that differential proliferation of higher-level units (the second criterion) often defines the group effect that influences the fitness of lower-level individuals chosen as a focus (the first criterion). But the two criteria need not correspond, leading to situations where we would identify group selection by one criterion, but deny the same process by the other. For example, under the first criterion of group effects on lower-level fitness, some higher-level properties of groups can influence lower units without causing any differential reproduction of the groups themselves. On this criterion, for example, some biologists have held that frequency dependent selection must be viewed, _ipso facto_, as an example of group selection—a claim simply incomprehensible under the alternative criterion of differential group proliferation. (The unresolved, and perhaps largely semantic, issue of whether kin selection should be interpreted as a form of group selection, or only an extension of conventional lower-level selection, also presupposes this criterion of group effect upon lower-level fitness—see Wilson and Sober, 1994.)

A predominantly sociological issue has often set preferences between these criteria. Paleontologists, and other students of species selection, myself included, have strongly advocated the criterion of differential reproduction for higher-level individuals as a strict and obvious analog of ordinary natural selection as conventionally understood. Neontologists and students of group selection have generally (though not always) preferred the criterion of “group effect on gene or organismal fitness,” both from fealty to Darwinian traditions for using organisms as a primary focus, and because certain contentious issues, especially the evolution of altruism, have generally been posed in organismal terms—“why can saintly Joe be so nice if he loses reproductive success thereby?”

Three major reasons lead to my strong preference for the criterion of differential proliferation correlated with properties of relevant evolutionary individuals that confer fitness in interaction with their environment. First, we thereby follow standard definitions of selection, which have always been based on causal pluralification, not on mere effect. Second, why would we ever
prefer an elaborate and indirect definition—in terms of effects on something else at a scale far removed from the causal interaction—over a simpler account rooted in the direct result of the causal process itself? Considered in these terms, the criterion of "group effect on organismal fitness" seems downright peculiar. We only entertain such a standard for contingent reasons of history and philosophical preference—the Darwinian tradition for focusing on organisms, and our larger scientific allegiance to reductionism. Third, we can too easily lose the force and location of causality when we study a phenomenon through indirect effects expressed elsewhere, rather than by immediate operation. True, we are supposed to assess the separate effects upon lower-level focal units—from deme membership, or species membership, for example. But since several higher levels may simultaneously affect a lower focal unit, we may not be able to untangle the differences, and we may end up with an account of consequences, rather than causes.

As an obvious example of these pitfalls, I point out that gene-selectionism, with all its fallacies, arises from an erroneous inversion in the criterion of "group effect on lower-level fitness." One begins with the basic statement that membership in higher-level units affects the fitness of genes. So far, so good. But if one then makes the error of assuming that replicators, rather than interactors, should be units of selection—and then chooses genes as fundamental replicators both by general reductionistic preference, and by allegiance to faithfulness in replication as a necessary criterion—then one becomes tempted to misidentify effects as causes. The gene selectionist then slides down the following slippery slope: why should I talk about higher-level interactors affecting gene fitness? why don't I just consider higher-level interactors as one aspect of the gene's environment? in that case, why should I talk about higher-level interactors as entities at all? environment is environment, however constituted, and whether clumped into interactors housing the genes or not? in fact, why even try to identify the environment's forms of clumpiness? why not, instead, simply average the gene's fitness over all aspects of environment to achieve a single measure of the gene's evolutionary prowess?

This line of argument, as its least attractive feature, relentlessly dissolves causality. We begin with the causal agents of selection—interactors at various hierarchical levels. (Even the most ardent gene selectionists, as I show on pages 631–632, cannot avoid discussing the causal process of selection in terms of these interactors.) We then represent interactors by their effects on genes. Next, we decide to consider interactors only as environments of genes. Then we lose interest in their nature and action because "environmental clumping" (the "expression" of interactors in this view) does not appear to represent an important issue. Finally, we dissolve the interactors entirely by deciding to average the fitness of genes across all aspects of the environment. And, before we notice what we have really done, causality has disappeared.

In a vigorous defense of gene selection against the hierarchical view of Wilson and Sober (1994), Dawkins (tongue-in-cheek to be sure) pretends to be "baffled" by "the sheer, wanton, head-in-bag perversity of the position that they champion" (commentary in Wilson and Sober, 1994, p. 617). Such a sense of strong psychological frustration must arise when you and your opponents seem to be saying the same thing, but in such utterly different ways, and to such radically different effect. Thus, Dawkins presents his gene-selectionist reformulation of Wilson and Sober's *Weltanschauung* (mine as well, by the way):

Selection chooses only replicators... Replicators are judged by their phenotypic effect. Phenotypic effects may happen to be bundled, together with the phenotypic effects of other replicators, in vehicles. Those vehicles often turn out to be the objects that we recognize as organisms, but this did not have to be so... There did not have to be any vehicles at all... The environment of a replicator includes the outside world, but it also includes, most importantly, other replicators, other genes in the same organism and in different organisms, and their phenotypic products.

(Note that I did not exaggerate or caricature in my previous summary; gene selectionists do regard "clumping" into vehicles as beside the point, and they do dissolve these vehicles—the true units of selection—into "environment" considered as the sum of contexts for any gene.)

Wilson and Sober (1994, p. 641) responded to Dawkins with their own frustration:

Dawkins remains so near, yet so far... We could not ask for a better summary of the gene-centered view. The question is, are vehicles of selection absent from this account or have they merely been reconceptualized as environments of the genes. The answer to this question is obvious at the individual [organism] level, because Dawkins acknowledged long ago that individuals [organisms] can be vehicles of selection... despite the fact that they are also environments of the genes. The answer is just as obvious at the group level... [Dawkins's] passage does not refute the existence of vehicles, but merely assumes that the vehicle concept can be dispensed with and that natural selection can be studied entirely in terms of average genic effects.

Is this brouhaha much ado about nothing? Are the two views—selection on a hierarchy of interactors, and representation of all selective forces in terms of gene fitnesses, with interactors treated as environments of genes—truly equivalent, and our decision just a matter of preference, or a question of psychological judgment about superior sources of insight? Is this twofold choice just another manifestation of Dawkins's old Necker Cube (see p. 640)—a flipping between two equivalent facets of reality, an example of conventionalism in philosophy?

The answer, I think, must be a clear and resounding "no." The two alternatives represent strikingly different views about the nature of reality and causality. We all agree that we need to know causes—and natural selection is a causal process. Gene selection confuses bookkeeping (properly done at the genic level) with causality (a question of evolutionary individuals purifying...
differentially, based on interaction of their phenotypes with the environment). If we dissolve interactors into an overall "environment" of the genes, and then average a gene's fitness across all environments—the procedure of gene selectionism—then we lose causality.

Wilson and Sober (1994, p. 642) also reject the purely pluralist, or Necker Cube view: "There is no room for pluralism on these substantive empirical issues...Group-level adaptations can be represented at the individual [organism] and gene level by averaging the fitness of lower level units across higher level units. Gene- and individual-level adaptations cannot be interpreted as group adaptations without committing the errors of naive group selection, but the gene's-eye view and the individual's-eye view cannot deny the existence of group-level adaptations (when groups are vehicles of selection) without being just plain wrong."

Arnold and Fristrup (1982, p. 115) make the same point for the intrinsic reality—and not just preferential status vs. other equivalent representations—of species selection: "The characters that increase individual [organismic] fitness do not necessarily cause speciation or prevent extinction. Thus, it is misleading to adopt the convention of expressing all higher level trends in terms of individual [organism] level fitness."

For all these reasons, I strongly advocate that we define higher-level selection as the differential proliferation of relevant evolutionary individuals based on causal interaction of their properties with surrounding environments—rather than by representing the effect of higher-level membership on the fitness of a designated lower-level individual. Only in this way will we avoid a set of confusions, and two pitfalls that easily follow, one after the other, with the first as a kindly delusion, and the second as an outright error: first, a falsely pluralistic belief in the equivalency of alternative representations at different levels; and, second, the siren song of gene selection as defining the only legitimate level of causal analysis in evolution. Only in this way will we achieve a clear and unified view that treats each level in the same manner, and approaches each evolutionary individual with the same set of questions. With this apparatus of analysis, we can attain a coherent and comprehensive theory of hierarchical selection—the most potentially fruitful, promising, and proper expansion of the Darwinian research program now before us.

** Shall emergent characters or emergent fitnesses define the operation of species selection?**

Once we agree to define higher-level selection by differential proliferation of relevant units based on interaction between their traits and the environment, then we must (above all) develop clear criteria for the definition and recognition of traits in the unfamiliar world of higher-level individuals. Since we encounter enough trouble in trying to define and parse traits for the kind of individuals we know best—integral, complex, and continuous organisms like ourselves—we should not be surprised that this issue becomes particularly refractory at higher levels, and thus acts as a considerable impediment to the development of a rigorous theory of hierarchical selection. In particular, what should count, for purposes of defining evolutionary interaction with the environment, as a trait of a species?

The developing literature on this subject has featured a rich and interesting debate between two quite different approaches that, nonetheless, can be united in a coherent way to form the basis of a unified macroevolutionary theory of selection: the "emergent character" approach, as particularly championed by Elizabeth Vrba (1983, 1984b, 1985; Vrba and Eldredge, 1984; Vrba and Gould, 1986); and the "emergent fitness" approach inherent in the classic paper of Lewontin (1970), developed and defended in the important work of Arnold and Fristrup (1982), given further mathematical form in Damuth (1985), and Damuth and Heisler (1988), and most fully codified and expressed by Lloyd (1988—see also Lloyd and Gould, 1993; and Gould and Lloyd, 1999).

Grantham (1995), in an excellent review of hierarchical theories of macroevolution, has christened this discussion "The Lloyd-Vrba Debate," so the issue has now even acquired a proper name. The codification makes me feel a bit strange, since I have written papers on the subject with both protagonists (Gould and Vrba, 1982; Vrba and Gould, 1986; Lloyd and Gould, 1993; Gould and Lloyd, 1999), and do not view the issue as dichotomous; though the two viewpoints are surely distinct, and I have changed my mind—as a former supporter of Vrba's "strict construction," who became convinced that Lloyd's more inclusive formulation forges a better match with conventional definitions of selection, and provides more promise for constructing an operational theory. But Lloyd does not disprove Vrba; rather, Vrba's exclusive domain becomes a subset of "best cases" in Lloyd's formulation. In this crucial sense, the theories sensibly intermesh.

Vrba's "emergent character" approach requires that a trait functioning in species selection be emergent at the species level—basically defined as origin by non-additive interaction among lower-level constituents. Since all science works within particular sociological and historical circumstances, we must understand that the greatest appeal of this strict criterion lies in its ability to "fend off" the conventional objection to species selection in a Darwinian and reductionistic world—namely, that the trait in question, although describable as characterizing a species, "really" belongs to the constituent, lower-level parts—and that the causal process therefore reduces to ordinary Darwinian natural selection on organisms or genes. For, when Vrba's criterion of emergence holds, one can't, in principle, ascribe the trait in question to lower levels. The trait, after all, does not exist at these lower levels. It makes a "first appearance" at the species level, for the trait arises through non-additive interaction of component lower-level parts or influences. If one species proliferates differentially within a clade by higher rates of speciation based upon such populational traits as geographic range, or density of packing among organisms, then we cannot ascribe selection to the organismic level—for organisms, by the logic of definition, cannot possess a population density, while the geographic range of a species need not correlate at all, or in any
simple way, with the size of an organism's personal territory during its lifetime.

The strength of the "emergent character" criterion lies in its ability to identify a set of hard-line, unambiguous cases for species selection. For we must speak of selection among species if the relevant trait not only doesn't exist at any lower level, but can't even be represented as a linear combination of lower-level parts—for the nonadditive interactions that build the populational trait only arise within the population, and make no sense outside such an aggregation.

But we soon begin to worry that such a criterion may be too restrictive in eliminating a wide variety of traits that we intuitively view as features of populations, but that do not arise by nonlinear interaction of subparts, and do not therefore qualify as emergent by Vrba's criterion (which also matches the standard definition of the important concept of emergence in philosophy). Species and other higher-level individuals also develop features that seem to "belong" to them as an entity, but that arise additively as "aggregate" or "sum-of-the-parts" characters. Consider the mean value of a trait? This figure belongs to no individual and becomes, in this legitimate sense, a character of the population. But a mean value doesn't "emerge" as a functional "organ" of the population by nonlinear interactions among organisms. A mean value represents an aggregate character, calculated by simple summation, followed by division.

And how shall we treat variability—an even more "intuitive" candidate for a species-level character that may be important in survival and proliferation of species? An individual organism doesn't possess a variability, so the property belongs to the species. But variability also represents an aggregate character—another average of a sum-of-the-parts. Do we not want to talk about species selection when species B dies because constituent organisms show no variability for a trait that has become strongly inadaptive in the face of environmental change—while species A lives and later multiplies because the same trait varies widely, and includes some states that can prosper in the new circumstances? Yes, species B dies because each of its parts (organisms) expires. In this sense, we can represent extinction as a summation of deaths for organismal reasons. But don't we also want to say that A survived by virtue of greater variability—a trait that does not exist at the organismal level, but that surely interacted with the new environment to preserve the species?

Vrba's solution, which I greatly respect but now regard as less useful than the alternative formulation, requires that we not designate differential proliferation of species based on aggregate characters of populations as species selection—but rather that we interpret such cases as upward causation from the traditional organismal level. Vrba (1980 et seq.) has coined and developed the term "effect hypothesis" for such situations—since the differential proliferation of species A vs. species B arises as an effect of organismal properties (of the individuals in species A that vary in the "right" direction), resulting in the survival of species A.

Vrba, and (I think) all other major workers in this area, have always regarded the effect hypothesis as a macroevolutionary theory because, in a heuristic and descriptive sense, one must apply the notion to species considered as items of evolutionary history. But events under the effect hypothesis are causally reducible to the traditional organismic level. (This kind of situation represents the minimal claim for an independent macroevolutionary theory—the need for descriptive engagement at the level of species, even if no distinct causality emerges at this higher level. This book defends the stronger claim for important causal uniqueness at the species level and above. Vrba, of course, also advocates this stronger version because she argues that some cases of differential species proliferation arise by the effect hypothesis, while others occur by true species selection based on emergent characters. I advocate a much larger role for causal uniqueness by defending the emergent fitness approach, a criterion that greatly expands the frequency and importance of species selection.)

To facilitate this distinction, Vrba and I developed a terminology to resolve a common confusion in evolutionary theory between the simple, and purely descriptive, observation of differential reproductive success—which we named "sorting"—and the causal claim—always and properly called "selection"—that observed success arises from interaction between properties of the relevant evolutionary individual and its environment (see Vrba and Gould, 1986). Evolutionary biology needs this distinction because students of the field have often—with misplaced confidence in selection's ubiquity and exclusivity—made a case for selection based on nothing more than an observation of differential reproductive success (sorting), without any attempt to elucidate the cause of such sorting. A leading textbook, for example, proclaimed that "selection...is differential survival and reproduction—and no more" (Futuyma, 1979, p. 292).

Under Vrba's criterion of emergent characters, differential species proliferation by the effect hypothesis counts only as sorting at the species level—since the characters responsible for selection belong to organisms, but transfer an effect to the species level by upward causation. On the other hand, differential species proliferation based on emergent species characters does count as selection at the species level. However, under the broader criterion of emergent fitness, any species-level trait that impacts an irreducible fitness to species in their interaction with the environment defines a true process of selection at the species level, whether the trait itself be aggregate or emergent.

In the "emergent fitness" approach, we do not inquire into the history of species-level traits that interact with the environment to secure differential proliferation. We do not ask where the traits originated in a structural or temporal sense—that is, whether such traits arose by emergence at the species level, or as aggregate features by summation of properties in component organisms or demes. We only require that these traits characterize the species and influence its differential rate of proliferation in interaction with the environment. In other words, we only demand that aspects of the fitness of the
species be emergent and irreducible to the fitnesses of component organisms. For cases where species function as interactors, or potential units of selection, Lloyd and Gould write (1993, pp. 595–596):

Interactors, and hence selection processes themselves, are individuated by the contributions of their traits to fitness values in evolutionary models; the trait itself can be an emergent group property or a simple summation of organismic properties. This definition of an entity undergoing selection is much more inclusive than in the emergent character approach, since an entity might have either aggregate or emergent characters (or both) . . . The emergent fitness approach requires only that a trait have a specified relation to fitness in order to support the claim that a selection process is occurring at that level. . . . In other words, the interactor’s fitness covaries with the trait in question.

In a classic example, much discussed in the literature (Arnold and Fristrup, 1982; Gould, 1982c; Lloyd and Gould, 1993; Grantham, 1995), several clades of Tertiary gastropods show trends to substantial decrease in relative frequency of species with planktotrophic larvae vs. species that brood their young. In one common explanation (by no means universally accepted), this reduction occurs by species sorting based on the lower speciation rate of planktotrophic species—an hypothesized consequence of the lower probability for formation of isolates in species with such widespread and promiscuous larval dispersal. The sorting clearly occurs by selection, since low speciation rate arises as a consequence of interaction between traits of interactors and their environment. But at what level does selection occur?

Under the emergent character approach, the case becomes frustrating and ambiguous. Does the crucial property of “low speciation rate” in planktotrophs result from an emergent species character? In one sense, we are tempted to answer “yes.” Organisms, after all, don’t speciate; only populations do—so mustn’t the trait be emergent at the population level? But, in another sense, low speciation rate arises as a consequence of population structures induced by planktotrophy, a presumed adaptation at the organismal level—so perhaps the key character can be reduced to simple properties of organisms after all.

I have gone round and round this example for twenty years, often feeling confident that I have finally found a clear resolution, only to recognize that a different (and equally reasonable) formulation yields the opposite interpretation. All other participants in this debate seem equally afflicted by frustration, so perhaps, the fault lies in the concepts, and not in ourselves that we seem to be underlings, unable to achieve closure.

However, if we invoke the broader criterion of emergent fitness, the problem gains a clear resolution in favor of species selection. A structural feature of populations, leading to a low frequency of isolation for new demes, must be treated as a character of populations in any conventional usage of language. As stated above, individual organisms don’t speciate; only populations do—so the character belongs to the species. However, the character may represent an aggregate rather than an emergent feature—thus debarring species selection under the emergent character approach. But, under the emergent fitness approach, so long as the character (whether aggregate or emergent) belongs to the species, and so long as the fitness of the species covaries with the character—and no one denies the covariation in this case—we have detected an instance of species selection.

Arnold and Fristrup (1982, p. 114) present this argument in a clear and forceful way:

The critical characters—larval strategies—may well have arisen for reasons that can be seen as adaptive in a traditional Darwinian sense. However, regardless of the mechanism by which they became fixed, these strategies behave as properties of species in that they result in distributions of rates of speciation and extinction within this group . . . It might be tempting to assume that there are fewer planktotrophic species because the individuals in these species were somehow less fit than the individuals in non-planktotrophic species. However, it is obvious that the same result could obtain even if planktotrophic and non-planktotrophic individuals [organisms] have equal fitnesses, by virtue of the population structures that are concomitants of these larval strategies. Thus, the observed distribution of species types within these gastropods is not predicted from individuals level fitness alone, underscoring the necessity of the higher level of analysis.

In other words, the relative frequency of planktotrophic species falls not because planktotrophic organisms must be less fit (they may, in fact, be more fit on average across the clade), but because a character fixed by organismic selection yields the effect of lowering the speciation rate at a higher level. The population structure produced by planktotrophy may not rank as an emergent character, but does confer an emergent fitness at the species level—a fitness irrelevant to individual organisms, which, to emphasize the obvious point one more time, do not speciate.

Finally, we may seal the case by citing Grantham’s important argument (1995, p. 301) that “species selection does not require emergent traits because higher-level selection acting on aggregate traits can oppose lower-level selection.” Vrba herself has argued (1989, p. 80) that “the acid test of a higher level selection process is whether it can in principle oppose selection at the next lower level.” Surely such an opposition can arise “in principle” (and probably in actuality) in this case—for planktotrophy could be positively selected at the organismic level, but may, through its strong effect on population structure, and the resulting consequences for rates of speciation, enjoin negative selection at the species level.

To summarize, we all agree that an independent theory of macroevolution must identify higher-level causal processes that are not reducible to (or simple effects of) causes operating at conventional lower levels of gene and organ-
this premise defines the theoretical salience of the debate about species selection—for if such a process exists, and can also be validated as both common in evolution and irreducible in principle, then macroevolutionary theory has been achieved. For this reason, evolutionary biologists, who usually eschew academic philosophy (as the mildly philistinistic culture of science generally dictates), have joined in such classical philosophical debates as the meaning of reduction and emergence.

Vrba’s criterion of emergent characters establishes an obvious case for irreducibility because the trait that causes species selection can claim neither existence nor representation at the conventional organismic level. Grantham writes (1995, p. 308): “When a component of species-level fitness is correlated with an emergent trait, this correlation cannot be reduced because the trait cannot be represented at the lower level.” But Lloyd’s broader criterion of emergent fitness also establishes irreducibility, even if the trait involved in the correlation between trait and fitness is reducible under the effect hypothesis. In Lloyd’s case, the fitness is irreducible (as shown practically in the previous example of gastropod lineages, where higher-level fitness based on speciation rate opposes lower-level fitness based on the same trait of larval adaptation). The technical point may be summarized in the following way: selection is defined by the correlation between a species-level trait and species-level fitness; therefore, the irreducibility of either component of the correlation establishes irreducibility for the selection process. Grantham notes (1995, p. 308): “Emergent traits are not, however, necessary for species selection. If an aggregate trait affects a component of species-level fitness (e.g. rate of speciation) and this component of fitness is irreducible, then the trait-fitness correlation will be irreducible.”

Vrba’s emergent character approach embodies one great strength, but two disarming weaknesses. This criterion does identify the most irrefutable, and in many ways the most interesting, subset of cases for species selection—examples based on genuine species adaptations (for an emergent character that evolved as a consequence of its value in fitness is, ipso facto, an adaptation); whereas nonemergent characters that contribute to species fitness via the effect hypothesis are exaptations (Gould and Vrba, 1982; Gould and Lloyd, 1999), at the species level (and adaptations at the lower level of their origin).

But the emergent character criterion suffers from two problems that would render the theory of species selection, if framed exclusively in its light, eternally contentious and, perhaps, relatively unimportant as well. First, by including only the “hardest-line” cases within the concept, we may be unduly limiting species selection to an unfairly small compass. (For example, and as an analogy, we wouldn’t want to restrict the concept of “adaptation” only to the small subset of true biomechanical optima—for most adaptations only hold the status of “better than,” not ne plus ultra). Second, emergence can often be extremely difficult to document for characters—so, in practice, the concept may be untestable in most circumstances. To differentiate between a truly emergent species character and an effect of a lower-level character, one often needs a great density of narrative information about the actual history of the lineage in question—information only rarely available in the fossil record, not to mention our spotty archives for living species.

By contrast, the emergent fitness approach enjoys the great virtue of fully general applicability. For, when one only has to consider current circumstances (the trait-fitness correlation), and need not reconstruct prior history (as the designation of emergence for a species-level character so often requires), then we can study any present reality that offers enough information for a resolution. We certainly use this most broadly applicable, nonhistorical approach in traditional studies of natural selection at the organismic level—that is, we identify current selective value whether the feature conferring differential reproductive success arose as an adaptation for its current contribution to fitness, or got coopted for its present role from some other origin or utility. (In other words, both preadaptations and spandrels—features that arose as adaptations for something else, or for no adaptive purpose at all—can function just as well in a regime of current selection as true adaptations forged by the current regime.) The historical origin of characters, and their later shifts in utility, constitute a central and fascinating question in evolutionary theory—and provide a main theme for Chapter 11 of this book. But we define the process of selection ahistorically—as differential reproductive success based on current interaction between traits of evolutionary individuals and their environments—that is, the concept of selection remains agnostic with respect to the historical origin of the traits involved.

The emergent fitness approach presents four favorable features that establish species selection as a central, fully operational, and vitally important subject in evolutionary biology—thereby validating both the necessity and the distinctness of macroevolutionary theory.

1. Rather than depending upon a documentation of prior history in the narrative mode (often untestable for lack of information), we move to a fully general mathematical model that can, in principle, identify components of higher-level selection in any case where we can obtain sufficient data on the current operation of a selection process. Arnold and Fristrup (1982) expanded Price’s (1970, 1972) covariance formulae to encompass a set of nested levels, and devised an approach closely allied to analysis of covariance, considering selection at one level as a “treatment effect” upon selection at an adjacent level. Damuth and Heisler (1988) developed a similar method, also based on covariances (or regression of fitness values on characters); this procedure has been expanded by Lloyd (1988; Lloyd and Gould, 1993). As Lloyd and Gould (1993, p. 596) describe the method: “This is done by describing interactors at the lower level first. If a higher-level interactor exists, the higher-level correlation of fitness and trait will appear as a residual fitness contribution at the lower level; we must then go to the higher level in order to represent the correlation between higher-level trait and higher-level fitness.”

Lest this method seem to fall into the very reductionistic trap that species selection strives to overcome—because we begin at the lowest level and only move higher if we find a residual fitness—I point out that we use this procedure only as a convenient and operational research method, and decidedly
not with the reductionistic hope that no residuals will appear, and that the
lowest level will therefore suffice for a full explanation. We may be stuck with
the technical term “residual” as a common statistical usage in such circum-
stances—but there is nothing conceptually residual about higher-level selec-
tion. Selection at lower levels cannot be designated as more true or basic,
with higher levels then superadded if necessary. The statistical “residual” of
our procedure exists as a separate but equal natural reality in our fascinating
world of hierarchical selection.

2. The emergent fitness approach establishes a large and general realm for
the operation of species selection. Any evolutionary trend that must be de-
dcribed, at least in part, as a result of species sorting automatically becomes
subject to the analytical apparatus here proposed, and therefore a candidate
for identification of species selection. (And I can hardly imagine that any im-
portant trend unfolds without a major—I would say almost always predomi-
nant (see Chapter 9)—component of species sorting, for extensive anagene-
sis rarely occurs in single lineages, and none can persist very long without
branching in any case.)

3. The emergent fitness approach allows us to use a single, familiar, and
minimalist definition of selection in the same manner at each level—dif-
ferrential proliferation of evolutionary individuals based on interactions of their
traits with the environment. We therefore achieve a unified theory of selection
at all scales of nature. The availability of a fully operational analytical appa-
ratus, connected with this definition, greatly enhances the scientific utility of
emergent fitness as a definition of species selection.

4. As an admittedly more subjective and personal point, the emergent
fitness approach allows us to encompass under the rubric of species selection
several attributes of populations that many participants in this debate have
intuitively wished to include within the causal compass of species acting as
evolutionary individuals, but which the more restrictive emergent character
approach rules out. Many of us have felt that two distinct kinds of species
properties should figure in species selection because, for different reasons,
such features cannot function at the lower and traditional level of organismic
selection. In the first category, emergent characters of species obviously can't
operate at the organismic level because they don't exist for organisms. These
features clearly serve as criteria of species selection in either the emergent
character or the emergent fitness approach.

In a second category, some important aggregate characters of species can't
function in selection at the organismic level, not because they have no expres-
sion at this lower level (for they clearly exist as organismic properties, at least
in the form of traits that aggregate additively to a different expression at the
species level), but because such properties do not vary among organisms, and
therefore supply no raw material for selection's necessary fuel. I speak here
of a common phenomenon recognized by different jargons in various sub-
disciplines of our field—autapomorphies for cladists, or invariant Bauplan
characters for structuralists. Suppose that each species in a clade has evolved
a unique state of a homologous character—and that, within each species,
all organisms develop the same state of the character, without meaningful
variation. In this situation, all variation for the homologous character oc-
curs among species, and none at all within species. If a trend now develops
within the clade when some species live and proliferate because they possess
their unique state of the character, while others die because their equally dis-
tinct and unvarying state has become maladaptive in a changed environment,
should we call such a result species selection—for each species manifests a
single attribute, and all variation occurs among species? Interestingly, de
Vries originally coined the term species selection (see pages 448–451) for pre-
cisely this situation, where no relevant variation exists within species, and all
variation occurs among species.

To summarize: in the first situation, the character doesn't exist at the or-
ganismal level, and each species develops only one state of the (emergent)
character because the character belongs to the species as a whole. Therefore,
selection for this character can only occur among species. In the second situa-
tion, the character doesn't vary at the organismal level, and each species in a
clade has evolved a unique and different state of the character. Again, selec-
tion can only occur among species. In either situation, each species manifests
one different and unvarying state of a feature that cannot operate in organ-
smic selection—so selection for this feature can only occur among species.

The emergent status of the character leads us to designate the first situation
as species selection without any ambiguity or alternative. But we balk at de-
signating the second situation as species selection because the relevant species-
level character (lack of variation) represents an aggregate, not an emergent,
feature. The emergent fitness criterion rescues us from this dilemma, and
forges an intuitive union between the two situations by designating both
as species selection. Lack of variation—the aggregate species character—in-
teracts with the environment to influence differential rates of proliferation
among species. This character imparts an emergent fitness to the species, and
therefore becomes an agent of species selection. (After all, the species doesn’t
die because organism A, or B, or C, possesses a trait that has become mal-
adaptive; the species dies because none of its parts (organisms) can develop
any other form of the trait—and this lack of variation characterizes the spe-
cies, not any of its individual organisms.)

I believe that such “species selection on variability”—the title that Lloyd
and I gave to our 1993 paper—will prove to be a potent style of selection at
this level. (When I was struggling with the issue of whether such an aggregate
character as variability could count as a property of species, I asked Egbert
Leigh, a brilliant evolutionist and the leading late 20th century disciple of
R. A. Fisher, whether he thought that variability could operate as a character
in species selection—and he replied: “if variability isn't clearly a character of
a species, then I don't know what is.”)

To cite just one hypothetical example that I have often used to illustrate
this issue and to argue for species selection on variability: Suppose that a
wondrously optimal fish, a marvel of hydrodynamic perfection, lives in a
pond. This species has been honed by millennia of conventional Darwinian
selection, based on fierce competition, to this optimal organismic state. The gills work in an exemplary fashion, but do not vary among individual organisms for any option other than breathing in well-aerated, flowing water. Another species of fish—the middling species—ekes out a marginal existence in the same pond. The gills don't work as well, but their structure varies greatly among organisms. In particular, a few members of the species can breathe in quite stagnant and muddy waters.

Organismic selection favors the optimal fish, a proud creature who has lorded it over all brethren, especially the middling fish, for ages untold. But now the pond dries up, and only a few shallow, muddy pools remain. The optimal fish becomes extinct. The middling species persists because a few of its members can survive in the muddy residua. (Next decade, the deep, well-aerated waters may return, but the optimal fish no longer exists to reestablish its domination.)

Can we explain the persistence of the middling species, and the death of the optimal form, only by organismic selection? I don't think so. The middling species survives, in large part, as a result of the greater variability that allowed some members to hunker down in the muddy pools. (We may even argue that the optimal fish always prevailed against most members of the middling species, even at the worst time, so that most middlings died quickly when the pond dried, while the optimals hung on longer, but eventually succumbed.) The middling species survived qua species because the gills varied among its parts (organisms), not because all its members gained advantage when the environment changed. (For most middling organisms continued to fare worse than the optimal fishes.) We may represent this story at the organismal level by discussing the gills of the few middling fishes that carried the species through the crisis. But the middling species prevailed by species selection on variability—for this greater variability imparted an emergent fitness to the interaction of the species with the changed environment.

Species selection on variability also possesses the salutary property of uniting the two major themes of this book, the concepts that I regard as the most important revisions now needed to mend and strengthen the two main legs of the essential Darwinian tripod: the hierarchical theory of natural selection as a vibrant expansion of Darwin's focus on the organismal level, and the centrality of constraint as a channeler of evolutionary direction in concert with natural selection (which can no longer maintain the exclusivity that strict Darwinians wished to impart). An important component for explaining the patterning of life's history lies in limitations and channels imposed and retained by developmental architecture—and these constraints do much of their work at higher levels, in large part by influencing "species selection on variability."

I close this discussion with three points that validate the status of species selection as an irreducible macroevolutionary force, and place the proposed criteria of emergent characters and emergent fitnesses under a common rubric.

The Fallacy of "Necker Cubing" The philosophical doctrine of conventionalism, as expressed by Dawkins (1982) in his Necker Cube metaphor (see pages 640–641), presents an important challenge to claims for an independent macroevolutionary theory based on higher-level selection. For if all cases of higher-level selection, however cogently defended, represent only one legitimate way to describe a process that can always be causally expressed in terms of selection at conventional lower levels as well, then why bother (except for the fun of it, or for the psychological insight thus provided) with the alternative higher level, when the traditional Darwinian locus invariably works just as well?

I do not doubt that some evolutionary events can be alternatively expressed (and I shall mention one category under my second point below), but Necker cubing will not apply to genuine cases of irreducible species selection because the nature of the world (not the conventions of our language) regulates the locus of causality. Two reasons debar the Necker cube for true cases of species selection. First, for Vrba's "hardest" category of species selection based on emergent characters, no expression at conventional lower levels can be formulated because the relevant species character does not exist at the usual Darwinian locus of organisms. Second, for Lloyd's broader category of species selection based on the emergent fitness associated with aggregate species characters, the "Necker cubers" commit a basic error in logic. They correctly note that the aggregate character can be represented at the organismic level—so they invoke the conventionalism of alternative and equally valid expression. But, as discussed on page 659, the species-level fitness imparted by the aggregate character, not the character itself, denotes the irreducible feature that defines species selection on this criterion.

In other words, Necker cubers commit the same error in this case that Dawkins made in his original use of the metaphor to claim that all organismal selection can also be expressed in terms of gene selection. The metaphor of the Necker cube only applies when the same thing attains equal and alternative representation, not when the cube's two versions represent genuinely different aspects of a common phenomenon. In Dawkins's original error, something can always be represented at the gene level—but that something counts as bookkeeping, not as the causality of selection, which remains organismal in his standard cases. Similarly, for aggregate species-level characters involved in selection, something can always be represented at the organismic level—but that something, in this case, only involves the composition of the character, not the causal process of selection, which occurs irreducibly at the species level as identified by emergent species-level fitnesses.

A Unified Picture of Species Selection In advocating such an expanded role for species selection, we must guard against the ultimate fallacy of claiming too much—for if we turn all forms of species sorting into species selection by verbal legerdemain, then we falsely "win" by definition, but actually lose by an overly imperialistic extension that permits no distinctions.
and therefore sacrifices all utility as an empirical proposition in science. Fortunately, we can unite both criteria of emergent fitnesses and characters into a unified scheme that establishes two realms of species selection, one more inclusive than the other, but that also identifies a domain of species sorting leading us to reject causation by species selection.

Grantham (1995) has presented such a scheme, reproduced here as Figure 8-4. (I had independently developed the same system, almost with the same picture, in preparing to write this chapter. I mention this not to compromise Grantham's originality or priority in any way—for priority is chronology, and his cannot be gainsaid!—but to express the firm and almost eerie satisfaction that such a “multiple” formulation brings (see Merton, 1965), and to offer this example as proof that the inherent logic of a complex argument often drives independent researchers to a definite and almost ineluctable result—validating in this case the coherence of this “take” on species selection.)

Grantham's diagram circumscribes two realms of species selection, labeled as “hierarchical explanations.” The A realm contains Vrba's firmest examples based on emergent characters, while the B realm adds Lloyd's cases based on the emergent fitnesses associated with aggregate species-level characters. (Vrba, of course, would restrict species selection to the A realm, and ascribe the B realm to the “effect hypothesis”—but everyone seems to agree on the structure and relationships of the realms.) The A realm seems firmer because emergent characters count as adaptations of species, and maintain no expression at lower levels. The B realm seems “looser” because these aggregate species characters can be represented at the organismic level, even though they may also rise by upward causation to become exaptations of species (Gould and Vrba, 1982; Vrba and Gould, 1986; Gould and Lloyd, 1999). But, in any case, the resulting species-level fitnesses are irreducible—so the B realm also represents species selection by standard definitions of selection as a causal process.

The C realm includes cases of species sorting based on aggregate species-level characters that impart only a reducible fitness at the species level—and therefore do not count as species selection. One might add a D realm at the base for cases describable as species sorting, but not associated with any higher-level character, either aggregate or emergent, and therefore not qualifying for consideration as species selection on any definition of species as evolutionary individuals and interactors. The D realm, which may be quite large, includes several categories, most obviously species sorting based on the higher-level analog of drift—or random differentials in survival and death of species within a clade (see my summary chart, pp. 718–720).

As for any scientific theory, we want, most of all, to be able to make clear and testable distinctions at the crucial boundary between cases that affirm and cases that fall outside the hypothesis under consideration—in this case, between the B and C realms separating irreducible species selection from species sorting reducible to organismic selection. In these formative days for the theory of species selection, we have not yet developed a full set of firm criteria for making these crucial allocations. But let me suggest one guidepost at the outset. Ever since this literature began, astute workers have developed a strong intuition that species sorting based on events of differential birth (speciation rates) will usually represent true species selection, while species sorting based upon differential death (extinction) will often be reducible to organismic level (see Gilinsky, 1981; Arnold and Fristrup, 1982; Vrba and Eldredge, 1984; Grantham, 1995; Gould and Eldredge, 1977; Gould, 1983c).

The source of this intuition—which may turn out to be both wrong, and superficially based—arises from a sense that the extinction of a species may often be adequately explained simply as the summed deaths of all organisms, each for entirely organismal reasons and with no significant contribution from any species-level property. When the last reproductive organism dies, the species becomes extinct. But how could a new species originate without some involvement of population-level features? After all, individual organisms do not speciate; only populations do. But individual organisms die, and the extinction of a species might, at least in principle, represent no more than the summation of these deaths. Grantham expresses this common intuition particularly well (1995, pp. 309–310):

The concept of “speciation rate” cannot be expressed at the organismic level because there is no simple set of organismic traits that determine speciation rate. Rather, a diverse set of organismic and population-level
traits (including dispersal ability, population structure, and behavioral compatibility between members of distant populations) affect gene flow and therefore affect speciation rates. Because of the large variety of factors affecting speciation rate . . . the higher level property of "speciation rate" is, at best, extraordinarily difficult to express in organismic terms.

The speciation rate of a taxon is irreducible . . . A species goes extinct if and only if every individual dies. Whereas differences in speciation rates cannot be expressed in organismic terms, differences in extinction rates will often be reducible (unless population-level traits such as variation matter).

Thus, I suspect that the A and B realms will be heavily populated with cases based on differential speciation, whereas the C realm will feature cases based on differential extinction.

A PERSONAL ODYSSEY Many historians of science, particularly feminists like Donna Harraway (1989, 1991), have forcefully argued that scholars can strike their most effective blows against the myth of pure objectivism by being candid about the interaction of their own autobiographies with their current claims—thus exposing the inevitable (and basically welcome) cultural and psychological embeddedness of science, while opening an author's prejudice both to his own scrutiny, and to the examination of his readers. To do so obsessively or promiscuously in a book of this sort would only clutter a text that would then become even more insufferably egocentric or idiosyncratic—so I have usually desisted (except for some parts of Chapter 1, and the dubious indulgence of my appendix to Chapter 9). But I will follow Harraway's recommendation in this particular case, because no other subject in evolutionary theory has so engaged and confused me, throughout my career, as the definition and elucidation of species selection. For no other problem have I made so many published mistakes, and undergone so many changes of viewpoint before settling on what I now consider a satisfactory framework. Moreover, my basic reason for current satisfaction rests upon an interesting correction from within my own body of work—and, though I remain heartily embarrassed for not grasping both the inconsistency and the necessary resolution many years earlier, I do take some pleasure in my eventual arrival—and I do think that the story may help to illustrate the intellectual coherence of the framework now proposed in this book.

I made two sequential errors of opposite import. When Niles Eldredge and I first formulated punctuated equilibrium, I was most excited by the insight that trends would need to be reconceptualized as differential success of species, rather than anagenesis within lineages (a theme only dimly grasped in Eldredge and Gould, 1972, but fully developed in Gould and Eldredge, 1977, after much help from Stanley, 1975, and later from Vrba, 1980). I then committed the common fallacy of extending personal excitement too far—and I made the error (as we all did in these early days of "species selection" under punctuated equilibrium) of labelling as species selection any pattern that needed to be described in terms of differential success for species treated (under punctuated equilibrium) as stable entities. In other words, we failed to distinguish selection from sorting, and used the mere existence of sorting at the species level as a criterion for identifying species selection. This definition of species selection must be rejected as clearly wrong—particularly for the invalid "promotion" of several cases properly viewed as effects of causes fully reducible to conventional organismic selection.

In reaction to this previous excess, I then retreated too far in the other direction, by restricting species selection too severely—i.e., only to cases based on characters emergent at the species level (Gould, 1983c; Vrba and Gould, 1986). My later work with Elizabeth Lloyd (Lloyd and Gould, 1993; Gould and Lloyd, 1999) convinced me that emergent characters, while properly identifying species selection, only identified a subset of genuine cases, and that emergent fitness, as defended in this section, provided a conceptually broader, and empirically more testable criterion.

In preparing this chapter, I finally realized why I had originally erred in restricting species selection to emergent characters. The source for amending Vrba and Gould (1986) lay in an earlier paper that I had written with Elizabeth Vrba (Gould and Vrba, 1982), particularly in the codification of adaptation (or the origin of a character directly for its current utility) and exaptation (or the cooptation of a preexisting character for an altered current utility) as subsets of the more inclusive phenomenon of aptation (any form of current utility, whatever the historical origin).

We developed this terminology, which has now been widely accepted (see extensive discussion in Chapter 11), in order to make a crucial, but often disregarded, distinction between "reasons for historical origin" and "basis of current utility." The common conflation of these entirely separate notions has engendered enormous confusion in evolutionary theory—a situation that we documented and tried to correct in our paper (Vrba and Gould, 1986). Hardly any principle in general historical reasoning (not only in evolutionary theory) can be more important than clear separation between the historical basis of a phenomenon and its current operation. For example, crucial components of current utility often arose nonadaptively as spandrels, or side-consequences, of other features actively constructed or evolved (Gould and Lewontin, 1979).

I felt so enlightened by this distinction, and so committed (as a paleontologist and historian) to the special role of historical origin, that I longed to apply this notion to the important concept of species selection. I therefore concluded that we should not speak of species selection unless the character that imparted the relevant fitness could be identified as a true adaptation at the species level—that is, as a feature belonging to the species as a higher-level Darwinian individual, and evolved directly for current utility in promoting the differential success of the species. Emergent species characters qualify as adaptations—and I therefore felt drawn to this narrow criterion for identifying species selection.

In so doing, I committed a basic logical error about the nature of selection.
However much I may love history, selection cannot be, and has never been, defined as a historical relationship of character and result. Selection must be defined by present operation, as identified by an observable differential in reproductive success based on the current interaction of a trait of a Darwinian individual with its environment. This definition includes no reference to the historical origin of any relevant trait, which may be either an adaptation or an exaptation. Damuth and Heisler (1988) emphasize this crucial point, with an apt literary flourish at the end to note the irrelevancy of a trait's "aristocracy" (depth of historical origin, or "blue-blooded" continuity) to the hierarchy of selection:

The historical origin of a character is irrelevant to the way that it functions in a selection process. Thus, the issue of whether a character is a group or individual "adaptation," and whether it has been shaped for its present role by any particular process, is of no importance in the study of the selection mechanism. There may certainly be historical significance in such observations about the origin of characters. Nevertheless, selection evaluates characters in terms of their current relationship to fitness only, not in terms of their history. There is hierarchy in the world of natural selection, but no aristocracy.

Once I recognized the irrelevancy of historical origin to the identification of selection—my only previous rationale for insisting that characters for species selection must be species-level adaptations, and therefore emergent at the species level—I understood that the "emergent character" criterion must be rejected as too restrictive (while correctly identifying the finest subset of cases for species selection), whereas the "emergent fitness" criterion must be preferred, as not only legitimately broader in scope, but also properly formulated in terms of conventional definitions of selection. In my own preferred nomenclature, species-level characters that are exaptations rather than adaptations can function perfectly well in species selection. Aggregate species-level characters originate as exaptations of species because they arise at the organismal level and pass upwards as effects to the species level. When I mistakenly thought that characters for species selection had to be species-level adaptations, I had excluded aggregate characters (as species-level exaptations), and therefore falsely rejected the emergent fitness approach (see Gould and Lloyd, 1999, for an elaboration of this argument).

In the early 1980's, my own students Tony Arnold and Kurt Fristrup had strongly urged the criterion of emergent fitness upon me, and I well remember my bitter disappointment that I could not convince them to use the restrictive criterion of emergent characters! (I had not yet developed the nomenclature of adaptation and exaptation, and therefore did not yet possess the personal tools for a conceptual resolution.) Thus, my error reflected an active commitment (not a passive consequence of inattention), maintained in the face of an available correction that I now regard as one of the finest papers ever published on the subject (Arnold and Fristrup, 1982). I did not grasp, for another decade, how the terminology developed by Vrba and me also detailed the criterion that we both preferred. To sum up: selection operates on current utilities, and remains agnostic about historical origins in utilizing both adaptations and exaptations with equal facility. Emergent species-level characters will generally count as adaptations, thus clearly available for species selection. But all aggregate species-level characters represent potential exaptations, and therefore become equally available for species selection under the proper criterion of emergent fitness.

I would, however, salvage a lesson from this odyssey of errors. Vrba and I were not wrong in identifying emergent characters as especially interesting (we only erred in deeming them necessary for species selection). Emergent characters belong exclusively to the species. As adaptations, they become part of the defining cohesion that permits a species to function as an evolutionary individual. Emergent characters thus stand out in designating the style of individuality maintained by species. Aggregate characters, on the other hand, do not clearly define a species as a functional entity (variability, for example, represents an attribute, not an "organ," of a species)—for aggregate characters belong as much to the component organizations, as to the entire species. Thus, emergent characters are special and fascinating (though not essential to the definition and recognition of species as legitimate Darwinian individuals—see Gould and Lloyd, 1999). Emergent characters do deserve primary consideration in discussions about the structural basis of species both as natural entities in general, and as the basic individuals of macroevolution in particular. But we do not require emergent characters to identify a process of selection.

As a final note, and as one contribution to recognizing the crucial and characteristic differences among Darwinian individuals at the six primary levels of the evolutionary hierarchy, we should suspect that species selection will emphasize exaptations, whereas organismal selection employs a higher relative frequency of adaptations—for species, as more loosely organized in functional terms than organisms, probably possess far fewer emergent characters than organisms. But species "make up" for their relative paucity of adaptations by developing a higher frequency of exaptations. Most of these exaptations derive their raw material from adaptations at the organismal level that cascade upwards to effects at the species level. By joining fewer adaptations (emergent characters) with more exaptations (usually based on aggregate characters), species may become just as rich as organisms in features that can serve as a basis for selection. Species selection may therefore become just as strong and decisive as conventional Darwinian selection at the level of organisms—a process whose power we do not doubt, and whose range we once falsely extended to encompass all of nature.

Hierarchical Theory of Selection

Species as Individuals in the Hierarchical Theory of Selection

HIERARCHY AND THE SIXFOLD WAY

A literary prologue for the two major properties of hierarchies

Our vernacular language recognizes a triad of terms for the structural description of any phenomenon that we wish to designate as a unitary item or