

Stephen Jay Gould on species selection: 30 years of insight

Bruce S. Lieberman and Elisabeth S. Vrba

Abstract.—Stephen Jay Gould made impressive contributions to macroevolutionary theory; one of the topics in this area that particularly interested him was how to define and recognize species selection. Here we explore how and why Gould's ideas on concepts related to species selection evolved over 30 years, from the punctuated equilibria paper of 1972 to his "Structure of Evolutionary Theory" magnum opus published in 2002. Throughout his career his ideas on species selection shifted between three phases. Initially, Gould favored a definition of species selection that was more descriptive. Later, he came to distinguish between species sorting, which he called species selection in the broad sense, and true species selection, which is tied to the concept of species-level adaptations. Finally, he came to view species selection in a broader, more inclusive way, effectively merging the two earlier viewpoints. His ideas on species selection changed over the years because he was trying to square his views on complex concepts like adaptation, natural selection, emergence, and the independence of macroevolutionary theory. Gould's thoughts on species selection not only help to define the history of debate on the concept but also help set a course for the future.

Bruce S. Lieberman. Department of Geology, 1475 Jayhawk Boulevard, 120 Lindley Hall, University of Kansas, Lawrence, Kansas 66045. E-mail: blieber@ku.edu

Elisabeth S. Vrba. Department of Geology and Geophysics, Kline Geology Lab, Post Office Box 08109, Yale University, New Haven, Connecticut 06520-8109

Accepted: 22 April 2004

Introduction

Stephen Jay Gould had a tremendous impact on the fields of paleobiology and evolutionary biology and some of his most important contributions are in the area of macroevolutionary theory, which he helped build into an exciting, vibrant research area. One of the most contentious and interesting research topics in macroevolution has been the levels of selection debate, especially the role that species selection played in shaping evolution. Gould thought that this was a particularly salient topic, one to which he devoted much thought and energy. Indeed, he "long regarded species selection as the most challenging and interesting of macroevolutionary phenomena, and the most promising centerpiece for macroevolutionary theory" (Gould 2002: p. 731), while admitting that "no other subject in evolutionary theory has so engaged and confused me, throughout my career, as the definition and elucidation of species selection" (Gould 2002: p. 670). Although he was not the first nor the only scientist to publish on this topic, he did make important contributions.

Gould's published scientific legacy pre-

serves 30 years of engaging, insightful commentary of relevance to species selection. Here, we explore how and why Gould's views on this topic evolved, and their relevance for understanding his scientific legacy. Although over the years Gould's opinion did change regarding the nature of species selection and how to define it, he always understood the complex scientific issues associated with the levels of selection debate; his positional shifts did not represent waffling but rather his attempt to grapple with issues like adaptation, natural selection, emergence, and the primacy of macroevolutionary theory.

Punctuated Equilibrium and the Early Development of a Macroevolutionary View of Species Selection

Species selection, or at least the related group selection concept, had been recognized as a possible though not necessarily significant evolutionary force by biologists midway through the twentieth century (e.g., Fisher 1958; Wynne-Edwards 1962; Williams 1966). The concept even sneaks into discussions in Darwin's writing (1859). It is safe to say, however, that the concept was not really legiti-

mized until the development of the theory of punctuated equilibrium by Eldredge (1971) and Eldredge and Gould (1972); this represented a significant turning point for the fortunes of the species selection concept. Punctuated equilibrium is a theory that has relevance to many paleobiological topics. One aspect of its significance is that it emphasized the reality of species (Eldredge 1979, 1985, 1989; Gould 1980, 1982a,b, 1990, 2002; Vrba 1980, 1984a, 1992); as documented by Eldredge and Gould (1972) species had previously been viewed as ephemeral entities. The theory of punctuated equilibrium makes it possible to individuate species in both space and time (Eldredge 1979, 1982; Vrba 1980; Gould 1982a). Indeed, it was Ghiselin's (1974) and especially Hull's (1980) emphasis on the fact that species were individuals that contributed in an important way to discussions about species selections (see also Hull 1988). Fixity and permanence, as opposed to evanescence, make it easier to view species as objects that could be selected (Lieberman 1995).

Punctuated equilibrium was also important to the topic of species selection because it suggested a revised ontology of trends, which are one of the most significant paleontological phenomena (Gould 1990). When Eldredge and Gould (1972) focused on the nature of trends in light of punctuated equilibrium, they argued that evolutionary trends might not be due to the gradual, anagenetic modification of evolutionary lineages; instead, trends would involve cladogenesis followed by the differential success of species exhibiting change in a particular direction. Stanley (1975) expanded this notion. He argued that in light of punctuated equilibrium the differential birth or death of groups of species should be called species selection because it implied the action of a process different from strict natural selection: in Stanley's (1975) concept, species selection favors some clades of species because their included organisms are better adapted than other organisms in related clades. In this view, trends produced by species selection actually represent adaptive success at the organism level. A similar concept was subsequently used by others, including Gould and Eldredge (1977), Stanley (1979),

Gould (1980), and Arnold and Fristrup (1982). Punctuated equilibrium triggered the development of "an expanded hierarchical theory (that) would not be Darwinism as strictly defined, but it would capture, in abstract form, the fundamental feature of Darwin's vision—direction of evolution by selection at each level" (Gould 1982a: p. 381).

Species Sorting and Species Selection

Sorting is a neutral description of differential birth and death. It contains no statement about causes, and these could in fact range from random drift to selection. In Table 1, the subset of species sorting that is most relevant to our discussion about species selection is nonrandom sorting of heritable variation. We further subdivide this into three categories. Two of these are relatively clear-cut cases that either do not, or do, represent species selection, respectively: (A) where the only selected characters are those of organisms (although in this and all other cases of sorting in sexual species it is important to recognize that the emergent species-level characters of reproductive systems are relevant to speciation and extinction); and (B2) where there are selected characters that are indisputably emergent at the species level. The middle ground, case B1, has proved to be more difficult to interpret, as we discuss below.

A brief history of the debate about species selection and its definition starts with Stanley (1975) and other treatments of species selection up to 1980 (Table 1: 1), and we list three cases that have been descriptively termed species selection. A contrasting view of these early treatments was offered by Vrba (1980), who distinguished between the effect hypothesis of species sorting and true species selection. Effect species sorting occurs when lineages vary in aggregate organismal characters and selective regimes, and that variation directly effects, and explains, differences in speciation and extinction rates. In this view (Vrba 1980, 1982), species selection can be invoked only when true species-level characters interact with the environment to produce species sorting and trends (Table 1: 2).

In the ensuing debate there emerged a general agreement that cases A and B2 need to be

TABLE 1. A history and classification of terminology applied to three modes of nonrandom species sorting, involving heritable character differences among species and clades. The three modes differ in the kinds of species characters, and therefore the processes, involved. The terms used by GOULD and others are in the body of the table: SS = species selection; and EH = the effect hypothesis. The linkage between characters and terms used in cited references was either argued explicitly (shown as entries without parentheses), or implied but not directly stated (shown as entries in parentheses).

Heritable character differences among species influence species sorting (namely, there is "emergent species' fitness" sensu Lloyd and Gould 1993):			
Authors	A. Species differ in aggregate characters (genotypes and phenotypes fixed in species)	B. Species differ in characters emergent at the species level:	
		B1. Degree of genetic/phenotypic variability of the species' gene pool	B2. Population structure and distribution within species
1. Eldredge and GOULD 1972; Stanley 1975, 1979; GOULD and Eldredge 1977; GOULD 1980	SS	(SS)	(SS)
2. Vrba 1980	EH	(SS)	(SS)
3. GOULD 1982b	?SS broad sense ?EH	?SS broad sense ?EH	SS narrow sense
4. Sober 1984	"SS of"	?	"SS for"
5. Eldredge 1985; Gilinsky 1986; Jablonski 1986; Kitchell et al. 1986; Vrba and GOULD 1986; Doolittle 1987; Werdelin 1987	EH	EH	SS
6. Vrba 1989	EH	SS	SS
7. GOULD 1990	?SS broad sense ?EH	?SS broad sense ?EH	SS narrow sense
8. Lloyd and GOULD 1993; GOULD 2002	SS broad sense ("emergent fitness SS")	SS broad sense ("emergent fitness SS")	SS narrow sense ("emergent character SS")
9. Lieberman and Vrba 1995; this paper	EH	SS	SS

distinguished, although the terms proposed for case A vary (Table 1: 3–9). Gould's early input in this debate was somewhat confusing. On the one hand, he acknowledged the distinction between effect species sorting, which is not based on species-level properties, and species selection. He wrote, "I strongly recommend that the term 'species selection' be confined to . . . selection among species based on species-level properties. I shall present an example of true species selection (p. 95) . . ." (Gould 1982b: 94). On the other hand, in the same paper he coined the term "*species selection* in the broad sense" (our emphasis) and

implied its equivalence with effect species sorting; further, his examples of "true species selection," namely "species selection in the narrow sense" (p. 95), included the case of organismal eurytopy and stenotopy for which the effect hypothesis was originally illustrated (Vrba 1980). Although Gould, and others, in subsequent treatments during the 1980s accepted the conceptual and terminological distinction between effect species sorting and species selection (Table 1: 5), a similar consensus did not emerge on the intermediate case, B1. For example, Vrba (1989: Table 2) grouped case B1 with B2 as species selection, and dis-

tinguished it from effect species sorting A (as we do in this paper, Table 1: 6, 9). By contrast, Lloyd and Gould (1993) and Gould (2002) treated A and B1 as species selection in the broad sense, and called it "emergent fitness species selection" (Table 1: 8).

In spite of these differences, on the whole the definition of the effect hypothesis led many to conclude that examples of species selection require emergent characters of species (see citations after 1980 in Table 1; also see Eldredge 1982, 1985, 1989; Vrba 1982, 1984a; Vrba and Eldredge 1984; Lieberman and Vrba 1995). This emphasis on emergent characters of species recognized the fundamental association between aptation and selection (Gould and Vrba 1982; Vrba 1984a, 1989; Eldredge 1985, 1989; Lloyd and Gould 1993; Gould 2002). In order to invoke species selection there must be a clade with a character that is a species-level aptation (Lieberman 1995).

The boundaries of the domain of emergent species characters, however, remain fuzzy. There is scientific consensus that emergent characters of species cannot be reduced to characters of the component organisms, and population size, structure, and distribution are such characters (e.g., Eldredge and Salthe 1984; Vrba and Eldredge 1984; Jablonski 1986, 1987; Vrba 1989: Table 2). There is debate, however, as to how simple differences in overall variability between species and clades (case B1 in Table 1) relate to species sorting.

One of us has argued (and we both agree on this) that "emergent characters that are candidates for aptation [at the species level include] rate of variation production (by mutation and recombination) [and] variation patterns of the gene pool itself, provided they can be transmitted to descendant species" (Vrba 1989: p. 131). Such characters can be significant because related species and clades commonly differ in their degree of variability. Most such differences are evanescent and either are not passed on to descendant species or have no causal bearing on species sorting. If, however, there are genetically based differences in gene pool variability between species and clades, and these differences persist for millions of years, such differences may be based on heritable among-organism dynam-

ics, perhaps relating to sexual reproductive interactions. These differences would qualify as emergent, species-level characters; if they influenced species sorting they might be species-level aptations, and then such a case would involve species selection.

The most problematic case relevant to the definition of species selection is when differences in levels of organismal variability cause species sorting involving differential extinction in one of two sister groups. Take, for example, two sister clades, X and Y, where the species in X have, as a species-level character, monomorphism in one or more habitat-related characters; further, and as a result, clade X has a higher extinction rate during times of climatic change. By contrast, the species-level polymorphism in these characters in the species of clade Y decreases their extinction probability during times of climatic change. (This example is actually not far fetched. Brooks [2002] argued that high genetically based variability within populations of some guppy fish has dampened speciation rate in these lineages in spite of a history of environmental change.) One might be tempted to conclude in this case that differing organismal characters and selection regimes led to effect species sorting. However, because of the presence of an emergent, heritable character associated with high variability in the species of clade Y, there is heritable, nonrandom species sorting, and this qualifies as species selection. Although we currently lean toward an interpretation of species selection in our hypothetical case, we expect that the study of the origin and long-term maintenance of organismal variability in species, and its macroevolutionary consequences, will result in expansion and sharpening of this concept.

Lloyd and Gould (1993) and Gould (2002) also concluded that if the degree of variability within species promotes species sorting, this would act as a species aptation and qualify as a case of species selection; however, they arrived at this conclusion in a different way. They did not consider or even require that such characters be emergent at the species level. Rather, they argued that such sorting involves "emergent fitness" at the species level, and that this is sufficient to qualify as "species

selection in the broad sense." We partly diverge from them in this interpretation and argue that in sexual species *all* nonrandom species sorting that is caused by heritable variation, including effect species sorting, involves emergent fitness. This is because the emergent fitness in effect species sorting arises as an incidental effect of the interaction of organismal selection with the boundaries imposed by closed gene pools.

In summary, the changes in the use of the term "species selection" (Table 1) are based on the fact that Eldredge and Gould (1972), and Stanley (1975) in more detail, had identified a legitimate and important pattern that had long been ignored by evolutionary biologists; however, this pattern, species sorting, did not necessarily imply that species were actually being selected (Vrba 1980; Eldredge 1982; Gould 1982b; Vrba and Gould 1986; Lieberman and Vrba 1995). Some of the cases that had been classified as species selection by Stanley (1975, 1979), Gould (1980), and Arnold and Frisrup (1982) but that no longer deserved such an appellation (Vrba 1980; Eldredge 1982) under the revised concept included trends caused by effects related to the direction of speciation, and differences in speciation and extinction rates that could be explained by the action of natural selection (Vrba 1980). An example of the latter includes diversity dynamics in two clades of African antelopes, the Aepycerotini and Alcelaphini, that were produced by the effect hypothesis rather than by species selection (Vrba 1984b, 1987).

Still, in the literature to date there may be several examples of species selection based on population structure and distribution (in the narrow sense *sensu* Gould 2002; B2 in Table 1); and we expect that many more will be found in the future as the number of macroevolutionary analyses increases and analytical methods improve. Some of the cases documented by Hansen (1978), Gilinsky (1981, 1986), Jablonski and Lutz (1983), and Jablonski (1986) may be included as examples. The mere existence, however, of an emergent population or species-level character does not necessarily prove the operation of species selection (Lieberman et al. 1993; Lieberman and Vrba 1995).

For example, Hansen (1978), Jablonski and Lutz (1983), and others have documented how in gastropods a non-planktonic larval type produces a population structure that favors population fragmentation and speciation. They predicted that through time the number of species with a non-planktonic larval type will increase relative to the number of species with a planktonic larval type not because the organisms in these species were more fit but rather because they were more likely to speciate (Gould 1982b, 2002). In one group of gastropods, the turritellids, the number of species with a non-planktonic larval type does increase through the Cenozoic relative to the number of species with a planktonic larval type. However, phylogenetic analysis suggested that the primary reason for the trend in the turritellids was not species selection but instead the repeated conversion of planktonic to non-planktonic species with absent or minimal reversion (Lieberman et al. 1993; Lieberman 1995). Instead, mechanisms involving either development, called cell-lineage drive (Lieberman et al. 1993; Lieberman 1995) using Buss's (1987) ideas on germ-line sequestration, or organismal adaptation (Strathmann 1978), seemed implicated. Therefore, at least some of the trend pattern in the turritellids is compatible with species sorting, but the trend was not caused by species selection (Lieberman and Vrba 1995).

The distinction between species selection and other forms of species sorting, and between different kinds of species selection, is worth considering in greater detail because Gould (1982b) argued that "the inevitable confusion between (species selection in the) broad and narrow sense is most unfortunate especially since the existence of true group selection in some (but not all) trends is an important component of our (Gould and Eldredge's 1977) argument for the independence of macroevolution" (Gould 1982b: p. 94). We partly disagree with this interpretation: the independence of macroevolution is affirmed not only by species selection but also by other processes such as effect sorting among species (Vrba 1980: p. 81). (We here agree with Grantham's [1995: p. 309] conclusion on the effect hypothesis as illustrated by African mammal

clades in Vrba 1984b, 1987: "The species-level sorting is merely an incidental effect of organismic selection. Although Vrba's explanation does not introduce a higher-level process, I would maintain that this explanation is not reducible.") Our view is more in line with Gould's recognition that "the key issue for the independence of macroevolution is not whether species selection operates in all trends (it does not), but whether the necessity, under punctuated equilibrium, of regarding trends as a higher-level sorting of species implies a new level in a hierarchy of evolutionary explanation" (Gould 1982b: p. 94). Thus, Gould agreed that it was important to recognize species selection as a special type of species sorting, and the mere existence of species sorting, the pattern emphasized by Stanley (1975), was enough to justify the importance of macroevolutionary theory. Macroevolution is given expanded meaning by punctuated equilibrium, which is a theory more about species and their reality and individuality (*sensu* Hull 1980) than about speciation (Lieberman 1995).

In the middle and late 1980s Gould's views on species selection restricted the term to what he called species selection in the strong sense, and he used a definition requiring the presence of characters emergent at the species level that interacted with the environment to produce differential speciation rates (i.e., the definition of Vrba 1980, 1984a, 1989; and Eldredge 1982, 1985). As we shall see, however, Gould came to feel that this definition differed from how natural selection was defined. We do not agree with his revised interpretation. Traditionally, natural selection was always acknowledged to involve the interaction between the environment and genetically based phenotypes—namely, emergent characters of organisms—with fitness consequences emergent at the organismal level. Gould felt that the emergent character definition unnecessarily constrained the purview of macroevolution, making it a field more about documenting patterns of species sorting than identifying novel examples of species selection. (Again, we differ because we suspect the domain of species selection [as circumscribed by cases B1 and B2 in Table 1] is large; there remains the challenge of distinguishing be-

tween the various causal processes of species sorting irrespective of the terminology used.) By 1990 Gould had come to "vacillate between a strict definition (of species selection) based on emergent characters and a more inclusive construction" (Gould 1990: p. 19) (Table 1: 7), and three years later he had come to embrace the more inclusive construction (Table 1: 8).

Species Selection and Emergent Fitness

The shift in Gould's thoughts on species selection was first thoroughly documented in a paper by Lloyd and Gould (1993) where the concept of emergent fitness was introduced (Table 1). This they distinguished from the more narrowly circumscribed species selection in the strict sense, which they referred to as the emergent character definition. They argued that under the emergent fitness definition a character emergent at the species level is no longer required; instead, some differential pattern of speciation or extinction rates is necessary, and this would have to be correlated with a trait emergent at any hierarchical level. This emergent fitness definition greatly expands the amount of evolution that would be due to species selection. Still included would be the emergent character type of species selection, but also other examples that had been treated as nonselective species sorting by Vrba (1980, 1984) and Vrba and Gould (1986) would now qualify as valid examples of species selection (Table 1: 8). Further, Lloyd and Gould (1993) argued that species-level variability, a character that they did not necessarily believe was emergent at the species level, is crucial to the expanded vision of the emergent fitness criterion of species selection. Lloyd and Gould (1993) postulated that variability within species might be heritable and could promote extinction resistance; conceivably, such characters might also promote increased speciation rates, though Lloyd and Gould (1993) did not discuss this.

Gould (2002) offered three reasons that motivated his development of, and preference for, the emergent fitness concept of species selection as opposed to the emergent character approach. Although we do not necessarily agree with him, they are the following: (1) he believed that the emergent fitness definition is

more in line with the way selection is identified at the organism level; (2) he felt that the emergent character approach limits species selection to a small number of cases (he considered that only category B2 in Table 1 qualifies; as noted above, Vrba's [1989] emergent character concept and our present one is actually more inclusive); and (3) he felt that convincingly demonstrating that characters are truly emergent at the species level is problematic. At least two crucial issues are raised by Lloyd and Gould's (1993) and Gould's (2002) emergent fitness approach: the concept of adaptation or exaptation and its relationship to species selection, and how to treat characters such as species-level variability.

Adaptation and Exaptation at the Species Level.—As defined by Gould and Vrba (1982) adaptations are characters that are currently enhancing fitness and that were constructed by natural selection to function in that particular role; thus, their selection context has not varied historically. By contrast, exaptations are characters that now perform a current function that is subject to selection, but they initially either were not shaped by selection at all or were shaped by selection for a different role. Lloyd and Gould (1993) and Gould (2002) argued that whereas the emergent character approach to studying species selection requires the identification of adaptations at the species level that interact with the environment and produce differential survival (extinction) and especially differential birth (speciation) rates, the emergent fitness approach only requires the identification of exaptations of species that arise at the organismal level and pass upwards as effects to the species level. We do not, however, see this as a valid distinction between the strict and broad species selection concepts. As argued by Vrba (1989: pp. 135–136), when using the strict concept of species selection, most species adaptations are likely to be exaptations, while true species adaptations, if they exist at all, must be much rarer.

Species-Level Variability and Species Selection.—The primary example that Lloyd and Gould (1993) and Gould (2002) invoked to demonstrate a case of their version of species selection involved two hypothetical species:

one with little variation that is well adapted to a particular narrow environment, and another with abundant variation that is moderately adapted to several environments. If there is an environmental perturbation, it is the second more poorly adapted, variable species that is most likely to survive, whereas the better adapted but less variable species is more likely to go extinct. Lloyd and Gould (1993) argued that this example represents emergent fitness without emergent species properties. Their example is closely related to the one we described above of sister taxa X and Y, differing in levels of organismal variability and therefore in extinction rate, which we explored above as a case of species selection. In discussing this variability-based example of "emergent fitness species selection," Gould concluded that "Vrba's solution . . . requires . . . that we interpret such cases as upward causation from the traditional organismal level . . . [consistent with the] 'effect hypothesis'" (Gould 2002: p. 658; see also Lloyd and Gould 1993). However, this is erroneous and based on a misunderstanding of Vrba (1989), who included "variation patterns of the gene pool itself, provided they can be transmitted to descendant species" (p. 131) as emergent species characters relevant to species selection.

Whatever one calls this example identified by Lloyd and Gould (1993) and Gould (2002), it is clear that it involves a type of pattern that cannot be explained by recourse to the traditional neo-Darwinian world view that prevailed before the development of punctuated equilibrium and the demonstration of the stability, reality, and individuality of species (see Hull 1980, 1988). Their hypothetical example involving species-level variability cannot be explained by natural selection operating in a world where species are evanescent. To understand it, organisms must instead be viewed in the context of species; Lloyd and Gould have presented a classic example of nonselective species sorting. Their example demonstrates how the existence of species can powerfully shape the course of the evolutionary process. Although we disagree with Lloyd and Gould (1993) and Gould (2002) in the particulars about their definition of species selection, preferring the concept Gould embraced

earlier (e.g., Vrba and Gould 1986), we share strong concordance with them that species provide the fundamental context-dependence for organisms that influences patterns and processes in the history of life. Even if selection never operated above the level of individual organisms (which we do not believe), still, the geometry of evolution will be very different if species are real and relatively stable entities, compared with a world where species are not real and stable through time (Lieberman and Vrba 1995).

Conclusions

The issues that Stephen Jay Gould raised throughout his career regarding the prevalence and nature of species selection are insightful and important. Indeed, this topic, along with the related topic that species are real entities, stable for most of their history, which derives from his and Eldredge's theory of punctuated equilibrium, permeates many of his scientific writings. His work in this area helped develop macroevolutionary theory and expand current visions of evolutionary biology. He did this not by focusing primarily on the complex adaptations that organisms possess. Although a legitimate area of research, this has been thoroughly explored by Darwin and others (and also considered by Gould in many of his publications). Instead, with this work Gould focused on the related and equally interesting issue of what promotes trends within clades whose organisms possess these adaptations, and how clades wax and wane over geological time. The latter issues are primarily within the direct purview of paleontology. The emphasis on the stability of species provided by punctuated equilibrium suggests that characters that increase organismic fitness do not necessarily enhance speciation or prevent extinction, and that an important part of evolutionary theory is the causes and consequences of species sorting (Eldredge 1979, 1982; Vrba 1980; Gould 1982b, 2002). In effect, then, the discontinuity of species in space championed by Dobzhansky (1937) and Mayr (1942), and also their stability through time, first championed by Eldredge (1971) and Eldredge and Gould (1972), implied that the causes for how adaptive diversity is distrib-

uted within and among clades might reside not simply at the organismic level (mediated by natural selection) but also at the species level (species sorting and species selection). Future debates in macroevolutionary theory will continue to address the nature and various causes of species sorting. In any event, it is clear that Stephen Jay Gould was at the vanguard of many macroevolutionary topics and helped define not only the present but also the future of the debate about the nature of macroevolutionary theory in general and species selection in particular. In closing, it is worth recognizing that one topic that Gould championed throughout his career (e.g., Gould 1989, 1996, 2002) was contingency, for "in contingency lies the power of each person . . . to make a difference . . . spelling . . . vast improvement" (Gould 2002: p. 1346). This principle of contingency, and the impact a single person can have on a scientific field, is wonderfully illustrated by Stephen Jay Gould's contributions to paleobiology.

Acknowledgments

We thank D. Ackerley, N. Eldredge, R. Kaesler, and one anonymous reviewer for comments on earlier versions of this paper. B.S.L.'s research was supported by National Science Foundation grant EAR 0106885, a Self Faculty Fellowship, and NASA Astrobiology grant NNG04GM41G.

Literature Cited

- Arnold, A. J., and K. Fristrup. 1982. The theory of evolution by natural selection: a hierarchical expansion. *Paleobiology* 8: 113–129.
- Brooks, R. 2002. Variation in female mate choice within guppy populations: population divergence, multiple ornaments and the maintenance of polymorphism. *Genetica* 116:343–358.
- Buss, L. W. 1987. The evolution of individuality. Princeton University Press, Princeton, N.J.
- Darwin, C. 1859. On the origin of species. (Facsimile of first edition.) Harvard University Press, Cambridge.
- Dobzhansky, T. 1937. *Genetics and the origin of species*. Columbia University Press, New York.
- Doolittle, W. F. 1987. The origin and function of intervening sequences: a review. *American Naturalist* 130:55–85.
- Eldredge, N. 1971. The allopatric model and phylogeny in Paleozoic invertebrates. *Evolution* 25:156–167.
- . 1979. Alternative approaches to evolutionary theory. *Bulletin of the Carnegie Museum of Natural History* 13:7–19.
- . 1982. Phenomenological levels and evolutionary rates. *Systematic Zoology* 31:338–347.
- . 1985. *Unfinished synthesis*. Oxford University Press, New York.

- . 1989. *Macroevolutionary dynamics*. McGraw Hill, New York.
- Eldredge, N., and S. J. Gould. 1972. Punctuated equilibria: an alternative to phyletic gradualism. Pp. 82–115 in T. J. M. Schopf, ed. *Models in paleobiology*. Freeman, Cooper, San Francisco.
- Eldredge, N., and S. N. Salthe. 1984. Hierarchy and evolution. *Oxford Surveys in Evolutionary Biology* 1:184–208.
- Fisher, R. A. 1958. *The genetical theory of natural selection*, 2d ed. Dover, New York.
- Ghiselin, M. T. 1974. A radical solution to the species problem. *Systematic Zoology* 23:536–544.
- Gilinsky, N. L. 1981. Stabilizing species selection in the Archaeogastropoda. *Paleobiology* 7:316–331.
- . 1986. Species selection as a causal process. *Evolutionary Biology* 20:248–273.
- Gould, S. J. 1980. Is a new and general theory of evolution emerging? *Paleobiology* 6:119–130.
- . 1982a. Darwinism and the expansion of evolutionary theory. *Science* 216:380–387.
- . 1982b. The meaning of punctuated equilibrium and its role in validating a hierarchical approach to macroevolution. Pp. 83–104 in R. Milkman, ed. *Perspectives on evolution*. Sinauer, Sunderland, Mass.
- . 1989. *Wonderful life*. Norton, New York.
- . 1990. Speciation and sorting as the source of evolutionary trends, or ‘things are seldom what they seem.’ Pp. 3–27 in K. J. McNamara, ed. *Evolutionary trends*. Belhaven Press, London.
- . 1996. *Full house*. Harmony Books, New York.
- . 2002. *The structure of evolutionary thought*. Harvard University Press, Cambridge.
- Gould, S. J., and N. Eldredge. 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology* 3: 115–151.
- Gould, S. J., and E. S. Vrba. 1982. Exaptation—a missing term in the science of form. *Paleobiology* 8:4–15.
- Grantham, T. A. 1995. Hierarchical approaches to macroevolution: recent work on species selection and the “effect hypothesis.” *Annual Review of Ecology and Systematics* 26:301–321.
- Hansen, T. A. 1978. Larval dispersal and species longevity in Lower Tertiary gastropods. *Science* 199:885–887.
- Hull, David L. 1980. Individuality and selection. *Annual Review of Ecology and Systematics* 11:311–332.
- . 1988. *Science as a process*. University of Chicago Press, Chicago.
- Jablonski, D. 1986. Larval ecology and macroevolution in marine invertebrates. *Bulletins of Marine Science* 39:565–587.
- . 1987. Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. *Science* 238:360–363.
- Jablonski, D., and R. A. Lutz. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Reviews* 58:21–89.
- Kitchell, J. A., D. L. Clark, and A. M. Gombos. 1986. The selectivity of mass extinction: causal dependency between life history and survivorship. *Palaios* 1:504–511.
- Lieberman, B. S. 1995. Phylogenetic trends and speciation: analyzing macroevolutionary processes and levels of selection. Pp. 316–337 in D. H. Erwin and R. L. Anstey, eds. *New approaches to speciation in the fossil record*. Columbia University Press, New York.
- Lieberman, B. S., and E. S. Vrba. 1995. Hierarchy theory, selection, and sorting. *BioScience* 45:394–399.
- Lieberman, B. S., W. D. Allmon, and N. Eldredge. 1993. Levels of selection and macroevolutionary patterns in the turritellid gastropods. *Paleobiology* 19:205–215.
- Lloyd, E. A., and S. J. Gould. 1993. Species selection on variability. *Proceedings of the National Academy of Sciences USA* 90:595–599.
- Mayr, E. 1942. *Systematics and the origin of species*. Columbia University Press, New York.
- Sober, E. 1984. *The nature of selection*. MIT Press, Cambridge.
- Stanley, S. M. 1975. A theory of evolution above the species level. *Proceedings of the National Academy of Sciences USA* 72: 646–650.
- . 1979. *Macroevolution: pattern and process*. W. H. Freeman, San Francisco.
- Strathmann, R. R. 1978. The evolution and loss of feeding larval stages in marine invertebrates. *Evolution* 32:894–906.
- Vrba, E. S. 1980. Evolution, species and fossils: how does life evolve? *South African Journal of Science* 76:61–84.
- . 1982. The evolution of trends. Pp. 239–246 in J. Chaline, ed. *Modalités, rythmes, et mécanismes de l'évolution biologique (Colloques internationaux du centre national de la recherche scientifique, No. 330)*. Editions du Centre National de la Recherche Scientifique, Paris.
- . 1984a. What is species selection? *Systematic Zoology* 33: 318–328.
- . 1984b. Evolutionary pattern and process in the sister-group Alcelaphini-Aepycerotini (Mammalia: Bovidae). Pp. 62–79 in N. Eldredge and S. M. Stanley, eds. *Living fossils*. Springer, New York.
- . 1987. Ecology in relation to speciation rates: some case histories of Miocene-Recent mammal clades. *Evolutionary Ecology* 1:283–300.
- . 1989. Levels of selection and sorting with special reference to the species level. *Oxford Surveys of Evolutionary Biology* 6:111–168.
- . 1992. Mammals as a key to evolutionary theory. *Journal of Mammalogy* 73:1–28.
- Vrba, E. S., and N. Eldredge. 1984. Individuals, hierarchies and processes: towards a more complete evolutionary theory. *Paleobiology* 10:146–171.
- Vrba, E. S., and S. J. Gould. 1986. The hierarchical expansion of sorting and selection: sorting and selection cannot be equated. *Paleobiology* 12:217–228.
- Werdelin, L. 1987. Jaw geometry and molar morphology in marsupial carnivores: analyses of a constraint and its macroevolutionary consequences. *Paleobiology* 13:342–350.
- Williams, G. C. 1966. *Adaptation and natural selection*. Oxford University Press, New York.
- Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behaviour. Oliver and Boyd, Edinburgh.