Hierarchy Theory, Selection, and Sorting

A phylogenetic perspective

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The hierarchical structure of nature has seldom been prominently emphasized in evolutionary theory, although it has been recognized by a broad range of evolutionary biologists (e.g., Dobzhansky 1937, Eldredge 1985, Mayr 1963). Its marginal role may be partly due to what is perceived as a paucity of examples and to the difficulty in formulating tests to analyze hierarchical structure. In this article, we discuss how a phylogenetic perspective can be used as a technique to study the hierarchical structure of nature. We analyze how sorting and selection act at levels in addition to those of classic organismic natural selection.

Various fields of biology have produced empirical and conceptual advances supporting the need to

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Information about clade shape and topology is important to any test of higher level selection

consider several hierarchical levels in evolutionary theory. In evolutionary biology, the development of the theory of punctuated equilibria (Eldredge and Gould 1972) was an important conceptual advance. It postulated that species are morphologically static throughout most of their history and have distinct and rapid births and deaths. The formulation of Eldredge and Gould imbues species with an existence in nature and through time. This theory about species formation and persistence, in conjunction with the recognition that species are spatiotemporally bounded entities—or individuals as defined by Ghiselin (1974)—indicates that factors influencing the births and deaths of species should be taken into account in evolutionary theory (Eldredge 1989a, b). It also implies that selection among species could occur, a possibility that Eldredge and Gould (1972) and Stanley (1975) explored. The debate, discussion, and analysis of the validity of species selection, as well as the determination of criteria to be used for its recognition, led in part to the fruition of a nascent hierarchical expansion.

Also relevant to this expansion was the discovery that selection operates, in a manner analogous to Darwinian natural selection, at several levels in addition to genes and organisms. For instance, the growth of molecular biology has led to the recognition that several regions of the genome—not only genes encoding phenotypes—can act as units of selection (e.g., Doolittle 1987, Doolittle and Sapienza 1980, Dover 1982, Orgel and Crick 1980). Levels where selection is now thought to work include cell lines and demes, in addition to noncoding DNA. In the past, scientists had suggested that selection might occur at each of these levels (e.g., Roux 1881, Smuts 1925, Wright 1931, Wynne-Edwards 1962), but their conclusions were either provisionally refuted or ignored.

The difference between sorting and selection

In order to continue a discussion on hierarchy theory and selection one must first define *sorting* and distinguish it from *selection*. Such a distinction is needed to recognize that both can occur at several levels.

Sorting is the pattern of differential survival and/or reproduction of entities. It occurs at levels including genes, cells, organisms, groups, and species (Vrba and Gould 1986). In contrast, selection is the interaction between heritable, varying, emergent characters of individuals and the environment that causes differences in birth and/or death rates of those individuals (Vrba 1989). Se-

lection is one of many processes that can produce a pattern of sorting.

To demonstrate that sorting is due to selection, it is necessary to show that there are heritable, variable character differences. It is also crucial to recognize the hierarchical level at which character differences that can be selected are manifested, or emergent. For instance, spots on a leopard are emergent at the level of the individual leopard. They are not emergent at the level of its cells or genes, though the spots certainly are the products of cellular and genetic processes. Similarly, a divided population structure in which a species is split up into many genetically distinct, isolated populations is a character emergent at the population level, because organisms do not have population structures although they have behaviors that may result in a certain population structure. With these clarifications, the definition of *selection* is valid whatever the hierarchical level of the selected entities or individuals under study. Thus, hierarchy theory embodies the essence of Darwin's selectionist argument, expanded to work at several hierarchical levels (Gould 1982).

Not all authors have operationalized this definition of *selection*. Some, such as Sober (1984) and Arnold and Fristrup (1982), have argued that the criteria used to recognize selection should not be identical across different hierarchical levels. In particular, they have argued that *group selection* should be given a broader interpretation so as to encompass instances of group context dependence, where an organism's fitness is affected by its presence in a particular group, but the group's fitness does not change apart from the additive fitness of the individuals it contains. Thus, their definition of *group selection* includes instances in which the group increases in size or in which the representation of particular characters possessed by organisms within a group increases, without the need for increases in the number of groups or the need for characters emergent at the group level (Vrba 1989). This definition may be plausible, but then group selection would not be analogous to Darwin's conception of natural selection acting on organisms.
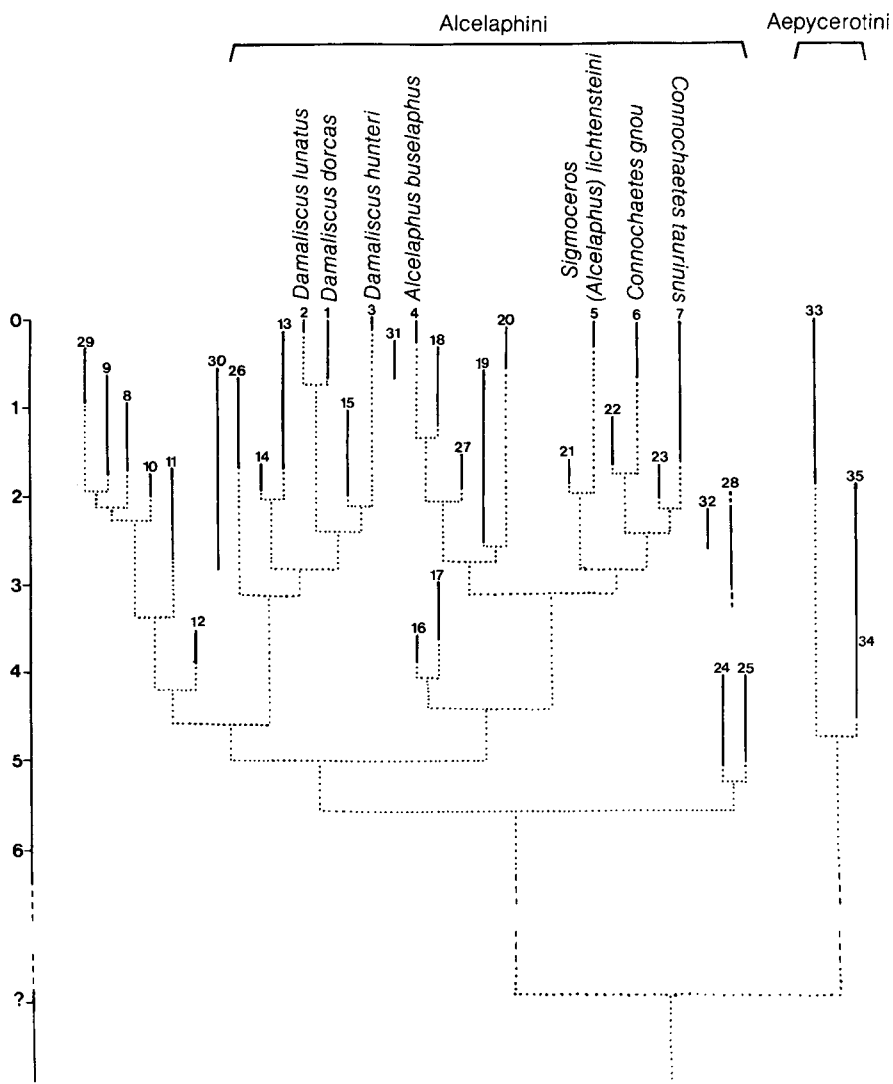

Figure 1. A phylogeny based on morphological data illustrating different rates of speciation in the Alcelaphini (wildebeests, hartebeests, and blesbuck) and Aepycerotini (impala) sister groups. Also shown are the durations of taxa. Figure adapted from Vrba (1984b). Morphological data support the alcelaphine-impala sister group relationship; however, molecular sequence data are ambiguous about the precise placement of the impala clade (Gatesy 1993).

Sober's (1984) and Arnold and Fristrup's (1982) definition of *group selection* is similar to that used in the studies of Wade (1977) and Wilson (1977). Wade and Wilson identified cases of group selection that we classify as cases of group sorting and/or context dependence, because in their examples the sorting of groups was either caused by properties of organisms or the groups were not even sorted but organisms were affected by their group membership (Mustapha Mond sorting, according to Vrba 1989). Cases of group sorting only equate with group selection if there are emergent group characters and

if their presence leads to differential group birth and/or death rates. However, the studies of Wade and Wilson have fundamental importance because they point out that the existence of groups in the natural world is vital to understanding evolutionary theory. In addition, their studies support the contention that groups and species exist and are a valid level in the hierarchy of life, not an artificial construct.
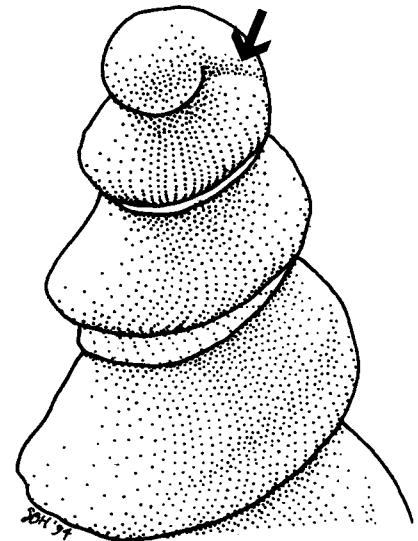
Hierarchical selection and sorting emphasized

Work in several areas has validated a hierarchical approach to the study
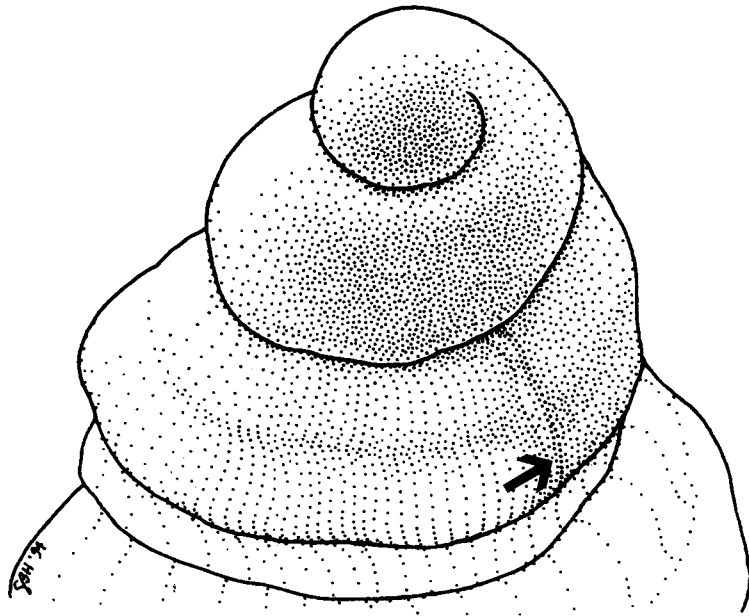
a
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Figure 2. An illustration of two representative shell morphologies in the Turritellidae showing the larval shell or protoconch, the transition to the juvenile stage, and the juvenile stage (X 100) for (a) a nonplanktonic species, with transition from larva to juvenile occurring after approximately 2.5 whorls and denoted by arrow and initiation of linear band of stipples; and (b) a planktonic species, with transition occurring after approximately 0.5 whorls and denoted by arrow and initiation of linear band of stipples.

of selection processes. The elucidation of the mechanism of molecular drive (Dover 1982) and the demonstration of selfish DNA (Doolittle and Sapienza 1980, Orgel and Crick 1980) imply selection acting within nuclear DNA molecules. In addition, selection occurs among mitochondrial DNA (Rand and Harrison 1986). Other important hierarchical perspectives indicate that large chunks of the genome can act as a single replicator, with chromosomes serving as units of selection (Nei 1987). The studies of Eberhard (1980, 1990) concluded that organelles within cells and bacterial plasmids can operate as units of selection. Also, cell-lineages within bodies can act as venues for selection processes. There are well-known examples within the immune system (e.g., Buss 1987).

One of the most contentious issues in the levels-of-selection debate is whether species selection occurs, and if it does whether it is an important force in the history of life. It is likely that many of the trends seen in the fossil and extant biota, particularly those involving differences in the diversity of clades, involve some sort of species sorting, and

their explication may in some cases be possible by recourse to species selection.

Some of the first cogent arguments for the role of species selection in evolution were presented by Stanley (1975), building upon the findings of Eldredge and Gould (1972). Stanley considered a pattern of differential species births and deaths to be a form of species selection that was analogous to natural selection. However, what he called *species selection* was not entirely analogous to Darwinian selection but referred to a type of species sorting. In particular, he did not focus on emergent properties of species that related to the differential birth and death of species but simply focused on differences in the amount of speciation and extinction (Eldredge 1989b).

In the search for cases of species selection, scientists have concentrated on two distinct evolutionary modes (Sober 1984). The first mode is based on the views of Wynne-Edwards (1962), who argued that species fitness was governed by resistance to extinction and species longevity. The second mode is based on the models of Wright (1931) and

posits that species fitness is directly related to the ability of species to produce additional species. These two modes correspond, respectively, to the differential survival and differential reproduction parts of our definition of *selection*.

In the quest to document species selection, some authors have concentrated on aspects of species survival (e.g., Eldredge and Cracraft 1980, Eldredge and Gould 1972), while other authors have emphasized aspects of species reproduction (e.g., Vrba 1984a, 1989). Thus far, the best prospects for elucidating species selection appear to lie with those studies that emphasize the differential proliferation of species, because emergent properties of species related to their reproduction are easier to identify than emergent properties of species related to their survival (Eldredge 1985, Vrba 1989).

An example of an emergent property of species related to their reproduction is the specific mate-recognition system (Lieberman 1992). It is a fertilization system that allows the initiation of reproductive interactions by signaling between mating partners or their cells (Paterson

1985). It is a group-level feature, because it requires a male and a female in order to operate (Lieberman 1992). A single organism cannot have a specific mate-recognition system, unless it is asexual.

Species selection has mainly been invoked to explain trends such as evolutionary patterns in which there are large numbers of species in one clade relative to the number in its closest relative clade or sister-taxon. There have been some explicit tests of the species selection hypothesis using clades known from the fossil and extant biota. One of these tests (Vrba 1980, 1984a) considered a trend in African bovids, the mammalian group including antelopes, wildebeests, and cows. In this test, one group of antelopes (the Alcelaphini), which includes the hartebeests and gnus, is known to be very diverse in the fossil and living biota compared with its closest extant group, the impala (Figure 1). When analyzed in detail, these differences in diversity were found not to be a consequence of emergent properties of antelope species, but rather they were due to different patterns of resource use by alcelaphine and impala organisms (Vrba 1989). Alcelaphine organisms are ecological specialists, while impalas are ecological generalists. These patterns of resource use by organisms led to a pattern of species sorting among antelope species (Vrba 1987, 1989). This trend in species diversity could be explained as an effect of organismal behavior rather than species selection, and this kind of species sorting was therefore termed the *effect hypothesis* by Vrba (1980).

These results suggest that species selection does not explain the difference in species diversity among the African bovids. However, organismal fitness is influenced by an organism's existence within a species. Existence of an organism within a species (or context dependence) implies a pattern different from selection strictly at the organismal level without the existence of groups, because patterns at a lower level cannot be smoothly extrapolated to a higher level. As evidence, there are far more species of alcelaphines than impalas, but the number of organisms within these two clades is esti-
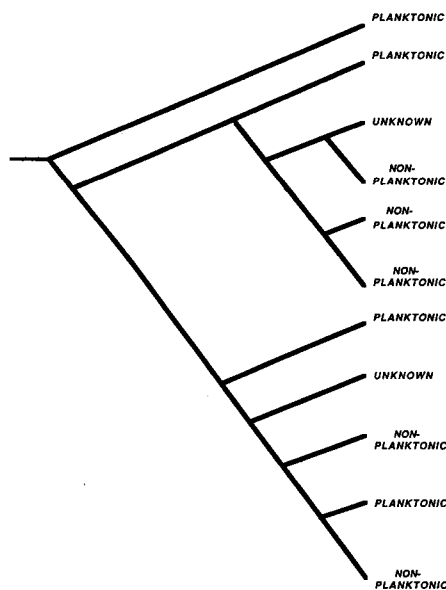

Figure 3. The shortest length tree for the turritellid gastropods produced by phylogenetic analysis of a portion of the 16s ribosomal RNA gene in the mitochondria with the larval type of each species substituted for the species name. From data in Lieberman et al. (1993).

mated to be equivalent (Vrba 1987). Thus, even if species selection does not operate, the existence of biological units of organization above the level of the individual organism can have evolutionary effects.

Studying levels of selection using phylogenies

One of the important roles ascribed to selection processes, particularly species selection, is the generation of trends. Such trends often take the form of diversity gradients in which taxa with a certain character, presumably emergent at the species level, are likely to have a large number of species when compared with their closest relatives that lack the character. However, this pattern does not by itself unequivocally support species selection (Lieberman 1995). It merely suggests species sorting, which may be explicable by one or more causal processes. Assays can be conducted to study trends and discriminate species sorting from species selection; however, these analyses must include a phylogenetic framework because the fundamental evidence for the existence of trends is information about clade

shape and topology, which is equivalent to phylogenetic patterns.

A phylogenetic approach was used by Lieberman et al. (1993) to analyze a frequently cited trend in the fossil and living marine gastropod biota that had typically been ascribed to species selection. They studied a group of marine gastropods, the Turritellidae, whose species generally possess one of two distinct larval types—planktonic and nonplanktonic (Figure 2). Information from population genetic studies on marine organisms suggests that the isolated, subdivided population structure produced by a nonplanktonic larval type is likely to lead to high speciation rates relative to those engendered by a planktonic larval type (Scheltema 1986). In addition, in the fossil and extant biota, turritellids with a nonplanktonic larval type outnumber those with a planktonic larval type by a factor of two or three. This information led Spiller (1977) and Jablonski and Lutz (1983) to ascribe this trend to species selection.

Lieberman et al. (1993) and Lieberman (1995) use phylogenies to determine both the polarity and distribution of planktonic and nonplanktonic larval types in the turritellid clade. A molecular phylogeny of the turritellids was determined, and the larval type of each gastropod species was mapped onto the phylogeny (Figure 3). This phylogeny predicts that in the turritellids a planktonic larval type is primitive and that a nonplanktonic larval type arose at least two times from planktonic turritellid lineages (assuming parsimonious character optimizations). Thus, a nonplanktonic larval type was not a single adaptation (sensu Coddington 1988) or a key innovation associated with elevated diversification rates in the turritellids.

Therefore, at the level of the Turritellidae, species selection cannot explain the trend in larval-type diversity. However, the separate acquisitions of a nonplanktonic larval type, if associated with subsequent elevated diversification, may have been driven by species selection. To determine this possibility, a comparison of diversification rates of planktonic and nonplanktonic species (based on information from

the fossil record) is needed.

In this case, the role of species selection must be minor, because in both the fossil and extant turritellids the ratio of nonplanktonic to planktonic species is only 2:1 or 3:1. This ratio can arise as a simple by-product of the other pattern manifest in the phylogeny (Lieberman et al. 1993).

The phylogeny in Figure 3 indicates an evolutionary asymmetry, with planktonic lineages giving rise to both nonplanktonic and planktonic taxa whereas nonplanktonic lineages chiefly give rise to nonplanktonic taxa. Such asymmetries or biases, recognized in other taxa, have been considered evidence for selection acting on individual organisms to prevent the reacquisition of a long planktonic[1] larval stage after the structures necessary for feeding during such a stage have been lost (e.g., Hansen 1982, Wray and Raff 1991). Lieberman et al. (1993) proposed that in the turritellid gastropods such asymmetries may also represent sorting or selection operating at the level of developing cell lineages. In the case of these gastropods, such sorting or selection would involve the timing of germ-line sequestration, which appears to be tied to larval type and the timing of larval metamorphosis (Lieberman et al. 1993). Species with a planktonic larval type have a long-lasting window in development (as defined by Buss 1987) during which they may be subject to heritable changes in ontogeny, while species with a nonplanktonic larval type have a narrow window and are likely to be buffered and resistant to developmental modification (Lieberman et al. 1993).

The trend witnessed in the turritellids would be produced by this mechanism in the following manner: Species with a planktonic larval type, if they sequester the germ-line at a late stage, can give rise to species with both planktonic and nonplanktonic larval types, while species with a nonplanktonic larval type would give rise almost exclusively to nonplanktonic species. Even assuming equal diversification rates in nonplanktonic and planktonic lineages (i.e., no species selection), nonplanktonic species

would still come to predominate (Lieberman et al. 1993).

This mechanism has been termed *cell-lineage drive* by Lieberman (1995) in analogy to Dover's (1982) molecular drive. Thus, it is the multiple origin of nonplanktonics and the asymmetrical transformation vector from planktonics to nonplanktonics, in conjunction with information about differences in diversity of the two larval types from the fossil and extant biota, that suggests species selection alone is not driving the trend in the turritellids. Determining if cell-lineage drive is actually operating in the turritellids would require experimental manipulations of development, studies of molecular markers of germ-line differentiation, and computer modeling experiments.

The results of these studies suggest that deterministic sorting or selection processes acting at hierarchical levels beyond that of the organism may produce trends. Species selection is still a valid hypothesis, but all tests of the hypothesis conducted thus far have indicated that either it does not apply to the particular case being studied or it is one among several selection processes operating. However, such studies are only in their infancy. Many additional cases await study, with phylogenetic analysis to provide the information about clade shape that is vital for evaluating hypotheses about trends in species diversity.

Conclusions

Acting at several hierarchical levels, selection processes and sorting may play a prominent role in shaping the major features of diversity and biological organization. We believe that all of the disciplines in biology (e.g., molecular, developmental, population genetics, zoology, and paleontology) are relevant for formulating and testing hypotheses about selection processes. However, when considering hypotheses about whether or not species selection acts to drive trends, the fundamental data required include information about clade shape and topology. Thus, an important component of any test of higher level selection is phylogenetic analysis.

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