

Paleontological Society

Micro- and Macroevolution: Scale and Hierarchy in Evolutionary Biology and Paleobiology

Author(s): David Jablonski

Source: *Paleobiology*, Vol. 26, No. 4, Supplement (Autumn, 2000), pp. 15-52

Published by: Paleontological Society

Stable URL: <http://www.jstor.org/stable/1571652>

Accessed: 28/10/2008 17:29

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=paleo>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.



Paleontological Society is collaborating with JSTOR to digitize, preserve and extend access to *Paleobiology*.

<http://www.jstor.org>

Micro- and macroevolution: scale and hierarchy in evolutionary biology and paleobiology

David Jablonski

Abstract.—The study of evolution has increasingly incorporated considerations of history, scale, and hierarchy, in terms of both the origin of variation and the sorting of that variation. Although the macroevolutionary exploration of developmental genetics has just begun, considerable progress has been made in understanding the origin of evolutionary novelty in terms of the potential for coordinated morphological change and the potential for imposing uneven probabilities on different evolutionary directions. Global or whole-organism heterochrony, local heterochrony (affecting single structures, regions, or organ systems) and heterotopies (changes in the location of developmental events), and epigenetic mechanisms (which help to integrate the developing parts of an organism into a functional whole) together contribute to profound nonlinearities between genetic and morphologic change, by permitting the generation and accommodation of evolutionary novelties without pervasive, coordinated genetic changes; the limits of these developmental processes are poorly understood, however. The discordance across hierarchical levels in the production of evolutionary novelties through time, and among latitudes and environments, is an intriguing paleontological pattern whose explanation is controversial, in part because separating effects of genetics and ecology has proven difficult. At finer scales, species in the fossil record tend to be static over geologic time, although this stasis—to which there are gradualistic exceptions—generally appears to be underlain by extensive, nondirectional change rather than absolute invariance. Only a few studies have met the necessary protocols for the analysis of evolutionary tempo and mode at the species level, and so the distribution of evolutionary patterns among clades, environments, and modes of life remains poorly understood. Sorting among taxa is widely accepted in principle as an evolutionary mechanism, but detailed analyses are scarce; if geographic range or population density can be treated as traits above the organismic level, then the paleontological and macroecological literature abounds in potential raw material for such analyses. Even if taxon sorting operates on traits that are not emergent at the species level, the differential speciation and extinction rates can shape large-scale evolutionary patterns in ways that are not simple extrapolations from short-term evolution at the organismal level. Changes in origination and extinction rates can evidently be mediated by interactions with other clades, although such interactions need to be studied in a geographically explicit fashion before the relative roles of biotic and physical factors can be assessed. Incumbency effects are important at many scales, with the most dramatic manifestation being the postextinction diversifications that follow the removal of incumbents. However, mass extinctions are evolutionarily important not only for the removal of dominant taxa, which can occur according to rules that differ from those operating during times of lower extinction intensity, but also for the dramatic diversifications that follow upon the removal or depletion of incumbents. Mass extinctions do not entirely reset the evolutionary clock, so survivors can exhibit unbroken evolutionary continuity, trends that suffer setbacks but then resume, or failure to participate in the recovery.

David Jablonski. *Department of Geophysical Sciences, University of Chicago, 5734 South Ellis Avenue, Chicago, Illinois 60637. E-mail: djablons@midway.uchicago.edu*

Accepted: 18 July 2000

Introduction

The landscape of evolutionary biology has changed significantly over the past quarter-century. Evolutionary and ecological studies now regularly incorporate serious considerations of history, scale, and hierarchy. This expansion of the working toolkit of the discipline—the near-routine application of ideas that were once barely developed, highly abstract, or in some circles outright anathema—

heralds a more profound integration of evolutionary biology, paleobiology, systematics, ecology, and developmental biology. Whatever the intellectual forebears of these ideas (and some of their roots are very deep), the growing number and diversity of studies that directly address such factors as intrinsic constraints, phylogenetic effects, differential origination and extinction rates, and local vs. regional effects represent a true operational expansion of evolutionary theory. As a window

onto a wide range of spatial and temporal scales, including extreme events not accessible to neontological study, paleontology is playing a vital role in this expansion and will certainly continue that role in the coming decades.

This is by no means to declare the demise of the highly successful microevolutionary paradigm, which is alive and well, but rather to say that the study of evolution continues to evolve and expand conceptually, and increasingly incorporates approaches that explicitly emphasize scale and hierarchy. These approaches, even those that can be traced back to Darwin, were barely visible when Tom Schopf and Ralph Johnson were mustering support for a new journal to be titled *Paleobiology*. Paleontology was one of the fields that provided a phenomenology, a conceptual base, and a battery of new quantitative methods, that fostered the expansion of evolutionary theory in the first quarter-century of this journal.

One way to survey the infusion of hierarchy and scale into evolutionary biology is through the classic darwinian two-step process: the origin and the sorting of variation. Other schemes are possible, of course, from the intrinsic/extrinsic dichotomy of causal mechanisms (e.g., Gould 1977a; Jablonski 2000a) to a nested set of temporal and spatial scales (e.g., Gould 1985; Bennett 1997), and those elements will inevitably appear here as well.

Origin of Variation

The origin of heritable variation, the raw material of the evolutionary process, is by definition a matter of genetics. One major issue in bridging scales and hierarchical levels, however, has been the correspondence between genotypic changes and the magnitude and direction of phenotypic transformation. A reasonable assumption underlying most models of evolution has been that the probability of a phenotypic change is inversely related to the complexity or magnitude of the genetic change required to generate it (among other factors, of course). Geneticists have long recognized that mutations of equal magnitude can have strikingly different phenotypic consequences depending on context, but this

awareness has been somewhat lost in the empirical evidence from quantitative genetics that many traits are underlain by a large number of genes of small and mainly additive effect. However, intensive study of developmental processes in multicellular organisms has led to a new appreciation of how modest genetic changes can be amplified and channeled developmentally to yield significant variations in the magnitude and direction of phenotypic change. We are only beginning to understand how and when to apply this expanding set of approaches to the origin of novel morphologies (and the absence or rarity of certain forms), but few would deny the potential to both illuminate and be illuminated by the fossil record of morphological evolution—not least because, as discussed below, that record exhibits nonrandom patterns in space and time.

Genetic Control Pathways and Networks

At one extreme in the nonlinearities between genotypic and phenotypic change are the high-level regulatory genes now under intense study by molecular developmental biologists. Some of these genes, such as the Hox clusters that help to pattern the body axis and appendages across the entire breadth of metazoan diversity, specify positional information and thereby regulate the transcription of a large number of downstream genes. Others sit near the top of a regulatory cascade, or perhaps more commonly within a regulatory network, that determines a specific tissue or structure. For example, perhaps 2500 genes are involved in building and maintaining the *Drosophila* eye (Halder et al. 1995; 18% of the fly's genome by Adams et al.'s [2000] count, although of course many are also used elsewhere), but experimental manipulation of a single gene—most famously *eyeless*, but also *eyes absent*, *dachshund*, and others—can yield well-formed eyes in the middle of wings and other improbable sites (see reviews by Gehring and Ikeo 1999 and Hodin 2000; and see Chow et al. 1999 for similar results in the frog *Xenopus*). Such high-level regulatory genes and even entire signaling pathways have been recruited as modular units ("cassettes") in the service of novel morphologies. Thus, the

hedgehog pathway that underlies the generation of limbs also participates in the production of eyespot patterns on butterfly wings (Keys et al. 1999); the *Toll* pathway has been recruited to the development of chick limbs, the operation of the vertebrate immune system, and the development of ventral structure in *Drosophila* (Gonzalez-Crespo and Levine 1994; Ghosh et al. 1998), and even the "master control gene" for eyes, *Pax-6*, plays multiple roles (e.g., Quinn et al. 1996; Duboule and Wilkins 1998; Hodin 2000; and see Heanue et al. 1999 and Relaix and Buckingham 1999 for an analogous situation involving *Pax-3*).

Many of the major molecular components of metazoan development appear to have arisen very early and been retained across taxa with very different bodyplans of varying complexity (reviews in Finnerty and Martindale 1998; Erwin 1999; Valentine et al. 1999; Holland 1999; Knoll and Carroll 1999, among others); although data are sketchier, the same appears to hold for plants (Purugganan 1998; Lawton-Rauh et al. 2000; Theissen et al. 2000). The extraordinary conservation (albeit in a highly dynamic fashion involving gene loss, gain, and duplication) and the multiple expression events and sites of these genes strongly suggests that the evolutionary action at this level is in the enhancer regions that govern the timing and intensity of gene expression (see Arnone and Davidson 1997 for an excellent review). The evolutionary impact of changes in the major regulatory genes will therefore be more complex than the extreme binary effects suggested by the homeotic mutants that abruptly transform segment identities. Instead, that impact should probably be visualized in terms of finer modulations in the expression of major regulatory genes, and therefore should include evolutionary changes that do not depend on the viability of extreme saltations and lone individuals (Gellon and McGinnis 1998; Akam 1998; Duboule and Wilkins 1998; Purugganan 1998, 2000; Gibson 1999; Li and McGinnis 1999; Ludwig et al. 2000). Possible examples of striking morphological changes that may have involved relatively subtle shifts in Hox expression patterns include the evolutionary differentiation of arthropod appendages (Averof and Patel 1997;

Shubin et al. 1997; Weatherbee et al. 1999), morphological transitions of vertebrae along the spinal column (Burke et al. 1995; Belting et al. 1998), the origin and diversification of tetrapod limbs (Shubin et al. 1997; Coates and Cohn 1998), and the suppression of those limbs and the homogenization of vertebral morphology along the body axis of snakes (Cohn and Tickle 1999; Greene and Cundall 2000). Vertebral identity and digit size and number appear to be dose-dependent functions of Hox gene products (Zakany et al. 1997), providing a mechanism for selection on high-level regulatory factors within populations, and thus a pathway for coordinated change effected by major genes but in a polymorphic population rather than a strictly typological context. Similar situations, again underlain by polymorphisms in regulatory genes, have been recognized by plants as well (e.g., Purugganan 1998, 2000; Lawton-Rauh et al. 2000).

These are very early days in the macroevolutionary exploration of developmental genetics. Careful study is needed in the inference of causal, evolutionary relationships between variations in Hox expression and morphological differences among taxa (e.g., Rogers et al. 1997). And the next step, taking insights derived from laboratory populations into natural evolutionary processes, has just begun. Gibson et al. (1999) found that crossing mutants of the Hox genes *Ubx* and *Antp* into natural populations of *Drosophila* could evoke a wide range of extreme phenotypes whose expression depended on the overall genetic context of the mutation, again showing how large-effect genes might impinge on morphological variation generated in the wild. More speculatively, DeSalle and Carew (1992) attribute some of the morphological extremes seen in Hawaiian drosophilid species, such as grotesquely reshaped heads and bizarre mouthpart appendages, to mutations in Hox genes because of their resemblance to *Antp* mutants in laboratory *D. melanogaster*—an attractive hypothesis that invites direct molecular study. Nevo et al. (1992) reported apparent Hox gene polymorphisms that significantly correlated with a wide array of morphological variables in the mole rat *Spalax ehrenbergi*, an early, pro-

vocative result that needs further work. On the other hand, Ahn and Gibson (1999a,b) found intraspecific variation in expression domains of Hox genes along the body axis of the three-spined stickleback, but this variation did not correlate with phenotypic variation. Finally, considerable within-species variation has been recorded for a number of major developmental genes in natural and domesticated plant populations, and several dramatic intraspecific variants have proven to be underlain by high-level developmental genes (for overview see Lawton-Rauh et al. 2000).

Evolution via changes in Hox-gene expression is hardly a prerequisite for a strong non-linearity between genetic and phenotypic change, of course, and both theory and evidence are accumulating that genes of large effect—many of them presumably involved in regulating development—do play a role in the origin of adaptations and the divergence of species (e.g., Gottlieb 1984; Orr and Coyne 1992; Palopoli and Patel 1996; Orr 1998). Much empirical work is still needed, of course, but an absolutely micromutational view of evolutionary change in natural populations seems increasingly untenable even for quantitative traits that are often seen as the bastion of the “many genes of equal and infinitesimal effect” approach championed by R. A. Fisher. One recent surprise, for example, has been the number of studies reporting quantitative trait loci (QTLs) of large phenotypic effect in both laboratory and natural populations (Orr 1998: p. 936; see also Paterson et al. 1997; Voss and Shaffer 1997; Doebley and Wang 1997; Bradshaw et al. 1998; Schemske and Bradshaw 1999; Goffinet and Gerber 2000). QTL analyses have their limitations, of course: they are only feasible among species or morphs that can be hybridized, they may not permit an absolute determination of the numbers of genes involved in important traits because minor factors may not be detected, and they can even be biased toward artificially inflating the effects of single QTLs or underestimating the number of genes involved in complex traits (Routman and Cheverud 1997; Lynch and Walsh 1998: p. 474–476; Via and Hawthorne 1998). On the other hand, laboratory selection experiments can be biased toward document-

ing polygenic changes (e.g., McKenzie and Batterham 1994). The growing weight of evidence suggests that genetic differences even among closely related taxa often involve genes of large effect that in the few cases of functional analysis are involved in regulating development (e.g., Doebley and Lukens 1998); corroboration for this view has been found in a number of “candidate loci” identified through mutations that are then mapped to QTLs accounting for natural variation in populations (e.g., Long et al. 1996; Mackay 1996; Nuzhdin et al. 1999). This calls for a more complex treatment of the raw material for evolutionary change, and for new models of how this raw material can influence the direction or pace of evolution, in concert with more traditional parameters like population size or structure—models that can be applied, tested, and refined paleontologically in many instances. One potential avenue might be to use neontological data on a well-fossilized group to pinpoint some of the phenotypic changes most likely to be underlain by large-effect genes, and then to test whether those changes can predict the evolutionary trajectories of clades in the fossil record. The interplay of evolutionary factors mentioned above might be assessed in a comparative framework in which several related clades are targeted that differ in such features as genetic population structure (see below for paleontological approaches to this parameter).

Heterochrony and Heterotopy

Heterochrony, a change in the rate or timing of developmental events, has received much attention as a potential avenue to dramatic morphological evolution. As Klingenberg (1998) points out, the pervasiveness of heterochrony hinges on its definition. Developmental biologists restrict heterochrony to changes in the relative timing of developmental events, emphasizing the dissociation between developmental units (e.g., Raff and Wray 1989; Raff 1996; Hall 1999), while evolutionary biologists and paleontologists have used a broader definition that also includes changes in the relative rates of developmental processes even when the order of events is unchanged (e.g., Gould 1977b; Alberch et al. 1979; McKinney

and McNamara 1991). Further difficulties are imposed by the hierarchy of biological organization: changes in timing at the molecular or cellular level need not produce heterochronic patterns at the whole-organism level, and the heterochrony at the organismal level need not involve changes in the timing of molecular events (e.g., some salamanders owe their paedomorphosis simply to the disabling of the production or reception of the hormone thyroxin, which is closer to a binary switch than a change in timing).

Global or systemic heterochrony—in which the entire phenotype is shifted relative to the ancestral ontogeny—has the greatest evolutionary potential, and is most readily detected, in species that undergo substantial phenotypic changes during ontogeny. Both continuous but nonlinear changes such as ontogenetic allometry and saltational changes such as metamorphosis (as in the classic example of neotenic salamanders that mature in the aquatic larval state) provide ample raw material for dramatic evolutionary events. This implies a little-explored predictive approach to differences in morphological diversification among clades, based on the nature of ancestral ontogenies. This might involve, for example, testing how well the ontogeny of individual organisms can predict the extent of morphological diversification of their descendant clades, a macroevolutionary equivalent of Wayne's (1986) classic conclusion that the great array of morphologically extreme dog breeds relative to cats is a consequence of their contrasting ontogenetic allometries (see also Wayne and Ostrander 1999).

The preceding example represents just one way in which the evolution of development at the individual level might indirectly shape large-scale patterns. Selection on life-history traits over ecological timescales, which as Gould (1977b) notes can often result in heterochrony, can also have far-reaching, indirect macroevolutionary effects, for example via changes in genetic population structures. For example, populations of obligate paedomorphic ambystomatid salamanders are genetically more distinct from one another than are metamorphosing populations (Shaffer 1984). Presumably the obligate paedomorphs tend to

stay in their aquatic neighborhoods, yielding lower rates of gene flow, and thus potentially higher speciation rates compared with metamorphosing relatives free to travel among ponds. Similarly, selection for small body size per se, energy economy, or short generation time in benthic invertebrates can evidently give rise to paedomorphs that are so small that they must evolve a low-dispersal, non-planktotrophic mode of development due to fecundity constraints (see Jablonski and Lutz 1983; Lindberg 1988); such a change in developmental mode would in turn be likely to result in high speciation and high extinction rates at the clade level, as discussed below (and see experiments showing that selection on egg size can in turn alter other aspects of larval biology, such as those of Sinervo and McEdward [1988] and Emler and Hoegh-Guldberg [1997]). Again, this intriguing intersection of micro- and macroevolution, where life-history theory meets heterochrony (an important but neglected insight in Gould 1977b; see also McKinney and McNamara 1991; McKinney and Gittleman 1995), would produce dramatic shifts not only in morphology but in evolutionary dynamics.

Although global or systemic heterochrony has enjoyed the most attention, local or specific heterochrony has been much more common (e.g., McKinney and McNamara 1991). Such changes in the rate or timing of development of particular structures within an organism can break allometric relationships and generate new and coordinated morphologies, again by drawing on established developmental interactions but this time within a localized region or developmental field. For example, the most successful crinoids in modern oceans, the stemless, mobile comatulids, were derived from the stemmed crinoid order Isocrinida; intermediates such as *Eocomatula* and *Paracomatula* suggest progressively earlier offset of stem formation, with the substratum-gripping cirri, which adorn the long stem in the isocrinids, finally arising from a single centro-dorsal ossicle on the base (Simms 1988a,b, 1994; Hagdorn and Campbell 1993). In mammals, the ossification of facial bones is accelerated relative to the central nervous system in marsupials compared with both mono-

tremes and placentals, correlated with the particular demands of neonate survival, including head movements during migration to the pouch, attachment to the teat, and suckling (Smith 1996, 1997; Nunn and Smith 1998). Such localized developmental changes, from the elongation of pterosaur digits to support a wing to the elongation of echinoid plates to create a protruding rostrum, represent coordinated changes in suites of complex tissues. Such dissociation and reintegration among local growth fields is still poorly understood but permits an enormous range of morphologies to be tapped by alterations of local growth fields. This does not mean that phenotypes are infinitely malleable, but that the scope for evolution via heterochronies of existing morphologies is far wider than implied by global heterochrony alone.

Calibration of ontogenetic trajectories against better metrics than the convenient but unreliable size criterion will be important for rigorous analysis of local and global heterochrony, particularly if life-history parameters are potential targets or by-products of selection. Fortunately, this can be achieved in paleontological material where accretionary growth leaves internal growth lines and a stable isotope record that can be calibrated at the level of monthly, seasonal, and annual periodicities (e.g., Jones 1988, 1998). In some taxa these can be tied to onset and perhaps frequency of reproduction, because reproductive growth interruptions can often be distinguished from disturbance checks (Kennish 1980; Harrington 1987; Sato 1995, 1999). Such skeletal chronometers have been used extensively in ecological studies of bivalves, but will be extremely valuable in evolutionary applications (for an exemplary study, see Jones and Gould 1999).

A final mechanism for coordinated morphological change is heterotopy, or alteration in the location of a developmental event. Heterotopy has received much less attention than heterochrony, but some authors have argued that spatial changes in development may prove to have greater evolutionary impact than temporal ones (e.g., Raff 1996; Zelditch and Fink 1996; Hall 1999). Although this perceived frequency is in part a consequence of

an expanded definition that may include virtually every developmental change that is not narrow-definition heterochrony (see Klingenberg 1998: p. 83), spatial changes in developmental events can certainly give rise to novel morphologies, as in the shifting of the scapula from outside to *inside* the ribcage in turtles (Burke 1989, 1991). Hall (1999: p. 388) goes so far as to say, "heterochrony tinkers, but heterotopy creates" and to anticipate that "heterotopy may be about to come into its own as heterochrony wanes and our knowledge of developmental mechanisms increases." This may be selling heterochrony a bit short (Hall goes on to note the intimate connections between heterochrony and heterotopy), but the recognition that the evolution of development involves more than just heterochrony—also being driven home by molecular work on gene regulation—is welcome. And, continuing one of the themes of this section, heterotopy is an effective evolutionary mechanism because, like heterochrony, it draws on preexisting developmental pathways and components: the spatial reordering of the turtle skeleton is striking by any measure, but the turtle tucks its scapula, identifiable as such during morphogenesis, under its ribcage rather than evolving a novel structure.

Epigenetics

Local heterochronies and heterotopies are effective evolutionary agents because of another aspect of developmental systems that contributes to the nonlinearities between genetic change and morphological effect: epigenetics in the classical sense, i.e., the local cell and tissue interactions that help to integrate the developing parts of an organism into a functional whole (for example the induction of vertebral cartilage formation by contact with the spinal cord [Hall 1983] or the growth response of both embryonic and postnatal bone to mechanical loading [Carter et al. 1998]). By drawing on a set of preprogrammed responses to local signals, such interactions allow the developing embryo to accommodate evolutionary changes in particular morphological elements without a host of independent but mutually beneficial mutations. We have little detailed knowledge of mechanisms, but strik-

ing epigenetic responses to experimental alterations in morphology have been described by many workers, and their evolutionary implications abundantly discussed (reviews include Rachootin and Thomson 1981; Raff and Kaufman 1983; Thomson 1988; Atchley and Hall 1991; McKinney and McNamara 1991; Hall 1999). Those experiments show that evolutionary changes in, for example, eye size need not be accompanied by independent mutations in genes governing bones, nerves, muscles, or blood vessels in the skull (see Twitty's famous transplant experiments reviewed by Müller 1990), and changes in vertebral posture need not involve independent mutations in genes that collectively control thoracic cross-sectional shape or the sites of muscle insertions on limb bones (see Slijper's bipedal goat, reviewed by Rachootin and Thomson 1981), because epigenetic interactions yield accommodations to those morphological changes.

The epigenetic interactions that help generate complex forms do have limits to the changes they can accommodate, as attested by many "failed" embryological manipulations or the more bizarre gene regulation experiments that haunt the pages of *Nature*, *Cell*, and similar journals. The macroevolutionarily important questions revolve around where those limits lie for particular clades or particular kinds of changes, and how evenly the potential directions of permissible change are distributed in morphospace. An approach along those lines will help to illuminate how two of the seemingly conflicting themes of development, modularity, and integration—at several hierarchical levels within the organism from molecular pathways to tissue inductions—conspire to produce evolutionary novelty.

Wanted: An Integrated Genetics

All of these aspects of genetics strongly underscore the nonrandom and nonlinear nature of variation that is the raw material for evolution. Any probability distribution of potential changes around a genotype (phenotype) will inevitably be inhomogeneous, reflecting evolutionary lines of least resistance that are conditioned by the underlying structure of developmental pathways at the molecular, cel-

lular, and tissue levels. The challenge is to take these new insights from the organismal level to the population, species, and clade level to forge a better understanding of the links and discontinuities among those levels.

A synthesis of developmental and population genetics will not be easy, as R. A. Fisher himself recognized ("I can no longer calculate it," he said when confronted with early evidence for nonadditive genetic variation [Mayr 1992]). A general mathematical theory may not much resemble our textbook versions of microevolutionary population genetics or quantitative genetics but will contain elements of both. Various, rather disparate, pioneering attempts suggest some potential components of such a program (e.g., Arthur 1988, 1997; Atchley and Hall 1991; Atchley et al. 1994; Schluter 1996; Nijhout and Paulsen 1997; Wagner et al. 1997; Orr 1998; Rice 1998). Given that our knowledge of the genotype–phenotype relation is still heavily biased toward laboratory strains of a few model organisms, far more extensive analysis of natural populations will be a critical step whose early phases were noted in the section on genetic hierarchies and networks, above.

A discouraging possibility is that so much taxon-specific information will be required that quantitative models, or even qualitative predictions, at the macroevolutionary scale will have little power. However, the strong commonalities among phyla in basic developmental genetics hold out some hope, and certain differences among clades suggest some simple hypotheses that might be explored. For example, protostomes have evolved the genetic machinery for generating complex morphologies by keeping genomes relatively small and increasing the number of times a gene is used during development, whereas deuterostomes have enlarged the genome by two rounds of duplication so that multiple copies of a given gene are available to diverge functionally (Akam 1998; Holland 1999; Valentine 2000; among many others). Do these differences in genetic architecture impinge on phenotypic evolution to produce differences in evolutionary style between the two main metazoan branches (e.g., in dissociability of structures—that is, the relative degree of

developmental independence of structures or organs within bodies, styles of heterochrony or heterotopy, etc.)? The two architectures may prove to be functionally equivalent from a macroevolutionary perspective, but demonstrating that they generate qualitatively as well as quantitatively similar variation would be equally interesting. Whether phenotypic evolution is gradual or discontinuous when regulatory changes give rise to major morphological novelties is still utterly uncertain, and probably depends on the types of characters involved. Reasonable arguments are available for either evolutionary dynamic and so data rather than theory will be required to determine relative frequencies.

Bridging the empirical and conceptual gap between developmental biology and macroevolution remains a challenge. Living and fossil organisms are all the products of developmental sequences that themselves had to evolve to yield the diverse forms of past and present taxa, but hypotheses on the nature and evolutionary impact of those developmental changes are difficult to test, and inferences on developmental changes in extinct clades can rarely be precise. Using our growing knowledge of gene-expression events within, for example, a *Drosophila* or crustacean embryo as a basis for understanding the morphological diversification of the arthropod clade (and vice-versa) represents a truly daunting shift in spatial and temporal scale. But here as elsewhere, paleontology has much to gain and much to offer. For example, paleontological comparisons across clades, habitats, or time intervals of the density distributions and sequences of novel morphologies around their ancestral starting points can make substantial contributions to understanding the large-scale consequences of the organization of developmental systems. This work will of course be most powerful if done in concert with actual developmental information from the clade in question, but paleontology's spectacular array of morphologies viewed in historical perspective can lead the way for a host of new questions and help to target organisms for developmental analyses likely to yield macroevolutionary insights.

Temporal and Spatial Variation in the Origin of Novelties

Given the many ways in which developmental changes can generate evolutionary novelties, the macroevolutionary expectation might be that novelties arise stochastically according to clade-specific pressures and opportunities. The highly nonrandom first appearances of novelties in the fossil record thus present an intriguing challenge. Although debate continues on the mechanisms behind these patterns, and more empirical work is sorely needed, these large-scale patterns in time and space hint at the potential paleontological contributions to a theory of evolutionary novelty.

Temporal Patterns.—The most striking burst of evolutionary creativity in the animal fossil record comes early in the Phanerozoic, with the Cambrian explosion of metazoan bodyplans. This extraordinary interval, which saw the first appearance of all but one of the present-day skeletonized phyla (along with an array of less familiar forms) in an interval of less than 15 m.y., has received considerable attention recently from both geological and developmental perspectives. The standing of the two major explanatory models, one involving intrinsic, developmental or genomic controls and the other involving extrinsic, environmental or ecological controls, has varied over the past decade, but resolution has been difficult (see Erwin et al. 1987; Jablonski and Bottjer 1990a; Valentine 1995; Conway Morris 1998; Erwin 1999, 2000a; Knoll and Carroll 1999; Valentine et al. 1999; Jablonski 2000a). The rival hypotheses need not be mutually exclusive, of course, for as Erwin (2000a) notes, "successful innovations require ecological opportunity, developmental possibility and an appropriate environmental setting." The problem therefore becomes a matter of assessing which of Erwin's triad of requirements—for example, open ecospace as set by the biota, intrinsic morphogenetic potential, or by favorable oxygen levels or other physical limiting factors—was the immediate trigger of the explosion. An equally intriguing and no less elusive problem is to determine which of them damped the production of bodyplan after-

wards, without actually damping diversification at lower levels—including further developmental modifications—so that the production of phyla ceased but lower-level taxonomic diversity soared to new heights during the Ordovician, and again in the post-Paleozoic. And of course the trigger might have been different from the damper.

Secondary pulses of evolutionary innovation occur in the wake of mass extinctions, adding further temporal structure to the origin of novelties. These repeated pulses, measured either as the first appearances of high-ranking taxa or increases in morphological disparity, strongly suggest a role for ecological opportunity in the origin of novelties (see also below). But is this sufficient to account for the Cambrian explosion, or were genomic factors also involved? Erwin et al. (1987) reasoned that taxonomic diversity but not genomic flexibility should have approached Cambrian levels after the Permo-Triassic extinction, allowing a test of the genomic and ecological hypotheses. However, they found that even the end-Permian debacle, although cutting deep into taxonomic diversity, failed to remove major functional groups from the marine biosphere and thus did not sufficiently mimic the ecological character of Cambrian seas for a definitive test.

Another approach is to sidestep taxonomic rank and examine the evolution of morphology more directly. The rapid filling of a quantitatively defined morphospace has been documented for a number of clades originating in the early Paleozoic (see Foote's 1997 review). More daunting is the task of quantifying larger and more heterogeneous groups such as the deuterostomes or the bilaterians for the purpose of gaining an overall picture of the deployment of morphological diversity through time—but see Thomas et al.'s (2000) analysis showing that 80% of the theoretical skeleton designs available to living and extinct metazoans were occupied by the Middle Cambrian.

Comparative approaches to morphospace occupation can be used to address the rival hypotheses for temporal trends in the origin of novelties. For example, Foote (1999) found that the post-Paleozoic rediversification of cri-

noids, although representing a rapid increase in morphological disparity, yielded a narrower set of architectural novelties than those established in their initial, early Paleozoic radiation. He took this as evidence for less constrained developmental inputs to the Cambrian explosion than in later times. Wagner (1995) also argued for the lability of different kinds of traits during the initial and later phases of Paleozoic gastropod diversification. These are intriguing results that appear to support a genomic component to the Cambrian explosion, but they are just a first step, in part because they lack an explicitly generative or developmental component. For example, a developmentally based partitioning of traits to compare the long-term behavior of those that might have been more subject to initial freedom and later limitation, relative to those that might have been subject to earlier entrenchment (as attempted by Jacobs 1990) would be valuable. Pinpointing appropriate characters for comparative analysis may not be straightforward, however. For example, Hughes et al.'s (1999) finding that the variability of thoracic segment number in trilobites depends on the number of segments in a given species rather than its phylogenetic position or geologic age undermines a particular argument (McNamara 1983) but cannot fully address the kinds of regulatory networks that were involved in the radiation of arthropod and related clades in the Early Cambrian.

Instead of focusing on particular characters, the role of genomic changes in the damping of the Cambrian explosion might be tested by tracking levels of morphological integration through the early Paleozoic (Erwin 1994)—that is, the morphometric correlation patterns within an organism (e.g., Olson and Miller 1958; Cheverud 1996). This may require a better understanding of developmental mechanisms than presently available, because phenotypic integration can be stable even when genotypic covariances are not (e.g., Turelli 1988; Shaw et al. 1995; Schlichting and Pigliucci 1998). However, Nemeschkal's (1999) finding that avian morphometric correlation patterns correspond to the expression domains of Hox and other developmental control genes is encouraging in its implication

that morphometric matrices can reflect developmental architecture (see also Leamy et al. 1999). Operational questions aside, the evolutionary role of morphological integration needs further theoretical and empirical study: maximal evolutionary lability may come at an intermediate level of integration, where the body is composed of locally integrated units that can behave as modules, as discussed above (e.g., G. P. Wagner 1996; Kirschner and Gerhart 1997). G. P. Wagner (1996) argues that the origin of multicellularity led to an decrease in integration as regional specialization of morphology led to differential gene expression, but developmental "burden" is held to increase through time as developmental interdependencies accumulate (e.g., Riedl 1978; Donoghue 1989). The two perspectives are of course potentially compatible, as they may represent very different scales (multicellularity vs. the developmental genetics of a single feature), but they do suggest that this issue would be worth exploring in greater depth.

Although direct comparisons are difficult, a major burst of novel plant architectures is associated with the invasion of land (e.g., Niklas 1997; Bateman et al. 1998). We need to develop criteria to determine whether the establishment of the major land plant designs was as profound an evolutionary event as the Cambrian explosion, as sometimes suggested. If so, we will probably need to confront the intrinsic/extrinsic debate here as well: were plant developmental systems more labile as late as the Devonian (in contrast to animal systems), or is the ecological opportunity afforded by the assembly of traits permitting terrestrial existence a sufficient explanation? Recent work suggests that the MADS-box genetic architecture that orchestrates plant development in ways reminiscent of Hox and other high-level regulatory genes in animals were in place early in land plant evolution (Theissen et al. 2000).

Evolutionary novelties at lower levels exhibit very different temporal patterns from major novelties, and may depend on different variables. As made clear by Valentine's (1969, 1973, 1980, 1990) seminal work on evolutionary and ecological hierarchies in the fossil record, this is immediately evident from the dis-

cordance between the diversity dynamics of marine taxa ranked as phyla and classes relative to the very different dynamics of those ranked as families and genera (see also Erwin et al. 1987). Such discordances are not simply an artifact of the greater inclusiveness of higher taxa (as suggested by Smith [1994], among others), because similar patterns emerge from taxon-free analyses of multivariate morphologic data (Foote 1993, 1996a, 1997, 1999; and see Lupia 1999 on an early burst of disparity followed by stability in angiosperm pollen, discordant with species-level diversity). Raup (1983) essentially recognized this as well by noting that the requirements of tree topology alone could not account for morphological divergences like the Cambrian explosion (that is, the topology of the tree cannot account for the autapomorphies on each branch).

The dynamics of novelty production at lower levels can be quite unexpected when examined in detail. For example, Jablonski et al. (1997) found the production of morphological novelties within the bryozoan orders Cyclostomata and Cheilostomata to be opposite in timing to that expected from the ecological-opportunity hypothesis that is the chief contender for explaining high-level originations. Cyclostomes generated novelties in a steady trickle despite their occurrence in the relatively low-diversity early Mesozoic world, whereas the cheilostomes produced novelties in a burst despite being embedded in the presumably more crowded, predator- and competitor-rich mid-Cretaceous environment. In this comparative study, ecological context mattered less than the relative speciation rates (and competitive abilities?) of the respective clades.

Spatial Patterns.—Evolutionary novelties also show spatial patterns in their first appearance in the fossil record. Like the major temporal patterns, onshore-offshore patterns show discordances between the first appearances of higher taxa and patterns of origination, extinction, and diversity accumulation at lower taxonomic levels: benthic marine orders tend to originate in onshore, disturbed habitats, regardless of the diversity dynamics of their constituent species, genera, and families (Jablonski and Bottjer 1990a,b, 1991; Droser et

al. 1993; Jablonski et al. 1997). Although much more work is needed, this pattern can also be seen in terms of derived characters (Jablonski and Bottjer 1990b is only a crude beginning) and in the morphological divergence of the founding species for two echinoid orders relative to the disparity among species in the ancestral group, showing how the onshore initiators of these orders "broke away from the bounds of [their ancestor's] morphospace from the very start" (Eble 2000: p. 68). In apparent agreement with these patterns, major land plant originations also appear to be concentrated in disturbed habitats, in both Paleozoic and Mesozoic settings (e.g., DiMichele and Aronson 1992 and Wing and Boucher 1998, respectively), although the botanical data have not been analyzed for the marine discordance across hierarchical levels.

The geography of first occurrences of major groups is particularly subject to sampling bias, but an attempt to take these into account found disproportionate appearances of marine invertebrate orders in tropical latitudes (Jablonski 1993). Similarly, phylogenetic analysis suggests that major plant lineages tend to originate in the Tropics and spread poleward, in that primitive members of clades tend to be tropical and derived taxa tend to be restricted to or best developed in the temperate zones (e.g., Judd et al. 1994, and in a very different tradition, Meyen 1992), although of course different dynamics could underlie this pattern (but see also Askin and Spicer 1995 on paleontological data). More work is needed, however, to test whether the latitudinal trend in higher-level originations significantly exceeds the probabilistic, per-taxon expectation, given that the latitudinal trend in species richness appears to have been present over most of the Phanerozoic, albeit with varying slope and subject to considerable sampling and preservation bias (e.g., Stehli et al. 1969; Humphreville and Bambach 1979; Kelley et al. 1990; Crame 1996; Walsh 1996).

Species and genera show less striking latitudinal origination patterns, and many clearly started in high latitudes (e.g., macroinvertebrates [Feldmann et al. 1993; Crame 1997], Neogene Foraminifera [Buzas and Culver 1986; Wei and Kennett 1986; Spencer-Cervato

et al. 1994], terrestrial plants [Wen 1999]). The relative fraction of high-latitude origination at low taxonomic levels has not been sufficiently quantified to compare with the preferential low-latitude appearance of the much smaller number of higher taxa, however. Plotting the mean or median geologic age, or alternatively the estimated net diversification rates, of extant lower taxa against latitude has given apparently conflicting results (e.g., for marine taxa [Wei and Kennett 1986; Flessa and Jablonski 1996 and references therein; Crame and Clarke 1997], terrestrial birds [Gaston and Blackburn 1996], birds and butterflies [Cardillo 1999]). Violation of assumed time-homogeneous dynamics may be one source of the conflict, but this entire area deserves more extensive study.

Potential mechanisms for spatial biases in evolutionary innovation are plentiful but difficult to test, and as with the temporal bias the jury is still out on whether this is a genetic or an environmental problem, or even whether the pattern is underlain by differential production or differential persistence of evolutionary novelties (or both). Environmental possibilities include high rates of local extinction and invasion and thus local opportunity for innovation, more variable and/or intense selection pressures, or the potential extinction-resistance of novelty-bearing species, in more disturbed habitats relative to more stable ones (e.g., Jablonski and Bottjer 1983, 1990b; Hoffmann and Parsons 1997). Latitudinal patterns might simply represent diversity-dependent novelty production at this spatial scale, or more complex combinations of novelty production and survival to produce the net effect recorded paleontologically (Jablonski 1993).

Genetic explanations for these patterns include the greater potential of small peripheral isolates—which would arguably be more frequently formed in disturbed, heterogeneous habitats—to have lower developmental stability or to break developmental canalization (Levin 1970; Jablonski and Bottjer 1983; Clarke 1993; Hoffmann and Parsons 1997). Most recently, Rice's (1998) model suggests that canalization might most readily be broken by strong truncation selection, when significantly

less than 50% of a population is selected to produce the next generation, a situation that might obtain most often with the enormous mortality of propagules in shallow-marine benthos (although the selective basis of that mortality and its overall impact relative to mortality in other populations is poorly understood [e.g., Rumrill 1990; Pechenik 1999]). The potential role of highly variable environments in fostering evolutionary innovation (e.g., Parsons 1993, 1994; Hoffmann and Parsons 1997; Hoffmann and Hercus 2000) has gained a new developmental wrinkle with the finding that some regulatory molecules that suppress phenotypic variation can be disabled not only by mutation but by environmental extremes such as high temperatures (Rutherford and Lindquist 1998; Wagner et al. 1999).

The connection between any of these mechanisms and the empirical macroevolutionary patterns remains highly speculative. However, they do suggest testable ways of making mechanistic sense of evolutionary patterns that are not smooth extrapolations up the taxonomic hierarchy. Comparative analyses of morphological divergences within and among clades, structured along environmental gradients, would be a valuable—and tractable—step in this area, particularly because the first appearances of most orders are not as divergent from likely ancestors as are the phyla of the Cambrian explosion. Complementary approaches that examine the first appearance of major groups in terms of derived characters or multivariate morphometrics relative to patterns within clades and across environments (along the lines of Eble 2000) would be valuable.

The discordance between high and low taxonomic levels in temporal and spatial patterns of origination, and between morphological diversification at different levels within nested clades and subclades, thus provides an intriguing set of patterns that require a hierarchical approach. The spatial component also demonstrates that large-scale evolutionary processes cannot be analyzed exclusively at the global scale, because unexpected—or at least previously undetected—structure resides at the regional scale and across environmental gradients (see also Miller 1998; Jablon-

ski 2000a). These aspects of the evolutionary process can also be seen in the sorting of variation.

Sorting of Variation

Species-Level Stasis and Change

Stasis and Its Causes.—As many authors have pointed out, microevolution can occur as rapidly as needed to account for virtually any speed observed in the fossil record (e.g., Charlesworth et al. 1982; Gingerich 1993; Kirkpatrick 1996; Hendry and Kinnison 1999; and many others). This has been abundantly demonstrated not only in the laboratory but in natural populations from Galapagos finches (Grant 1986; Grant and Grant 1995) to Bahamian anoles (Losos et al. 1997) to mosquitoes in the London Underground (Byrne and Nichols 1999), although as discussed above simple extrapolations of these changes may not provide the best model for all of the inhomogeneities in the origins of major novelties. The more challenging question then becomes, why are evolutionary rates generally so slow in the fossil record? This question pertains both to the species level, which is the domain of punctuated equilibrium and its alternatives (Gould 1982; Gould and Eldredge 1993), and to the clade level, where large-scale evolutionary trends often unfold with excruciating slowness when viewed on microevolutionary timescales (e.g., Stanley 1979; McShea 1994). The relation between potential mechanisms at the different levels has been discussed mainly in broad generalities, but few workers have attempted to address whether the factors that cause, for example, species-level stasis seen in many members of the horse lineage (e.g., Prothero and Shubin 1989) are also responsible for the slow rate of body size increase in the clade. Averaged over the duration of the entire clade, this size increase was so slow as to be virtually indistinguishable from drift (see Lande 1976, and Stanley's [1979, 1982] punctuational reinterpretation, seconded by Stebbins 1982; and also Lieberman et al. 1994, who found rates so slow in a Devonian brachiopod lineage that they would have involved only three selective deaths per 10 million individuals if treated as a continuous trend).

Over the past quarter-century, evolutionary stasis has proven to be a pervasive morphological pattern in the fossil record (reviewed in Erwin and Anstey 1995a; Gould and Eldredge 1993; Hallam 1998; Jackson and Cheetham 1999). However, few of the hypotheses on the forces that maintain this stasis at the species and higher levels have been conclusively tested and again, different mechanisms may obtain in different clades. The research questions have shifted to testing for among-clade and among-habitat differences in frequencies of evolutionary tempo (abrupt vs. gradual change) and mode (anagenetic vs. cladogenetic, sometimes termed phyletic vs. branching), the roles of intrinsic and extrinsic factors that might govern those differences, and whether the direction of phenotypic change during sustained anagenesis or cladogenesis is related to the morphologic behavior of the species or its constituent populations during preceding intervals.

Given pervasive stasis, the stunning diversity and subtlety of biological adaptations must often arise episodically, in the punctuations between stable species, either in single punctuational episodes—which, of course may encompass tens or hundreds of thousands of years (e.g., Jackson and Cheetham 1999: Table 1)—or in cumulative series. This process need not rely entirely on isolation itself as the trigger for adaptive change, but may also draw on geographic variation within established species. Consider, for example, Futuyma's (1987) very attractive but still untested suggestion that speciation events cordon off local adaptations into discrete gene pools, thereby packaging ordinarily ephemeral characters into more stable evolutionary units (see also Eldredge 1989, 1995). The apparently episodic nature of this process, at least in terms of the morphologies accessible in the fossil record, underscores the need to understand stasis.

At the species level, stasis over geologic timescales has been attributed to variation in both rate and direction of change. Variation in the rate of change involves truly slow evolutionary rates between the punctuations, with temporal stability generally attributed to constant selection for intermediate phenotypes,

interrupted by rapid anagenetic or cladogenetic shifts (maximum observed rates of change may also be artificially reduced by the size of the time bin encompassing both stasis and directional change). Less often considered is the possibility that directional selection fluctuates so rapidly that populations cannot respond, with the net effect of stasis at the mean phenotype; another alternative would be time-averaging of samples rather than selection pressures, detectable if not geologically then perhaps by exceptional apparent population variances (see Kidwell and Aigner 1985).

Sustained stabilizing selection must be the force behind habitat tracking as a mechanism for stasis (Eldredge's 1985, 1989, 1995 hypothesis), in which species remain morphologically static as they move with a favorable environment during climatic and other changes. The tracking process seems well supported in the Pleistocene (e.g., Valentine and Jablonski 1993; Coope 1995; Clark 1998; see also discussions in Price et al. 1997 and Jackson and Overpeck this volume). Intrinsic differences among taxa in their ability to keep up with shifting environments have not been explored as an explanation for differences in evolutionary tempo and mode; this may be unimportant, however, if we can generalize from rates of movement in Pleistocene plants and animals (e.g., Clark 1998). For widespread species, a more realistic model might be cline translocation (coined by Koch 1986), in which a set of populations that vary along an environmental gradient shift in and out of a sampling area to give the appearance of oscillatory or even directional change as the species overall maintains a constant morphology (see for example Stanley and Yang's 1987 extensive study of late Cenozoic bivalves, in which the total range of multivariate oscillations through the history of each lineage was very similar to its present-day geographic variation).

Most species-level lineages appear to lack directionality rather than evolutionary lability; that is, they show high total rates of evolution while accumulating little net change. The most frequently invoked model is that of oscillating directional selection (e.g., Ginger-

ich 1993; Sheldon 1996; Hendry and Kinnison 1999), a process well documented in some modern populations (e.g., Grant and Grant 1995; Via and Shaw 1996; among many others). Such evolutionary dynamics can be modeled and in principle tested against drift and other forces, although paleontological applications are still being developed and in some instances seem highly model-dependent (see Bookstein 1987, 1988; and Roopnarine et al. 1999; but see Cheetham and Jackson's [1995] overview of their superb multidisciplinary analysis of Neogene bryozoan evolution). A less-explored, explicitly hierarchical alternative involves the spatial structure within species: gene flow among highly dynamic local populations within a species might allow little net overall change (e.g., Eldredge 1985, 1989; Lieberman et al. 1995). Although molecular and other data suggest that few species lack some internal spatial structure (e.g., Hanski 1999; Avise 2000), it is not clear whether the particular metapopulation dynamics required by this model for stasis are truly pervasive in nature (e.g., S. Harrison 1998; Maurer and Nott 1998).

Also controversial is whether the apparent bounds on oscillatory stasis represent intrinsic limits of the organisms or reversals in selection pressure. I am not going to venture into the dense and tangled literature of evolutionary constraints, but the widespread existence of evolutionary trade-offs (as, for example, between age and size at first reproduction, when selection favors both early reproduction *and* large size [e.g., Stearns 1992]) seems to be a strong endorsement for some form of intrinsic constraint, at least in the short run (for morphological examples, see Nijhout and Emlen 1998). The detection of such trade-offs, however, generally carries little information on mechanisms underlying constraints, and, as with genotypic and phenotypic variance-covariance matrices (e.g., Shaw et al. 1995; Arnold and Phillips 1999), we do not know how stable they are over evolutionary time. Some must be nearly absolute, others may be quite transient and context-dependent. Plant and animal breeders hit limits all the time, and the failure to break the egg-a-day barrier in chickens (Lerner 1953), or to increase thoroughbred

racing speeds significantly over the past 70 years (Gaffney and Cunningham 1988), is not for lack of intense directional selection or high heritability of relevant traits.

Experimental work on host specificity in phytophagous insects suggests that intrinsic factors may be important in wild populations as well. Many insects exploit a restricted diet, presumably owing to plants' defensive compounds, but experiments in some groups have detected no significant relation (or, less often, a *positive* relation) between insects' performance on their host plants and their performance on other species, undermining a trade-offs hypothesis; a lack of genetic variation may actually be a limiting evolutionary factor in this instance (Futuyma et al. 1995; but see Keese 1998). This is not a trivial issue, given Farrell's (1998) contention that the overwhelming species richness of beetles is related to the macroevolutionary consequences of host shifts in phytophagous clades. The general relation between trade-offs, genotypic covariances, and other apparent limitations to evolutionary responsiveness on the one hand, and patterns of morphologic change in species over geologic timescales on the other, is clearly an attractive target for combined paleontological/neontological analysis of particular clades. To cut through the terminological morass, all of these features can be put under the rubric of *developmental constraints*, which might be defined as the resistance, owing to the configuration of developmental networks and pathways, of the phenotype to selection in certain directions. In principle this can be distinguished from *canalization*, which might be defined as the resistance, owing to the buffering or redundancy of developmental processes, of the phenotype to mutation or to environmental variation (and see Gibson and Wagner 2000 for a valuable overview).

Distribution of Stasis and Change.—The distribution of evolutionary tempos and modes at the species level remains poorly known, not least because rigorous research in this area is such a daunting task. Few studies have fully addressed all of the issues, but, drawing on the discussions of Gould and Eldredge (1977), Fortey (1985), Clarkson (1988), Erwin and An-

stey (1995a), and Jackson and Cheetham (1999), an appropriate protocol would include

1. Large samples in a closely spaced time-series
2. Objective delimitation of species as operational units
3. Stratigraphic control independent of the target clade
4. Independent evidence on sedimentation and preservation rates that might vary to create artificial punctuations or protracted transitions
5. An assessment of within-species geographic variation
6. A phylogenetic hypothesis

The characterization of morphospecies has become increasingly rigorous with the availability of multivariate morphometric methods. An encouraging development has been the generally good correspondence between biological units and the morphospecies of the shelly macroinvertebrates used in most analyses of evolutionary tempo and mode at these scales. This is not the place for an extensive discussion of species concepts, but from an evolutionary perspective species-level units are most useful if they are essentially independent lineages (e.g., Simpson 1961; Wiley 1981; Mayden 1997; de Queiroz 1998, 1999, and references therein). For the outcrossing biparental species that provide most of the animal and protistan fossil record and a sizeable but unknown fraction of the plant record, that independence often involves reproductive isolation or genetic cohesion, and so coincides with any broadly defined biological species concept that can accommodate isolation, recognition, cohesion and related viewpoints (e.g., Templeton 1989, 1998; Ghiselin 1997; Coyne and Orr 1998; R. G. Harrison 1998; de Queiroz 1998). However, that evolutionary independence need not be compromised even if those barriers are not absolute (to give just two examples, the fossil record shows that cottonwoods and balsam poplars have been generating hybrids in western North America since the Miocene but have remained distinct entities [Eckenwalder 1984] and that two lineages of Neogene cyprinid fishes hybridized for 2 m.y. without subverting the evolutionary identities of the parent lineages [Smith 1992]),

and other processes besides the traditional isolating barriers may impose or contribute to evolutionary independence as well (e.g., Van Valen 1976; Hull 1997; among many others).

Analyses within paleontologically important phyla where morphometrically defined species correspond closely to biologically, usually genetically defined ones include: the cheilostome bryozoans *Stylopoma*, *Steginoporella*, and *Parasmittina* (Jackson and Cheetham 1990, 1994, who also used an extraordinary set of breeding experiments, and see also Hageman et al. 1999); the benthic foraminifer *Glabratella* (Kitazato et al. 2000, also based on breeding experiments; but see below for the uncertain situation with planktic Foraminifera); the gastropods *Amalda* (Michaux 1987, 1989, who also found congruent phylogenies using both data sets), *Nucella* (Collins et al. 1996, albeit with considerable intraspecific shell variation), *Littorina* (Rugh 1997, who compared shell morphology with such biological species indicators as genital and egg-capsule features), and *Lacuna* (Langan-Cranford and Pearse 1995, again using breeding experiments); the corals *Porites* (Potts et al. 1993; Budd et al. 1994, again with congruent phylogenies) and *Montastraea* (Weil and Knowlton 1994; Knowlton et al. 1997); the decapod *Synalpheus* (Duffy 1996, using allozymes); the articulate brachiopod *Terebratulina* (Cohen et al. 1991, using both allozymes and mtDNA); and even the notoriously nondescript inarticulate brachiopod *Glottidia* (Kowalewski et al. 1997, who lacked genetic data and relied on previous biospecies definitions). One can only hope for a steady stream of such studies, including a new round on vertebrates such as Steppan's work (1998) on the rodent *Phyllotis*, using mtDNA versus skeletal morphometrics.

These accumulating results suggest that the paleontologist need be at no greater remove from biological units than any other systematist lacking a full molecular treatment of the taxonomic units under study. And by providing concrete support for the biological reality of the morphological differences between related fossil species, they imply that the morphological punctuations in fossil lineages—an empirical pattern open to multiple interpretations—do tend to correspond to speciation

events. Anagenetically evolving lineages lacking speciation-scale punctuations can be more problematic, of course, and when broken into arbitrary taxonomic segments may imply an artificially punctuational pattern (see Sheldon 1993). However, this pitfall will be avoided as long as phenotypic change is the final arbiter on questions of evolutionary tempo and mode at the species level, as seen in most recent studies including the examples cited here and by Jackson and Cheetham (1999).

On the other hand, sibling or cryptic species—that is, biological species that are virtually undetectable morphologically—are common in many taxa, both terrestrial and marine (e.g., Knowlton 1993; Avise 2000). To some authors, this imperfect correspondence between morphospecies and biologically discrete species dictates the collapse of the entire enterprise (e.g., Levinton 1988; Hoffman 1989), but this simply is not true, so long as the questions are posed appropriately. For example, a lineage is punctuational if most morphological change occurs in the context of speciation when viewed over geologic timescales. But this does not require that the converse be true, that all speciation events are accompanied by morphological change. More problematic is the generation of temporally and spatially persistent, discrete morphotypes that can arise abruptly but are not reproductively isolated, that is, are not evolutionarily independent entities (e.g., Palmer 1985; Trussell and Smith 2000). The examples cited above suggest that paleontologists are becoming adept at partitioning their morphological units in ways that are genealogically significant, but the ranking of discrete morphologies remains a potential problem and needs more attention. The same is true for character-based neontological species concepts, of course, particularly those based on “smallest diagnosably distinct units” (Cracraft 1989, 1997; Nixon and Wheeler 1990; Davis and Nixon 1992; Luckow 1995), where the taxonomic ranking and evolutionary roles of those units also can be controversial (e.g., Theriot 1992; Hull 1997; Knowlton and Weigt 1997; R. G. Harrison 1998).

The most robust analyses will be those that compare rates and patterns of morphospecies

production among clades (particularly within the same geological arena, so that many potential taphonomic biases are held constant), rather than depending on absolute values. Significant differences detected in comparative analyses will be misleading only if the frequency of sibling species has a strong inverse relation to the frequency of morphospecies origination. Little or no evidence of such a relation exists, although a formal analysis would be valuable. The sparse literature on important components of the fossil record, such as marine invertebrates and terrestrial vertebrates, conveys the general impression that the numbers of morphospecies and sibling species are, if anything, *positively* correlated among clades. If this is true, or if the relation is random so that no systematic bias is introduced, then cryptic species will not be a serious problem for comparative studies of evolutionary tempo and mode, at least in large data sets.

Geographic variation has been the Achilles' heel of many paleontological studies of evolution at the species level. Analyses centered on one or a few closely spaced stratigraphic sections or cores risk confounding the lateral movements of trends in intraspecific variation with evolutionary change, the methodological pitfall created by the cline translocations mentioned above (and the potential for local populations to exhibit independent morphological trajectories without net species-level directionality adds another hierarchical level to be considered [see Lieberman et al. 1995; Bralower and Parrow 1996]). This problem was recognized over 40 years ago (Newell 1956; Arnold 1966), but its remedy is generally so labor intensive that only a few studies have risen to the challenge (but see, gratefully, Stanley and Yang 1987; Cheetham and Jackson 1995, 1996). A formidable obstacle is the inverse relation between acuity of stratigraphic resolution and geographic distance, particularly along environmental gradients or among disjunct regions: the temporal acuity often achieved by closely spaced samples in a single section declines significantly when correlating among sections (see Behrensmeier and Hook 1992 and Behrensmeier et al. 2000 [this volume] on analytical time-averaging). This Paleontologi-

cal Uncertainty Principle—the trade-off between temporal resolution and geographic coverage—seems to be little appreciated outside the field but has implications for virtually every kind of paleobiological analysis. Quantitative stratigraphic methods, significant refinements in radiometric dating techniques, and tuning of correlations to Milankovitch cycles (e.g., Shackleton et al. 1999) will yield increasingly fine correlations, but resolution will tend to approach a limit on the order of thousands of years, if only because natural time-averaging operates at about this scale for most micro- and macrofossil records (see Kidwell and Flessa 1995; Martin 1999).

All of the end-member combinations of evolutionary tempo and mode have now been observed in fossil species transitions, and so the challenge is to assess the frequencies of the different patterns, and to test for the influence of biological traits, environmental factors, and other potential controlling variables. This effort is complicated by the strong imbalance in the evidence required to demonstrate gradualism versus stasis (see Fortey 1985, 1988; Clarkson 1988; Sheldon 1993, 1996; Pearson 1995; Wagner and Erwin 1995). Stasis can often be convincingly documented by samples from a succession of discrete sedimentary packages, even when the packages are separated by depositional hiatuses or unfavorable environments. Further, quantifying geographic and other intraspecific variation is less critical if even the local pattern is one of temporal stability. Stasis is unlikely to be artificially generated or removed by time-averaging, where successive populations are homogenized within a single sedimentary bed. Short-term directional changes can be collapsed into a single artificially variable assemblage, but trends extending over more than 10,000 years (depending on depositional environments, of course) and thus significant relative to the average duration of morphospecies, will generally be retained, and situations that would obliterate them can be recognized by independent evidence (e.g., Kidwell and Aigner 1985; Bell et al. 1987; Kidwell and Flessa 1995).

Ironically, then, gradualism is more difficult to demonstrate conclusively in the fossil rec-

ord than the alternatives, even though it was long taken to be the dominant style of evolutionary change! That said, distinguishing between true punctuated equilibrium, i.e., punctuated cladogenesis, and punctuated anagenesis, in which morphological change occurs episodically but without lineage branching, is not always straightforward either. This distinction cuts to the heart of the question of speciation's role in evolutionary change: the anagenetic mode can accommodate a broad range of intraspecific evolutionary processes (e.g., Gould 1982; Wright 1982a,b; Lande 1986; and a host of others since then). As noted above, however, establishing the coexistence of ancestor and descendent species, or of multiple sister species, requires a detailed phylogeny and well-resolved stratigraphic range endpoints. Like all paleontological analyses it also hinges on the ranking of morphologically defined units: taxonomic lumpers will tend to reduce the number of branching events, while splitters are more likely to convert anagenetic patterns to cladogenetic ones by increasing the number of contemporaneous taxonomic units. The growing inventory of studies linking morphology to genetically defined species suggests that the splitters have been closer to the biological reality (with past excesses and missteps, of course). Although some cladists have rejected the possibility of identifying ancestral species on theoretical grounds (e.g., Englemann and Wiley 1977; Frost and Kluge 1994; Norell 1996), increasingly rigorous protocols have become available for the recognition of potential ancestors for both fossil and living organisms (e.g., Paul 1992; Theriot 1992; Fisher 1994; Smith 1994; Marshall 1995; P. J. Wagner 1995, 1996a; Foote 1996b; Omland 1997). The data are still sparse but suggest that ancestral species can be detected and that temporal overlap with descendants, as expected for punctuated cladogenesis, is not uncommon. The challenge now is to refine and apply methods that will permit a quantitative assessment of when, where, and how often the different evolutionary patterns obtain in nature. A vast and nearly uncharted territory is open for modeling the interplay of sampling and paleobiological pattern (see Holland and Patzkowsky 1999), but most urgently needed

is a new battery of carefully designed and selected empirical studies.

Attempts to assess the relative frequency of evolutionary tempo and mode are premature, but some possibilities and problems can be defined. As already noted, stasis and punctuation appear to be the pervasive phenotypic patterns in marine macrofossils, although the relative proportions of anagenesis and cladogenesis remain unclear (e.g., Hallam 1998; Jackson and Cheetham 1999). Although more rigorous quantification would be valuable, there is little reason to doubt Fortey's (1985) report that gradualism occurs in fewer than 10% of the 88 trilobite species that have a meaningful stratigraphic range in the Ordovician Valhallfonna Formation, Spitsbergen, or Johnson's (1985) assessment, backed up by his data-rich monograph (Johnson 1984), that only one of the 34 scallop lineages in the northern European Jurassic shows possible gradual change in morphology. On the other hand, the famous Jurassic oyster *Gryphaea* shows a more complex mixture of stasis and gradualism (Johnson and Lennon 1990; Johnson 1993, 1994), and whether this complexity—and contrast with other contemporaneous bivalves—reflects the intensity of research prompted by *Gryphaea*'s notoriety as a classic evolutionary exemplar, difficulties of phylogenetic analysis in a morphologically difficult and heterochrony-prone group, or a true biological difference, remains uncertain.

Sheldon (1993, 1996) made the intuitively appealing suggestion that benthic species in more stable offshore environments might be more subject to gradual change, but empirical evidence is slim: Sheldon's trilobite study involves parallel changes in a single character in a set of lineages from a single restricted area in which the environment is changing upsection, albeit subtly (see Sheldon 1987, 1988). Better documented is the long-standing observation that pelagic species are more likely to show gradual change than benthic ones (Johnson 1982; Fortey 1985; Clarkson 1988; Jackson and Cheetham 1999). Fortey (1985) contrasts the evolution of a pelagic trilobite with that of co-occurring benthic species, but the richest data for gradualistic change come from microfossils. Three caveats obtain here:

first, geographic coverage remains a weakness of many analyses of pelagic organisms, although this is becoming less true; second, stasis and punctuations do occur in many microfossil lineages (see tabulations in Erwin and Anstey 1995a and Jackson and Cheetham 1999), even when hiatuses are taken into account (see MacLeod 1991); and third, so little is known about the population genetics, or even how individuals are packaged into species, in these unicellular groups that interpretation of paleontological patterns is doubly difficult (e.g., Tabachnick and Bookstein 1990; Norris et al. 1996; Huber et al. 1997; Darling et al. 1999, 2000; de Vargas et al. 1999; but see Kitazato et al. 2000 for encouraging results on a genus of benthic forams, and recall that some genetic analyses are finding that detailed morphometry of, for example, test porosity may help to capture genetic units [e.g., Huber et al. 1997; de Vargas et al. 1999]).

The record for land vertebrates is difficult to interpret because many studies lack one or more of the elements enumerated above (for cautionary notes see, for example, Schankler 1981; Heaton 1993). Some mammal lineages do appear to present robust examples of gradualistic change at the species level, however (see reviews by Barnosky [1987], Martin [1993], Chaline et al. [1993], and Carroll [1997]). For example, Chaline and Laurin (1986) found gradualism in a Plio-Pleistocene vole lineage over a broad geographic area, with quantitative data on cheek-tooth morphology in a series of time planes extending over an area from Spain and Britain to northern Italy, Poland, and the Czech Republic, with additional qualitative data from localities as far east as Moldova and western Siberia. But as with microfossils, mammals are not purely gradualistic in evolutionary tempo; indeed analyses of entire faunas or assemblages of clades suggests that stasis and punctuation is pervasive and perhaps prevalent (e.g., Barnosky 1987; Flynn et al. 1995; Prothero and Heaton 1996). Again the key issue is relative frequency and the factors that impose different frequencies among clades.

Attempts to assess the frequency of different types of speciation based exclusively on modern species have their own pitfalls. As

Wagner and Erwin (1995) note, phylogenetic tree topology alone cannot reliably distinguish evolutionary tempo and mode. Inferences based on molecular data as a source of temporal estimates show considerable promise but remain model-dependent, not only in terms of molecular-rate constancy but in assumptions about the pattern of morphological change between nodes (e.g., Garland et al. 1999). Finally, estimates of the relative frequency of allopatric and other types of speciation based on the present-day deployment of modern species (e.g., Lynch 1989; Barraclough and Vogler 2000) are undermined by the geographic volatility of species in the recent geologic past and by extinction. Only species that have split since the last glaciation, say in the last 10,000 years, are likely to capture the relative spatial distributions of sister species at the time of speciation. Species that split, say, 2 m.y. ago have been subject to perhaps 20 episodes of geographic shuffling with the waxing and waning of Pleistocene glaciation (e.g., Valentine and Jablonski 1993; Roy et al. 1996; Jackson and Overpeck this volume), so that the relative frequencies of geographic range overlap today probably say more about competitive interactions between close relatives than about speciation events (see also Chesson and Zink 1994). Taxa separated by major geographic barriers like the Rocky Mountains or the Isthmus of Panama are reasonable candidates for allopatric speciation, of course, but these more ancient splits are subject to the problems of extinct species more closely related to one or the other living ones—i.e., of intervening speciation events that represent the true spatial and temporal pattern of lineage splitting (e.g., Schneider 1995; Jackson and Budd 1996).

With all of these caveats, and in light of the sparse and uneven nature of the data, it is unsurprising that no clear taxonomic or environmental pattern has emerged for the distribution of evolutionary tempo and mode at the species level. Perhaps, in an obvious if unsatisfyingly context-specific hypothesis, species histories depend on their geographic extent and genetic population structure—i.e., on scale and hierarchy. If gradual anagenesis is simply the expected paleontological outcome

of homogeneous directional selection, in other words, true Fisherian mass selection, then this sets some requirements on the spatial scale of gene flow relative to that of environmental variation and thus makes predictions on the distribution and genetic structure of gradualistic taxa. On the other hand, for those species that maintain genetic cohesion over different environments, or among regions with disparate selective pressures through time, the interplay of local adaptation and gene flow—intermittent or regular—will tend to impose fluctuations around a mean rather than directionality (an argument raised by Eldredge 1985, 1989; and also consistent with Futuyma 1987). Such a return to the textbook basics could explain why lineages on islands (e.g., Lister 1989) and in isolated basins (e.g., Geary 1995; and Povel 1993 in part) exhibit gradualism while related taxa in more extensive or scattered habitats often show stasis and punctuation. It also provides an approach to the presence of contrasting evolutionary patterns in co-occurring lineages, which would be unexpected if the physical environment alone (e.g., habitat stability [Sheldon 1993, 1996]) determined tempo and mode. In our present state of ignorance it may even explain the gradualistic evolution of many planktic microfossils, which may often evolve as enormous populations that occupy different depth zones in one or more otherwise relatively homogeneous oceanic water masses (e.g., Lazarus et al. 1995; but see Norris et al. 1996 and other foraminiferal references cited above). The Plio-Pleistocene vole data are, however, an apparent counterexample: Chalain and Laurin (1986) note with surprise the gradualistic trajectory of their lineage despite its likely subdivision into semi-isolated populations. This may be the exception that proves the rule, however, if the particular phenotypic changes they measured, involving increasing hypsodonty and elaboration of enamel patterning on the tooth crown, can be attributed to selection imposed by long-term vegetation changes throughout the study area.

As already noted, the relative frequency of anagenesis and cladogenesis has yet to be established. Intuitively, even excluding “pseudoextinction” (i.e., anagenetic transformation

obscured by taxonomy), species extinction rates seem to be sufficiently high that frequent branching is required for lineages to persist over geologic timescales. A number of paleontological analyses of tempo and mode that consider clades of sufficient size and phylogenetic resolution for analysis do show significant numbers of species arising cladogenetically, with stratigraphic range overlaps between putative ancestors and descendants, or between sister species (see Erwin and Anstey 1995a; Jackson and Cheetham 1999; also Stanley et al. 1988; Wagner 1998). Nonetheless, all of these references, and many more besides, also contain examples of punctuated anagenesis, so that the apparent prevalence of stasis in many situations may or may not be matched by the prevalence of cladogenesis, as required by the punctuated equilibrium model. Clearly, analyses modeled on the Cheetham and Jackson (1995) studies and focused on other groups well represented in the fossils record, say bivalves or gastropods, would be valuable. Especially useful in light of the potential role of gene flow and its relation to the spatial scale of environmental variation would be to track lineages with contrasting evolutionary tempo and mode through the Neogene fossil record to their present-day populations.

Taxon Sorting

The prevalence of intraspecific oscillatory evolution and of evolutionary stasis means that the direction of speciation is difficult to predict from within-species evolutionary trajectories. Further, wherever punctuated cladogenesis is prevalent, long-term evolutionary trends will not be simple extrapolations of intraspecific evolution but instead must involve some form of sorting among species (stepwise, punctuated anagenesis patterns are less clear-cut and might also involve sorting among populations or even highly episodic, species-wide changes propelled entirely at the organismic level). That such differential speciation and extinction rates among clades might in principle shape large-scale evolutionary patterns appears to be generally accepted (e.g., Sober 1984; Maynard Smith 1989; Williams 1992). Equally important, as Slatkin

(1981) noted, differential rates can drive taxon sorting even in gradualistic systems depending on the extent of variation generated by cladogenesis and anagenesis. As in so many macroevolutionary questions the issues are the frequency of this sorting among species, the circumstances under which it occurs, and the nature of dynamics across hierarchical levels, i.e., identification of focal levels and upward and downward causation (e.g., Vrba and Gould 1986; and see Grantham 1995 for an especially thoughtful and clear review).

Species Selection and Related Processes

The term "species selection" has been used in both broad and narrow senses, sometimes by a single author. One approach, drawing on the insights of Lewontin (1970) and Hull (1980) and advocated by Vrba and Gould (1986) among others, is to maintain the neutral term "species sorting" for any pattern shaped by differential origination and extinction. Others would apply the term "species selection" here instead because fitness, i.e., differential birth and death, is being expressed at the species level, as the "emergent fitness" of species—speciation and extinction rates—within clades (e.g., Lloyd and Gould 1993; Stidd and Wade 1995; Gould and Lloyd 1999). Alternatively, species sorting can be divided into two categories depending on the hierarchical level of the characters that influence speciation and extinction rates. Then, in "effect macroevolution" differential rates are governed by organismal-level traits such as body size or habitat preferences, while in species selection the differential rates are governed by emergent, heritable properties at the species level (see Vrba 1984, 1989; Jablonski 1987; Grantham 1995).

Emergence and Heritability.—The concept of emergence in evolutionary biology has been difficult, but a simple operational approach is to recognize a feature as emergent at a given level if its evolutionary consequences do not depend on how the feature is generated at lower levels. (This approach is similar to Brandon's 1982, 1988 application of Salmon's 1971 statistical concept of "screening-off," and to a parallel view, "multiple realizability," that recently has been criticized as insufficiently pre-

cise in some circumstances; for discussion see Sober 1999; Sterelny and Griffiths 1999.) A classic example at the organismal level involves selection experiments in *Drosophila* where Robertson (1959) concluded that equivalent changes in wing size could be achieved either by changes in cell size or by changes in cell number, with variance in wild populations usually owing mainly to cell number, and in his experimental groups mainly to cell size (see also Stevenson et al. 1995). As the organism was the focal level of the experiment, the large-winged phenotype was the emergent property under selection, and not the cellular or genetic levels underpinning the evolutionary changes. Outside the lab, evolution of the emergent organismal property of DDT resistance is underlain by many alternative responses at the cellular level, from changes in cell walls that exclude the DDT molecule, to changes in cell metabolism that neutralize DDT when it penetrates the cell, to changes in cell physiology that sequester DDT before it can be effective (e.g., McKenzie and Batterham 1994; Feyereisen 1995).

By the same token, geographic range is an emergent property at the species level, not simply because most geographic ranges are determined by the overall distribution of conspecifics rather than by the movements of single bodies, but also because the evolutionary consequences of broad or narrow geographic ranges tend to be similar regardless of how those ranges are mediated at the organismal level (at least within broad groups, such as benthic marine invertebrates). For example, widespread species of marine gastropods are geologically longer-lived than restricted species, and the establishment and maintenance of these different ranges are statistically related to modes of larval development—an organismal trait—that differ in dispersal capabilities (Hansen 1978, 1982; Jablonski and Lutz 1983; Jablonski 1986a, 1987, 1995; Scheltema 1989, 1992; Gili and Martinell 1994; Kohn and Perron 1994). Jablonski (1987) found geographic range to be heritable at the species level (that is, closely related species showed significant correlations in the magnitudes in their geographic ranges), completing the requirements for evolution by selection at any

level: the existence of heritable variation in a feature that, by interaction with the environment, imparts differential success. Cheetham and Jackson (1996) also found widespread species of bryozoans to be geologically long-lived relative to restricted species; in fact their widespread species, taken as occupying >4 regions, have a median duration of about 7.5 m.y. while the narrowly distributed species a median duration of about 2 m.y., each remarkably close to the high- and low-dispersal molluscan species, respectively, as cited above. But here the differences in geographic ranges presumably derive from the rafting of adults (e.g., Watts et al. 1998). Thus, differential taxonomic survival depends on the emergent, species-level property, i.e., the scale of the species' range and not on the underlying organismal traits.

Genetic population structures, again not a property of single organisms, can be viewed in the same way. Jablonski (1986a, 1995) attributed high per-taxon speciation rates seen in gastropod lineages having low larval dispersal ability, as inferred from their larval shells, to their genetically fragmented populations (an argument broadly supported by genetic analyses of benthic marine invertebrates [see Pechenik 1999; Bohonak 1999]). Similarly, Wilson et al. (1975) suggested that mammals with complex social structures should have genetically more fragmented populations and thus higher speciation rates than those with more open breeding systems. And more recently, Belliure et al. (2000) found that natal dispersal ability in birds is inversely related to population differentiation and therefore, they argued, to speciation propensity. If these very different routes to highly subdivided populations yield similar macroevolutionary dynamics, this again would argue for genetic population structure as an emergent property at the clade level. The consistent relationship between dispersal ability and genetic population structure in plants (Govindaraju 1988) and animals (Bohonak 1999, in his valuable meta-analysis of 333 species across all animal groups and environments) suggests that this will be a profitable avenue for macroevolutionary research. Perhaps this general mechanism underlies the decrease in speciation rate

observed by Dodd et al. (1999) when angiosperm lineages switch from animal pollination to wind pollination, for example.

Recent molecular work has shown that even widely dispersing marine species can sometimes, perhaps usually, have subdivided rather than panmictic populations (e.g., Palumbi 1996; Geller 1998; Benzie 1999a; Avise 2000). This does not mean, however, that high-dispersal species are as readily subdivided as low-dispersal ones. The key issue is the stability and long-term evolutionary effects of that population structure relative to taxa with low dispersal abilities. The consistent relationships among larval type, geographic extent, and speciation/extinction rates in Cretaceous, Paleogene, and Neogene taxa (which appear to be robust to sampling [Jablonski 1988; Marshall 1991]) suggest that in at least some settings the population structures detected by mtDNA analysis may be transient or in any case do not have predictable macroevolutionary effects (see also the diversity of analyses tabulated by Bohonak 1999). An intriguing pattern that needs a more detailed evolutionary perspective is the discovery that genetic connectedness among Pacific populations of benthic invertebrates does not conform to present-day ocean circulation patterns but may be a Pleistocene holdover (Benzie and Williams 1997; Palumbi et al. 1997; Benzie 1999a,b). Spatial scale may also be important here: the vast but highly discontinuous environments of the Indo–West Pacific may impart a different evolutionary dynamic from that documented in the more linear shelves and the more continuous two-dimensional epicontinental seas that provided the paleontological data (see Valentine and Jablonski 1983).

Clearly, further analyses of evolutionary sorting of taxa would benefit greatly from a more detailed phylogenetic framework. Duda and Palumbi (1999) rightly note that the further analyses of such patterns in a phylogenetic context would be valuable. However, their emphasizing an evolutionary bias toward the production of species having low-dispersal larvae, rather than species sorting for the larval modes for Pacific *Conus*, is difficult to interpret because they lack data on extinct species and their model does not take

into account empirical evidence for higher extinction and origination rates in low-dispersal lineages.

Another unresolved problem is that marine bivalves do not exhibit the same relation between larval types and species-level dynamics as the co-occurring gastropods (e.g., Jablonski and Lutz 1983; Stanley 1990). Perhaps this is because modes of larval development in bivalves are more tightly linked phylogenetically to feeding types, body sizes, and other factors that might also influence evolutionary rates. Jablonski (1986a, 1995) showed that larval modes in marine gastropods override those of adult feeding types, and if the opposite is true for bivalves then the two groups in tandem might provide a valuable system for exploring the interplay of rate-determining traits at different hierarchical levels.

The heritability of species-level traits remains a neglected area. Jablonski (1987) and Ricklefs and Latham (1992) found geographic ranges to be heritable in marine mollusks and terrestrial plants, respectively. Their comparisons of closely related species were designed as a phylogenetic analogue to the sib-sib comparisons of quantitative genetics (and see also Peterson et al. 1999, who successfully predict geographic distributions of sister species based on a model of ecological niche conservatism). Gaston and Blackburn (1997) did not find strong species-level heritability in birds using nested ANOVAs, a very different design that also has precedents in quantitative genetics but lacks a detailed phylogenetic framework, necessarily omits extinct species and Pleistocene range adjustments, and compares taxa in different geographic situations, unlike Jablonski's analysis, which is a macroevolutionary analogue of a common-garden experiment. More work is needed to assess the strengths and weaknesses of the different approaches and where they might be applied most robustly.

The Limits of Species Selection and Species Sorting.—The domain of strict-sense species selection, which depends on emergent characters, is much narrower than broad-sense species selection, which depends only on emergent fitnesses (i.e., differential origination and extinction rates regardless of the hierarchical level at

which they are determined [see Vrba and Gould 1986; Lloyd and Gould 1993; Grantham 1995; Stidd and Wade 1995]). Beyond that, we simply do not know the relative frequencies of different sorting processes, overall or among clades. The theoretical literature has outstripped the empirical database, in part simply because of the scale of the databases required for rigorous analyses. However, if geographic range is arguably a species-level character, then the macroecological literature is rich in potential examples that might fit the species-selection paradigm, because so many features of living organisms can be related to geographic range and thus are candidates for hitchhiking on species sorting processes (see for example Brown 1995; Brown et al. 1996; Gaston 1998). Other components of rarity as classified by Rabinowitz (1981; Rabinowitz et al. 1986) might also be examined in this list: population sizes or densities may be emergent properties (e.g., Vrba and Eldredge 1984; and here too a large macroecological literature exists, ripe for macroevolutionary analysis, e.g., Brown 1995; Blackburn and Gaston 1997, 1999), whereas habitat specificity may reside more fully at the organismal level (e.g., Vrba 1987).

One important issue needing more attention is the stability of such species-level characteristics. Jablonski (1986b, 1987) gave evidence that marine species achieve their geographic-range magnitudes rapidly relative to their geologic durations. Tracking the magnitude, rather than the position, of geographic ranges during Pleistocene or other environmental oscillations would be interesting, as would testing for evolutionary rate differences among taxa that differ in the *amplitude* of their range-size changes over time. Population density should also be tested more fully for long-term stability (e.g., Arneberg et al. 1997). Both exciting and daunting is the loose covariation of geographic range, abundance, and body size (Brown 1995, 1999; Gaston and Blackburn 1999; Lawton 1999), and the question of how these effects spanning hierarchical levels and spatial scales interact, and become linked or decoupled on ecological and evolutionary timescales.

Given that the history of most lineages is ev-

idently dominated by stasis and punctuation, other potential species-level features that might be heritable owing to factors like population sizes or genetic population structure include relative morphological inertia (and so the average duration of stasis in the phyletic mode, or the amplitude of oscillations within stasis, if these are set intrinsically) and perhaps even the size-frequency distribution of morphological divergences of daughter isolates. Sex ratios may be another example of higher-level trait, although possibly played out at an intermediate focal level if interdemic differences in sex ratios are common in some groups (e.g., Delph 1990; Graff 1999). Is the relative genetic or morphological variability of species an emergent species-level trait, or is it simply the summation of organismic properties and therefore an aggregate trait as argued by Lloyd and Gould (1993)? It depends on how that variation arises, and how sorting processes operate on that trait, and empirical work is needed here.

The potential for species sorting (= broad-sense species selection) seems extensive, given the abundant evidence for differences in intrinsic extinction and origination rates among clades (e.g., McKinney 1997; Kammer et al. 1998; Sepkoski 1998; see also "extinction risk" studies on extant organisms, e.g., Bennett and Owens 1997 and references therein). Here, too, phylogenetic hypotheses can provide a valuable framework for rigorous analysis, and methods are being developed for rigorous testing of differential origination and extinction rates in a phylogenetic context (e.g., Kirkpatrick and Slatkin 1993; Slowinski and Guyer 1993; Sanderson and Donoghue 1996; Harvey and Rambaut 1998; Paradis 1998). These methods have mostly been applied to extant taxa, where the estimation of evolutionary dynamics is made difficult by unrecorded extinction that must be ignored or assumed to be constant through time, but some also show promise for the testing of species-sorting hypotheses in the fossil record.

Species sorting, including narrow-sense species selection, will generally play a different evolutionary role from the microevolutionary sorting of organisms within populations: it will tend to determine diversity differentials

among clades rather than shape adaptations. Species sorting may not construct a complex eye or a long neck, but it may determine how many species possess complex eyes or long necks over evolutionary timescales. This has two immediate implications. First, the setting of species sorting and microevolution as rival hypotheses or mechanisms is often inappropriate. And second, the mapping of species densities in morphospace need not reflect the topology of the adaptive landscape. That is, the frequency distribution of morphologies within or among clades may not be a simple indication of relative fitnesses at the organismal level.

But is sorting at the species level unequivocally ruled out as a mechanism for organismal adaptation? Rice (1995) showed that the efficacy of species sorting in character evolution depends on the speciation rate per generation, the mutation rate, and the survival rate of reproductive isolates (and the genetic complexity of the trait under consideration). Thus, species sorting would be more likely to influence character evolution directly in organisms with long generation times; for example Asian elephants fit this model, given reasonable mutation rates and selection coefficients, and a very broad taxonomic domain is possible if speciation rates are sufficiently high (Rice 1995). Perhaps a more pervasive way for species sorting to influence the evolution of complex characters is by determining the persistence and proliferation of taxa bearing characters shaped by individual selection, so that the process of assembling those characters can proceed beyond the duration of individual species (Raup 1994; Rice 1995). This means that rate differentials among clades might be important even if, as Hallam (1998) argues, many individual clades generate only a few species per unit time.

Hierarchical analyses of large-scale changes in morphology would be valuable for improving our understanding of the relative roles of processes at different levels and the potentially complex interactions between them. The infaunalization of bivalves, the evolution of tree-like growth habits with the initial assembly of terrestrial forests, and the escalation of defensive morphologies in marine benthos during

the increase in predation pressure described by Vermeij (1987) as the Mesozoic Marine Revolution (MMR) would all be possible subjects. To use the last of these biotic transitions as an example (and see also Signor and Brett 1984), long-lived bivalve or gastropod genera that appear to persist through much of the MMR, such as *Aphrodina*, *Cyprimeria*, or *Solariella*, might be targeted to test whether any given species shows anagenetic change in antipredatory adaptations independent of local environmental changes. (Kelley 1989, 1991, did find intraspecific trends, but within a much later, Neogene, interval.) If species tend to be static, several alternative dynamics should be tested. A mechanism below the species level might involve directional, stepwise anagenesis, shaped by widely spaced episodes of directional selection or within-species shifting-balance processes. Next up the hierarchy would be the sorting of species to convert clades to better-defended morphologies. Operating at an even higher level would be clade sorting, in which preferential extinction of poorly defended clades or preferential origin of well-defended ones might shape the overall biota. As many authors have noted (e.g., Stanley 1973; McShea 1994; P. J. Wagner 1996b), such analyses cannot focus only on mean morphologies or the appearance of derived character states; an important component of the sorting dynamics may involve the retention of less heavily defended morphologies. Finally, spatial scale will be important in understanding mechanisms, in terms of both the establishment of well-defended species—which Roy (1996) found to vary regionally in timing and which may have been promoted by environmental perturbations (see also Miller 1998)—and the fates of less derived forms (which Vermeij [1987] argues have shifted geographically or environmentally through time).

Such large-scale evolutionary interactions of predators and prey raise the broader issue of clade interactions and how they might drive taxon sorting. As Sepkoski (1996) made clear, negative clade interactions need not produce straightforward reciprocal diversity patterns (the “double wedge pattern” of Benton 1987), but instead can be manifest in com-

plex coupled logistic patterns, and perhaps most importantly depressed but still positive diversification rates (see also Miller and Sepkoski 1988). Still open to investigation is exactly how local ecological interactions—as many of these clade interactions surely must entail—actually scale up to determine origination and extinction rates. Simple intuitive arguments are easy: competition decreases population sizes and/or intrinsic growth rates, thereby making species more vulnerable to stochastic extinction; origination rates might be depressed in the same way, if biotic interactions reduce the population sizes of isolates and thus decrease their probability of surviving to achieve speciation. On the other hand, clade interactions via predation could arguably operate in the same fashion, although Vermeij (1994) explicitly rejects the role of escalation in extinction on mainly theoretical grounds. How negative ecological interactions actually determine per-taxon origination and extinction rates seems an important area for research.

Such analyses in the fossil record are complicated by the highly diffuse nature of many of the interactions under consideration: escalation in molluscan defenses is a response to the collective diversification of durophagous arthropods, mollusks, vertebrates, and other groups, so that simple responses to specific enemies will be unusual, difficult to detect, and probably fleeting in geologic terms. Targeting competitive interactions for combined micro/macroevolutionary analysis will also be complicated by the well-established observation that taxonomic distance is not a reliable proxy for interaction intensity (e.g., Brown and Davidson 1977; Brown et al. 1979a,b on seed-eating ants vs. rodents; Kodric-Brown and Brown 1979 on hummingbirds vs. insects; Schluter 1986 on finches vs. bees; Jackson and Hughes 1985 on spatial competition in marine encrusting communities among several phyla). Paleontologists have been aware of this—Bambach's (1983) "megaguilds" are decidedly polyphyletic, for example—but the study of the large-scale evolutionary effects of biotic interactions remains a difficult task. One powerful approach deserving more extensive application is the projection back into the fossil

record of interactions that have been experimentally dissected in modern communities (e.g., Aronson 1992, 1994; Lidgard et al. 1993; Sepkoski et al. 2000).

Incumbency.—Macroevolutionary incumbency effects, such as the damping of diversification among mammals for the first two-thirds of their history (presumably by incumbent archosaurs), are perhaps the most compelling evidence of the macroevolutionary effects of competitive interactions (Jablonski and Sepkoski 1996; Jablonski 2000a). Such effects represent very different dynamics from those underlying the reciprocal diversity patterns discussed above, of course: in double-wedge or coupled logistic models, taxon A progressively excludes taxon B by virtue of A's competitive superiority; in incumbency interactions, taxon A excludes B by virtue of A's ecological preemption of resources, which need not reflect competitive superiority on a level playing field (as emphasized by Rosenzweig and McCord [1991]). The double-wedge pattern is not exclusively the hallmark of the rise of a competitive dominant, however: piecemeal extinction of the dominant incumbent may create cumulative opportunities for surviving taxa, for example. Other kinds of progressive replacements might also be underlain by incumbency effects, as Valentine (1990) suggested for the Phanerozoic decline in evolutionary rates in the marine biota: over the long run, extinction-resistant clades will tend to preempt high-volatility clades (see Sepkoski 1998 for a somewhat different view).

The acceleration in evolutionary rates, taxonomically and morphologically, among previously established clades following an extinction event (e.g., Miller and Sepkoski 1988; Patzkowsky 1995; Foote 1997; McKinney 1998; Sepkoski 1998) is the primary macroevolutionary measure of incumbency effects. Considerable evidence supports a spatial analogue, in which asymmetries in biotic interchanges appear to reflect regional differences in extinction intensities, both in the fossil record (e.g., Vermeij 1991) and in present-day biotas (e.g., Case 1996). However, not all invasions are mediated by prior extinction (see for example Williamson 1996; Lonsdale 1999), and at least for the end-Cretaceous extinction,

invasion intensities need not correlate to local extinction intensities (Jablonski 1998). More work is needed that tackles the difficult task of separating the effects of diversity loss *per se* from regional differences in environmental change; in other words, is differential diversity loss the promoter of asymmetrical biotic interchanges, or another symptom of the effects of differential environmental perturbation? Incumbency effects may represent one of the strongest bridges between ecology and macroevolution, and cross-scale and spatially explicit analyses of how those effects are maintained, broken, or circumvented would be valuable, not only for theoretical reasons, but in order to address the pressing issues of present-day biotic interchange.

Extinction Events As Filters and Promoters

So much has been written lately on the evolutionary role of extinction events that I will touch on only a few points here (see Raup 1994; Jablonski 1995, 2000a,b; Erwin 1998, 2000b for an entry into this literature). First and foremost, we still have much to learn about the role of extinction events in evolution. Perturbations occur at all intensities and spatial scales, and as discussed above they promote biotic change in important ways, but effects are difficult to predict from magnitude alone (see Miller 1998). The differential response of large-scale biotic units like clades and regional biotas to seemingly similar perturbations at different times—whether asteroid impacts or climate changes—reflects the fundamental nonlinearities that typify most complex systems. Thresholds, and especially the importance of antecedent events, are probably an essential component to a system where four sea-level oscillations cause little change in marine community composition but a fifth brings significant turnover; asteroid impacts that form craters of 50 km have no perceptible effect on the global biota but a crater of 300 km corresponds to a Cretaceous/Tertiary (K/T) scale event; and even apparently similar mass extinction intensities can have differing effects on biosphere structure and function (Droser et al. 1997).

On the other hand, as Levin (1999: pp. 180–184) notes, there is little evidence that large-

scale biotic systems, let alone global biotas, evolve to the perpetual edge of collapse like the canonical sandpile, as suggested by Bak and colleagues (e.g., Sneppan et al. 1995; Solé et al. 1999). The resilience of these biotic systems to many perturbations, and their relatively loose organization as manifested in the relatively fluid composition of Pleistocene and many earlier communities, argues against a state of self-organized criticality, and more generally argues that the major turnover events in the history of life were externally driven (rather than the product of internal dynamics). Such avalanche models may apply on local scales and the short term, but hierarchy and scale defeat their universality, because the necessary biotic interconnectedness falls away rapidly at larger scales. Spatially heterogeneous dynamics can be seen, for example, in the geographic complexities of macroevolutionary and macroecological patterns like the Ordovician radiations, the marine Mesozoic revolution, the recovery from the end-Cretaceous mass extinction, and the demise of the Pleistocene megafauna (Roy 1996; Miller 1997a,b, 1998; Jablonski 1998; Martin and Steadman 1999).

The major mass extinctions probably account for less than 5% of the species turnover in the geologic past, and their disproportionate evolutionary effects probably derive from their removal of not just minor constituents of the biota, but also established incumbents. Analyses are still sparse, but contrasts between survivorship patterns during mass extinctions and those prevalent during times of low extinction intensity have been recorded for each of the major extinction events (Jablonski 1995, 2000a,b). This does not mean that certain features favored during times of “background” extinction could never also be advantageous during mass extinction events, but even partial discordances in survivorship can have profound and lasting effects, given the intensities involved. The monotonic rather than bimodal frequency distribution of extinction intensities in the geologic past (e.g., Raup 1991), and some of the similarities in survivorship among mass extinctions despite apparently different triggers, suggests that the scale of the perturbation and the operation of

threshold effects were important factors in the observed changes in selectivity.

Patterns of selectivity are difficult to assess, however, because traits can be lost as a by-product of selection on other features (or, of course, purely stochastic survivorship [Raup 1994]). For example, what was it about the end-Ordovician extinction that selected against broad selenizones in snails (P. J. Wagner 1996b), or about the end-Cretaceous extinction that selected against schizodont hinges in bivalves, elongate rostra in echinoids, or complex sutures in cephalopods? All of these losses or declines are more likely to represent correlations rather than direct causation, but they had long-term morphological effects, and additional examples are plentiful.

Finally, the long-term effects of mass extinctions are set not only by the victims and survivors of an event, but also by the dynamics of the recovery process. Here, of course, is where the incumbency effects are most vividly illustrated, by the diversifications that unfold with the removal of previously dominant taxa. As discussed by Jablonski (2000b), however, clade dynamics across extinction events can exhibit several different patterns, including (1) unbroken continuity, as in the escalation of antipredatory defenses in marine bivalves across the K/T boundary (Hansen et al. 1999); (2) continuity with setbacks, as in the increase in cheilostome bryozoan abundance relative to cyclostomes across the K/T boundary (McKinney et al. 1998) or the increase in suture complexity in Paleozoic ammonoids (Saunders et al. 1999); (3) failure to rebound and eventual extinction, as in the demise of the prolecanitid ammonoids in the Early Triassic after surviving the end-Permian debacle (Page 1996); or (4) unbridled diversification, as seen most famously in the radiation of mammals after the end-Cretaceous demise of the dinosaurs and other reptilian groups. The apportionment of survivors among these different trajectories needs much more analysis before we can understand the evolutionary roles of extinction events.

That said, mass extinctions have lasting effects across many scales. As Erwin (1998) argues, the Permo-Triassic extinction permanently restructured marine and terrestrial

ecosystems, so that the raw material for microevolution and the web of potential biotic interactions was profoundly shaped by the taxonomic losses of that time (although Sepkoski [1996, 1998] held that those changes were inevitable given differential turnover among groups, and were merely hastened by the mass extinction). Similarly, the end-Cretaceous extinction removed the rudists and nearly exterminated the trigonoid bivalves, but its lasting influence can also be seen in the age distribution of living marine bivalve genera, which shows a secondary peak corresponding to the early Cenozoic. This 60-m.y. evolutionary echo is less dramatic than the mammalian rise to dominance that began at the same time, but it reflects a similar evolutionary process (Flessa and Jablonski 1996).

Conclusion

The relation between micro- and macroevolution is complementary and not mutually exclusive, with effects cascading both upwards and downwards over long timescales. The conceptual expansion of evolutionary biology with the advances in our understanding of the origin and sorting of variation has benefited many disciplines and is promoting a fuller integration across those scales and hierarchical levels. I have touched only indirectly on many of the important methodological advances discussed elsewhere in this issue: in phylogeny estimation, in dissection of developmental processes, in calculation of confidence limits on diversification rates and patterns, and in quantifying the relation of paleontological patterns to the fabric of the stratigraphic record. These developing methodologies, and the host of new questions that are emerging at the interface of biology and geology, will provide rich research opportunities for the next 25 years of *Paleobiology*.

Acknowledgments

This paper benefited from discussions with many colleagues, most recently A. K. Behrensmeyer, B. Chernoff, D. H. Erwin, M. Foote, T. A. Grantham, S. M. Kidwell, K. Roy, A. B. Smith, J. W. Valentine, P. J. Wagner, S. L. Wing, and, in the final throes, the NCEAS Working Group on Ecological Processes and Evolution-

ary Rates (P. M. Brakefield, N. Eldredge, S. Gavrillets, J. B. C. Jackson, R. E. Lenski, B. S. Lieberman, M. A. McPeck, W. Miller, and J. N. Thompson); few if any of these people agree fully with the views expressed here. D. J. Futuyma, S. M. Kidwell, D. W. McShea, and J. W. Valentine provided valuable reviews. I thank the editors of *Paleobiology* for inviting me to write this paper, and for their patience during its elephantine gestation period; Natasha Atkins significantly improved the clarity and accuracy of the text. Supported by the National Science Foundation and a John Simon Guggenheim Memorial Fellowship.

Literature Cited

- Adams, M. D., et al. 2000. The genome sequence of *Drosophila melanogaster*. *Science* 287:2185–2195.
- Ahn, D.-G., and G. Gibson. 1999a. Axial variation in the threespine stickleback: relationship to *Hox* gene expression. *Development, Genes and Evolution* 209:473–481.
- . 1999b. Expression patterns of the threespine stickleback *Hox* genes and insights into the evolution of the vertebrate body axis. *Development, Genes and Evolution* 209:482–494.
- Akam, M. 1998. *Hox* genes, homeosis and the evolution of segment identity: no need for hopeless monsters. *International Journal of Developmental Biology* 42:445–451.
- Alberch, P., S. J. Gould, G. F. Oster, and D. B. Wake. 1979. Size and shape in ontogeny and phylogeny. *Paleobiology* 5:296–317.
- Arneberg, P., A. Skorping, and A. F. Read. 1997. Is population density a species character? Comparative analyses of the nematode parasites of mammals. *Oikos* 80:289–300.
- Arnold, H. 1966. Grundsätzliche Schwierigkeiten bei der biostatigraphischen Deutung phyletischer Reihen. *Senckenbergiana Lethaea* 47:537–547.
- Arnold, S. J., and P. C. Phillips. 1999. Hierarchical comparison of genetic variance–covariance matrices. II. Coastal–inland divergence in the garter snake, *Thamnophis elegans*. *Evolution* 53:1516–1527.
- Arnone, M. L., and E. H. Davidson. 1997. The hardwiring of development: organization and function of genomic regulatory systems. *Development* 124:1851–1864.
- Aronson, R. B. 1992. Biology of a scale-independent predator–prey interaction. *Marine Ecology Progress Series* 80:1–13.
- . 1994. Scale-independent biological processes in the marine environment. *Oceanography and Marine Biology, an Annual Review* 32:435–460.
- Arthur, W. 1988. *A theory of the evolution of development*. Wiley, Chichester, England.
- . 1997. *The origin of animal body plans*. Cambridge University Press, Cambridge.
- Askin, R. A., and R. A. Spicer. 1995. The Late Cretaceous and Cenozoic history of vegetation and climate at northern and southern high latitudes: a comparison. Pp. 156–173 in National Research Council Board on Earth Sciences and Resources, *Effects of past global change on life*. National Academy Press, Washington, D.C.
- Atchley, W. R., and B. K. Hall. 1991. A model for development and evolution of complex morphological structures. *Biological Reviews* 66:101–157.
- Atchley, W. R., S. Z. Xu, and C. Vogl. 1994. Developmental quantitative genetic models of evolutionary change. *Developmental Genetics* 15:92–103.
- Averof, M., and N. H. Patel. 1997. Crustacean appendage evolution associated with changes in *Hox* gene expression. *Nature* 388:682–686.
- Avise, J. 2000. *Phylogeography*. Harvard University Press, Cambridge.
- Bambach, R. K. 1983. Ecospace utilization and guilds in marine communities through the Phanerozoic. Pp. 719–746 in M. J. S. Tevesz and P. L. McCall, eds. *Biotic interactions in recent and fossil benthic communities*. Plenum, New York.
- Barnosky, A. D. 1987. Punctuated equilibria and phyletic gradualism: some facts from the Quaternary fossil record. *Current Mammalogy* 1:109–147.
- Barracough, T. G., and A. P. Vogler. 2000. Detecting geographical pattern of speciation from species-level phylogenies. *American Naturalist* 155:419–434.
- Bateman, R. M., P. R. Crane, W. A. DiMichele, P. R. Kenrick, N. P. Rowe, T. Speck, and W. E. Stein. 1998. Early evolution of land plants: phylogeny, physiology, and ecology of the primary terrestrial radiation. *Annual Review of Ecology and Systematics* 29:263–292.
- Behrensmeier, A. K., and R. W. Hook. 1992. Paleoenvironmental contexts and taphonomic modes. Pp. 15–136 in A. K. Behrensmeier et al., eds. *Terrestrial ecosystems through time*. University of Chicago Press, Chicago.
- Behrensmeier, A. K., S. M. Kidwell, and R. A. Gastaldo. 2000. Taphonomy and paleobiology. *Paleobiology* 26:103–147.
- Bell, M. A., M. S. Sadagursky, and J. V. Baumgartner. 1987. Utility of lacustrine deposits for the study of variation within fossil samples. *Palaios* 2:455–466.
- Belliure, J., G. Sorci, A. P. Møller, and J. Cloubert. 2000. Dispersal distances predict subspecies richness in birds. *Journal of Evolutionary Biology* 13:480–487.
- Belting, H. G., C. S. Shashikant, and F. H. Ruddle. 1998. Modification of expression and cis-regulation of *Hoxc8* in the evolution of diverged axial morphology. *Proceedings of the National Academy of Sciences USA* 95:2355–2360.
- Bennett, K. D. 1997. *Evolution and ecology: the pace of life*. Cambridge University Press, Cambridge.
- Bennett, P. M., and I. P. F. Owens. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? *Proceedings of the Royal Society of London B* 264:401–408.
- Benton, M. J. 1987. Progress and competition in macroevolution. *Biological Reviews* 62:305–338.
- Benzie, J. A. H. 1999a. Genetic structure of coral reef organisms: ghosts of dispersal past. *American Zoologist* 39:131–145.
- . 1999b. Major genetic differences between crown-of-thorns starfish (*Acanthaster planci*) populations in the Indian and Pacific Oceans. *Evolution* 53:1782–1795.
- Benzie, J. A. H., and S. T. Williams. 1997. Genetic structure of giant clam (*Tridacna maxima*) populations in the west Pacific is not consistent with dispersal by present-day ocean currents. *Evolution* 51:768–783.
- Blackburn, T. M., and K. J. Gaston. 1997. A critical assessment of the form of the interspecific relationship between abundance and body size in animals. *Journal of Animal Ecology* 66:233–249.
- . 1999. The relationship between animal abundance and body size: a review of the mechanisms. *Advances in Ecological Research* 28:181–210.
- Bohonak, A. J. 1999. Dispersal, gene flow, and population structure. *Quarterly Review of Biology* 74:21–45.
- Bookstein, F. L. 1987. Random walk and the existence of evolutionary rates. *Paleobiology* 11:258–271.
- . 1988. Random walk and the biometrics of morphological characters. *Evolutionary Biology* 23:369–398.
- Bradshaw, H. D., K. G. Otto, B. E. Frewen, J. K. McKay, and D.

- W. Schemske. 1998. Quantitative trait loci affecting differences in floral morphology between two species of monkeyflower (*Mimulus*). *Genetics* 149:367–382.
- Bralower, T. J., and M. Parrow. 1996. Morphometrics of the Paleocene coccolith genera *Cruciplacolithus*, *Chiasmolithus*, and *Sullivania*: a complex evolutionary history. *Paleobiology* 22: 352–385.
- Brandon, R. N. 1982. The levels of selection. Pp. 315–323 in P. Asquith and T. Nichols, eds. *PSA 1982, Vol. 1. Philosophy of Science Association, East Lansing, Mich.*
- . 1988. The levels of selection: a hierarchy of interactors. Pp. 51–71 in H. Plotkin, ed. *The role of behavior in evolution*. MIT Press, Cambridge.
- Brown, J. H. 1995. *Macroecology*. University of Chicago Press, Chicago.
- . 1999. *Macroecology: progress and prospect*. *Oikos* 87: 3–14.
- Brown, J. H., and D. W. Davidson. 1977. Competition between seed-eating rodents and ants in desert ecosystems. *Science* 196:880–882.
- Brown, J. H., D. W. Davidson, and O. J. Reichman. 1979a. An experimental study of competition between seed-eating desert rodents and ants. *American Zoologist* 19:1129–1143.
- Brown, J. H., O. J. Reichman, and D. W. Davidson. 1979b. Granivory in desert ecosystems. *Annual Review of Ecology and Systematics* 10:201–227.
- Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* 27:597–623.
- Budd, A. F., K. G. Johnson, and D. C. Potts. 1994. Recognizing morphospecies in colonial reef corals. 1. Landmark-based methods. *Paleobiology* 20:484–505
- Burke, A. C. 1989. Development of the turtle carapace: implications for the evolution of a novel Bauplan. *Journal of Morphology* 199:363–378.
- . 1991. The development and evolution of the turtle body plan: inferring intrinsic aspects of the evolutionary process from experimental embryology. *American Zoologist* 31:616–627.
- Burke, A. C., C. E. Nelson, B. A. Morgan, and C. Tabin. 1995. *Hox* genes and the evolution of vertebrate axial morphology. *Development* 121:333–346.
- Buzas, M. A., and S. J. Culver. 1986. Geographic origin of benthic foraminiferal species. *Science* 232:775–776.
- Byrne, K., and R. A. Nichols. 1999. *Culex pipiens* in London Underground tunnels: differentiation between surface and subterranean populations. *Heredity* 82:7–15.
- Cardillo, M. 1999. Latitude and rates of diversification in birds and butterflies. *Proceedings of the Royal Society of London B* 266:1221–1225.
- Carroll, R. L. 1997. *Patterns and processes of vertebrate evolution*. Cambridge University Press, Cambridge.
- Carter, D. R., B. Miki, and K. Padian. 1998. Epigenetic mechanical factors in the evolution of long bone epiphyses. *Zoological Journal of the Linnean Society* 123:163–178.
- Case, T. J. 1996. Global patterns in the establishment and distribution of exotic birds. *Biological Conservation* 78:69–96.
- Chaline, J., and B. Laurin. 1986. Phyletic gradualism in a European Plio-Pleistocene *Mimomys* lineage (Arvicolidae, Rodentia). *Paleobiology* 12:203–216.
- Chaline, J., P. Brunet-Lecomte, S. Montuire, L. Viriot, and F. Courant. 1993. Morphological trends and rates of evolution in arvicolids (Arvicolidae, Rodentia): towards a punctuated equilibria/disequilibria model. *Quaternary International* 19: 27–39.
- Charlesworth, B., R. Lande, and M. Slatkin. 1982. A neo-Darwinian commentary on macroevolution. *Evolution* 36:474–498.
- Cheetham, A. H., and J. B. C. Jackson. 1995. Process from pattern: tests for selection versus random change in punctuated bryozoan speciation. Pp. 184–207 in Erwin and Anstey 1995b.
- . 1996. Speciation, extinction, and the decline of arborescent growth in Neogene and Quaternary cheilostome Bryozoa of tropical America. Pp. 205–233 in J. B. C. Jackson, A. F. Budd, and A. G. Coates, eds. *Evolution and environment in tropical America*. University of Chicago Press, Chicago.
- Chesser, R. T., and R. M. Zink. 1994. Modes of speciation in birds: a test of Lynch's method. *Evolution* 48:490–497.
- Cheverud, J. M. 1996. Developmental integration and the evolution of pleiotropy. *American Zoologist* 36:44–50.
- Chow, R. L., C. R. Altmann, R. A. Lang, and A. Hemmati-Bri-vanlou. 1999. *Pax6* induces ectopic eyes in a vertebrate. *Development* 126:4213–4222.
- Claridge, M. F., H. A. Dawah, and M. R. Wilson, eds. *Species: the units of biodiversity*. Chapman and Hall, London.
- Clark, J. S. 1998. Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. *American Naturalist* 152:204–224.
- Clarke, G. M. 1993. The genetic basis of developmental stability. 1. Relationships between stability, heterozygosity and genomic coadaptation. *Genetica* 9:15–23.
- Clarkson, E. N. K. 1988. The origin of marine invertebrate species: a critical review of microevolutionary transformations. *Proceedings of the Geologists' Association* 99:153–171.
- Coates, M. I., and M. J. Cohn. 1998. Fins, limbs, and tails: outgrowths and axial patterning in vertebrate evolution. *Bio-Essays* 20:371–381.
- Cohen, B. L., P. Balfe, M. Cohen, and G. B. Curry. 1991. Molecular evolution and morphological speciation in North Atlantic brachiopods (*Terebratulina* spp.). *Canadian Journal of Zoology* 69:2903–2911.
- Cohn, M. J., and C. Tickle. 1999. Developmental basis of limblessness and axial patterning in snakes. *Nature* 399:474–479.
- Collins, T. M., K. Frazer, A. R. Palmer, G. J. Vermeij, and W. M. Brown. 1996. Evolutionary history of northern hemisphere *Nucella* (Gastropoda, Muricidae): molecular, morphological, ecological, and paleontological evidence. *Evolution* 50:2287–2304.
- Conway Morris, S. 1998. The evolution of diversity in ancient ecosystems: a review. *Philosophical Transactions of the Royal Society of London B* 353:327–345.
- Coope, G. R. 1995. Insect faunas in Ice Age environments: why so little extinction? Pp. 55–74 in J. H. Lawton and R. M. May, eds. *Extinction rates*. Oxford University Press, Oxford.
- Coyne, J. A., and H. A. Orr. 1998. The evolutionary genetics of speciation. *Philosophical Transactions of the Royal Society of London B* 353:287–305.
- Cracraft, J. 1989. Speciation and its ontology: The empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. Pp. 28–59 in Otte and Endler 1989.
- . 1997. Species concepts in systematics and conservation biology—an ornithological viewpoint. Pp. 325–339 in Claridge et al. 1997.
- Crame, J. A. 1996. Antarctica and the evolution of taxonomic diversity gradients in the marine realm. *Terra Antarctica* 3:121–134.
- . 1997. An evolutionary framework for the polar regions. *Journal of Biogeography* 24:1–9.
- Crame, J. A., and A. Clarke. 1997. The historical component of marine taxonomic diversity gradients. Pp. 258–273 in R. F. G. Ormond, J. D. Gage, and M. V. Angel, eds. *Marine biodiversity: patterns and processes*. Cambridge University Press, Cambridge.
- Darling, K. F., C. M. Wade, D. Kroon, A. J. L. Brown, and J. Bijma. 1999. The diversity and distribution of modern planktic fo-

- raminiferous small subunit ribosomal RNA genotypes and their potential as tracers of present and past ocean circulations. *Paleoceanography* 14:3–12.
- Darling, K. F., C. M. Wade, I. A. Stewart, D. Kroon, R. Dingle, and A. J. L. Brown. 2000. Molecular evidence for genetic mixing of Arctic and Antarctic subpolar populations of planktonic foraminifers. *Nature* 405:43–47.
- Davis, J. I., and K. C. Nixon. 1992. Populations, genetic variation, and the delimitation of phylogenetic species. *Systematic Biology* 41:421–435.
- Delph, L. F. 1990. Sex-ratio variation in the gynodioecious shrub *Hebe strictissima* (Scrophulariaceae). *Evolution* 44:134–142.
- de Queiroz, K. 1998. The general lineage concept of species, species criteria, and the process of speciation. Pp. 57–75 in Howard and Berlocher 1998.
- . 1999. The general lineage concept of species and the defining properties of the species category. Pp. 49–89 in R. A. Wilson, ed. *Species: new interdisciplinary essays*. MIT Press, Cambridge.
- DeSalle, R., and E. Carew. 1992. Phyletic phenocopy and the role of developmental genes in morphological evolution in the Drosophilidae. *Journal of Evolutionary Biology* 5:363–374.
- de Vargas, C., R. Norris, L. Zaninetti, S. W. Gibb, and J. Pawlowski. 1999. Molecular evidence of cryptic speciation in planktonic foraminifers and their relation to oceanic provinces. *Proceedings of the National Academy of Sciences USA* 96: 2864–2868.
- DiMichele, W. A., and R. B. Aronson. 1992. The Pennsylvanian-Permian vegetational transition: a terrestrial analogue of the onshore-offshore hypothesis. *Evolution* 46:807–824.
- Dodd, M. E., J. Silvertown, and M. W. Chase. 1999. Phylogenetic analysis of trait evolution and species diversity variation among angiosperm families. *Evolution* 53:732–744.
- Doebley, J., and L. Lukens. 1998. Transcriptional regulators and the evolution of plant form. *Plant Cell* 10:1075–1082.
- Doebley, J., and R.-L. Wang. 1997. Genetics and the evolution of plant form: an example from maize. *Cold Spring Harbor Symposium in Quantitative Biology* 62:361–367.
- Donoghue, M. J. 1989. Phylogenies and the analysis of evolutionary sequences, with examples from the seed plants. *Evolution* 43:1137–1156.
- Droser, M. L., G. Hampt, and S. J. Clements. 1993. Environmental patterns in the origin and diversification of rugose and deep-water scleractinian corals. *Courier Forschungsinstitut Senckenberg* 164:47–54.
- Droser, M. L., D. J. Bottjer, and P. M. Sheehan. 1997. Evaluating the ecological architecture of major events in the Phanerozoic history of marine invertebrate life. *Geology* 25:167–170.
- Duboule, D., and A. S. Wilkins. 1998. The evolution of 'bricolage.' *Trends in Genetics* 14:54–59.
- Duda, T. F., and S. R. Palumbi. 1999. Developmental shifts and species selection in gastropods. *Proceedings of the National Academy of Sciences USA* 96:10272–10277.
- Duffy, J. E. 1996. Species boundaries, specialization, and the radiation of sponge-dwelling alpheid shrimp. *Biological Journal of the Linnean Society* 58:307–324.
- Eble, G. J. 2000. Contrasting evolutionary flexibility in sister groups: disparity and diversity in Mesozoic atelostomate echinoids. *Paleobiology* 26:56–79.
- Eckenwalder, J. E. 1984. Natural intersectional hybridization between North American species of *Populus* (Salicaceae) in sections *Aigeiros* and *Tacamahaca*. III. Paleobotany and evolution. *Canadian Journal of Botany* 62:336–342.
- Eldredge, N. 1985. *Unfinished synthesis*. Oxford University Press, New York.
- . 1989. *Macroevolutionary dynamics*. McGraw-Hill, New York.
- . 1995. Species, speciation, and the context of adaptive change in evolution. Pp. 39–63 in Erwin and Anstey 1995b.
- Emlet, R. B., and O. Hoegh-Guldberg. 1997. Effects of egg size on postlarval performance: experimental evidence from a sea urchin. *Evolution* 51:141–152.
- Englemann, G. F., and E. O. Wiley. 1977. The place of ancestor-descendant relationships in phylogeny reconstruction. *Systematic Zoology* 26:1–11.
- Erwin, D. H. 1994. Early evolution of major morphological innovations. *Acta Palaeontologica Polonica* 38:281–294.
- . 1998. The end and the beginning: recoveries from mass extinctions. *Trends in Ecology and Evolution* 13:344–349.
- . 1999. The origin of bodyplans. *American Zoologist* 39: 617–629.
- . 2000a. Macroevolution is more than repeated rounds of microevolution. *Evolution and Development* 2:78–84.
- . 2000b. Lessons from the past: biotic recoveries from mass extinctions. *Proceedings of the National Academy of Sciences USA* (in press).
- Erwin, D. H., and R. L. Anstey. 1995a. Speciation in the fossil record. Pp. 11–38 in Erwin and Anstey 1995b.
- . 1995b. *New approaches to speciation in the fossil record*. Columbia University Press, New York.
- Erwin, D. H., J. W. Valentine, and J. J. Sepkoski Jr. 1987. A comparative study of diversification events: the early Paleozoic versus the Mesozoic. *Evolution* 41:1177–1186.
- Farrell, B. D. 1998. "Inordinate fondness" explained: why are there so many beetles? *Science* 281:555–559.
- Feldmann, R. M., D. M. Tshudy, and M. R. A. Thomson. 1993. Late Cretaceous and Paleocene decapod crustaceans from James Ross Basin, Antarctic Peninsula. *Paleontological Society Memoir* 28. *Journal of Paleontology* 67(Suppl. to No. 1).
- Feyereisen, R. 1995. Molecular biology of insecticide resistance. *Toxicology Letters* 82–3:83–90.
- Finnerty, J. R., and M. Q. Martindale. 1998. The evolution of the Hox cluster: insights from outgroups. *Current Opinion in Genetics and Development* 8:681–687.
- Fisher, D. C. 1994. Stratocladistics: Morphological and temporal patterns and their relation to phylogenetic process. Pp. 133–171 in L. Grande and O. Rieppel, eds. *Interpreting the hierarchy of nature*. Academic Press, Orlando, Fla.
- Flessa, K. W., and D. Jablonski. 1996. The geography of evolutionary turnover: a global analysis of extant bivalves. Pp. 376–397 in D. Jablonski, D. H. Erwin, and J. H. Lipps, eds. *Evolutionary Paleobiology*. University of Chicago Press, Chicago.
- Flynn, L. J., J. C. Barry, M. E. Morgan, D. Pilbeam, L. L. Jacobs, and E. H. Lindsay. 1995. Neogene Siwalik mammalian lineages: species longevities, rates of change, and modes of speciation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 115:249–264.
- Footo, M. 1993. Discordance and concordance between morphological and taxonomic diversity. *Paleobiology* 19:185–204.
- . 1996a. Perspective: evolutionary patterns in the fossil record. *Evolution* 50:1–11.
- . 1996b. On the probability of ancestors in the fossil record. *Paleobiology* 22:141–151.
- . 1997. The evolution of morphological diversity. *Annual Review of Ecology and Systematics* 28:129–152.
- . 1999. Morphological diversity in the evolutionary radiation of Paleozoic and post-Paleozoic crinoids. *Paleobiology Memoirs* No. 1. *Paleobiology* 25(Suppl. to No. 2).
- Fortey, R. A. 1985. Gradualism and punctuated equilibria as competing and complementary theories. *Special Papers in Palaeontology* 33:17–28.
- . 1988. Seeing is believing: gradualism and punctuated equilibria in the fossil record. *Science Progress* 72:1–19.
- Frost, D. R., and A. G. Kluge. 1994. A consideration of episte-

- mology in systematic biology, with special reference to species. *Cladistics* 10:259–294.
- Futuyma, D. J. 1987. On the role of species in anagenesis. *American Naturalist* 130:465–475.
- Futuyma, D. J., M. C. Keese, and D. J. Funk. 1995. Genetic constraints on macroevolution: the evolution of host affiliation in the leaf beetle genus *Ophraella*. *Evolution* 49:797–809.
- Gaffney, B., and E. P. Cunningham. 1988. Estimation of genetic trend in racing performance of thoroughbred horses. *Nature* 332:722–724.
- Garland, T., P. E. Midford, and A. R. Ives. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. *American Zoologist* 39:374–388.
- Gaston, K. J. 1998. Species-range size distributions: products of speciation, extinction and transformation. *Philosophical Transactions of the Royal Society of London B* 353:219–230.
- Gaston, K. J., and T. M. Blackburn. 1996. The tropics as a museum of biological diversity: an analysis of the New World avifauna. *Proceedings of the Royal Society of London B* 263:63–68.
- . 1997. Age, area and avian diversification. *Biological Journal of the Linnean Society* 62:239–253.
- . 1999. A critique for macroecology. *Oikos* 84:353–368.
- Geary, D. H. 1995. The importance of gradual change in species-level transitions. Pp. 67–86 in Erwin and Anstey 1995b.
- Gehring, W. J., and K. Ikeo. 1999. *Pax-6*: mastering eye morphogenesis and eye evolution. *Trends in Genetics* 15:371–377.
- Geller, J. B. 1998. Molecular studies of marine invertebrate biodiversity: Status and prospects. Pp. 359–376 in K. E. Cooksey, ed. *Molecular approaches to the study of the ocean*. Chapman and Hall, London.
- Gellon, G., and W. McGinnis. 1998. Shaping animal body plans in development and evolution by modulation of *Hox* expression patterns. *BioEssays* 20:116–125.
- Ghiselin, M. T. 1997. *Metaphysics and the origin of species*. State University of New York Press, Albany.
- Ghosh, S., M. J. May, and E. B. Kopp. 1998. NF-kappa B and rel proteins: evolutionarily conserved mediators of immune responses. *Annual Review of Immunology* 16:225–260.
- Gibson, G. 1999. Insect evolution: Redesigning the fruitfly. *Current Biology* 9:R86–R89.
- Gibson, G., and G. Wagner. 2000. Canalization in evolutionary genetics: a stabilizing theory? *BioEssays* 22:372–380.
- Gibson, G., M. Wemple, and S. van Helden. 1999. Potential variance affecting homeotic Ultrabithorax and Antennapedia phenotypes in *Drosophila melanogaster*. *Genetics* 151:1081–1091.
- Gili, C., and J. Martinell. 1994. Relationship between species longevity and larval ecology in nassariid gastropods. *Lethaia* 27:291–299.
- Gingerich, P. D. 1993. Quantification and comparison of evolutionary rates. *American Journal of Science* 293-A:453–478.
- Goffinet, B., and S. Gerber. 2000. Quantitative Trait Loci: a meta-analysis. *Genetics* 155:463–473.
- Gonzalez-Crespo, S., and M. Levine. 1994. Related target enhancers for dorsal and NF-kappa-B signalling pathways. *Science* 264:255–258.
- Gottlieb, L. D. 1984. Genetics and morphological evolution in plants. *American Naturalist* 123:681–709.
- Gould, S. J. 1977a. Eternal metaphors of paleontology. Pp. 1–26 in A. Hallam, ed. *Patterns of evolution*. Elsevier, Amsterdam.
- . 1977b. *Ontogeny and phylogeny*. Harvard University Press, Cambridge.
- . 1982. 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.
- . 1985. The paradox of the first tier: an agenda for paleobiology. *Paleobiology* 11:2–12.
- Gould, S. J., and N. Eldredge. 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology* 3:115–151.
- . 1993. Punctuated equilibrium comes of age. *Nature* 366:223–227.
- Gould, S. J., and E. A. Lloyd. 1999. Individuality and adaptation across levels of selection: how shall we name and generalize the unit of Darwinism? *Proceedings of the National Academy of Sciences USA* 96:11904–11909.
- Govindaraju, D. R. 1988. Relationship between dispersal ability and levels of gene flow in plants. *Oikos* 52:31–35.
- Graff, A. 1999. Population sex structure and reproductive fitness in gynodioecious *Sidalcea malviflora malviflora* (Malvaceae). *Evolution* 53:1714–1722.
- Grant, P. R. 1986. *Ecology and evolution of Darwin's finches*. Princeton University Press, Princeton, N.J.
- Grant, P. R., and B. R. Grant. 1995. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution* 49:241–251.
- Grantham, T. A. 1995. Hierarchical approaches to macroevolution: recent work on species selection and the “effect hypothesis.” *Annual Review of Ecology and Systematics* 26:301–322.
- Greene, H. W., and D. Cundall. 2000. Limbless tetrapods and snakes with legs. *Science* 287:1939–1941.
- Hagdorn, H., and H. J. Campbell. 1993. *Paracomatula triadica* sp. nov.—an early comatulid crinoid from the Otapirian (Late Triassic) of New Caledonia. *Alcheringa* 17:1–17.
- Hageman, S. J., M. M. Bayer, and C. D. Todd. 1999. Partitioning phenotypic variation: genotypic, environmental and residual components from bryozoan skeletal morphology. *Journal of Natural History* 33:1713–1735.
- Halder, G., P. Callaerts, and W. J. Gehring. 1995. Induction of ectopic eyes by targeted expression of the *eyeless* gene in *Drosophila*. *Science* 267:1788–1792.
- Hall, B. K. 1983. Epigenetic control in development and evolution. Pp. 353–379 in B. C. Goodwin, N. Holder, and C. C. Wylie, eds. *Development and evolution*. Cambridge University Press, Cambridge.
- . 1999. *Evolutionary developmental biology*, 2d ed. Kluwer Academic, Dordrecht, Netherlands.
- Hallam, A. 1998. Speciation patterns and trends in the fossil record. *Geobios* 7:921–930.
- Hansen, T. A. 1978. Larval dispersal and species longevity in Lower Tertiary gastropods. *Science* 199:885–887.
- . 1982. Modes of larval development in early Tertiary neogastropods. *Paleobiology* 8:367–372.
- Hansen, T. A., P. H. Kelley, V. D. Melland, and S. E. Graham. 1999. Effect of climate-related mass extinctions on escalation in molluscs. *Geology* 27:1139–1142.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford.
- Harrington, R. J. 1987. Skeletal growth histories of *Protothaca staminea* (Conrad) and *Protothaca grata* (Say) throughout their geographic ranges, northeastern Pacific. *Veliger* 30:148–158.
- Harrison, R. G. 1998. Linking evolutionary pattern and process: the relevance of species concepts for the study of speciation. Pp. 19–31 in Howard and Berlocher 1998.
- Harrison, S. 1998. Do taxa persist as metapopulations in evolutionary time? Pp. 19–30 in McKinney and Drake 1998.
- Harvey, P. H., and A. Rambaut. 1998. Phylogenetic extinction rates and comparative methodology. *Proceedings of the Royal Society of London B* 265:1691–1696.
- Heanue, T. A., R. Rashef, R. J. Davis, G. Mardon, G. Oliver, S. Tomarev, A. B. Lassar, and C. J. Tabin. 1999. Synergistic regulation of vertebrate development by *Dach2*, *Eya2*, and *Six1*,

- homologs of genes required for *Drosophila* eye formation. *Genes and Development* 13:3231–3243.
- Heaton, T. H. 1993. The Oligocene rodent *Ischyromys* of the Great Plains: replacement mistaken for anagenesis. *Journal of Paleontology* 67:297–308.
- Hendry, A. P., and M. T. Kinnison. 1999. Perspective: the pace of modern life: measuring rates of contemporary microevolution. *Evolution* 53:1637–1653.
- Hodin, J. 2000. Plasticity and constraints in development and evolution. *Journal of Experimental Zoology (Molecular and Developmental Evolution)* 288:1–20.
- Hoffman, A. 1989. *Arguments on evolution*. Oxford University Press, Oxford.
- Hoffmann, A. A., and M. J. Hercus. 2000. Environmental stress as an evolutionary force. *BioScience* 50:217–226.
- Hoffmann, A. A., and P. A. Parsons. 1997. *Extreme environmental change and evolution*. Cambridge University Press, Cambridge.
- Holland, P. W. H. 1999. The future of evolutionary developmental biology. *Nature* 402(Suppl.):C41–C44.
- Holland, S. M., and M. E. Patzkowsky. 1999. Models for simulating the fossil record. *Geology* 27:491–494.
- Howard, D. J., and S. H. Berlocher, eds. *Endless forms: species and speciation*. Oxford University Press, New York.
- Huber, B. T., J. Bijma, and K. Darling. 1997. Cryptic speciation in the living planktonic foraminifer *Globigerinella siphonifera* (d'Orbigny). *Paleobiology* 23:33–62.
- Hughes, N. C., R. E. Chapman, and J. M. Adrain. 1999. The stability of thoracic segmentation in trilobites: a case study in developmental and ecological constraints. *Evolution and Development* 1:24–35.
- Hull, D. L. 1980. Individuality and selection. *Annual Review of Ecology and Systematics* 11:311–332.
- . 1997. The ideal species concept—and why we can't get it. Pp. 357–380 in Claridge et al. 1997.
- Humphreville, R., and R. K. Bambach. 1979. Influence of geography, climate and ocean circulation on the pattern of generic diversity of brachiopods in the Permian. *Geological Society of America Abstracts with Programs* 11:447.
- Jablonski, D. 1986a. Larval ecology and macroevolution of marine invertebrates. *Bulletin of Marine Science* 39:565–587.
- . 1986b. Background and mass extinctions: the alteration of macroevolutionary regimes. *Science* 231:129–133.
- . 1987. Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. *Science* 238:360–363.
- . 1988. Response [to Russell and Lindberg]. *Science* 240:969.
- . 1993. The tropics as a source of evolutionary novelty: the post-Palaeozoic fossil record of marine invertebrates. *Nature* 364:142–144.
- . 1995. Extinction in the fossil record. Pp. 25–44 in J. H. Lawton and R. M. May, eds. *Extinction rates*. Oxford University Press, Oxford.
- . 1998. Geographic variation in the molluscan recovery from the end-Cretaceous extinction. *Science* 279:1327–1330.
- . 2000a. The interplay between physical and biotic factors in evolution. In A. Lister and L. Rothschild, eds. *Evolution on planet Earth: the impact of the physical environment*. Linnean Society and Academic Press, London (in press).
- . 2000b. Lessons from the past: Evolutionary impacts of mass extinctions. *Proceedings of the National Academy of Sciences USA* (in press).
- Jablonski, D., and D. J. Bottjer. 1983. Soft-substratum epifaunal suspension-feeding assemblages in the Late Cretaceous: Implications for the evolution of benthic paleocommunities. Pp. 747–812 in M. J. Tevesz and P. L. McCall, eds. *Biotic interactions in Recent and fossil benthic communities*. Plenum, New York.
- . 1990a. The ecology of evolutionary innovations: the fossil record. Pp. 253–288 in M. H. Nitecki, ed. *Evolutionary innovations*. University of Chicago Press, Chicago.
- . 1990b. The origin and diversification of major groups: environmental patterns and macroevolutionary lags. Pp. 17–57 in P. D. Taylor and G. P. Larwood, eds. *Major evolutionary radiations*. Clarendon, Oxford.
- . 1991. Environmental patterns in the origins of higher taxa: the post-Paleozoic fossil record. *Science* 252:1831–1833.
- Jablonski, D., and R. A. Lutz. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Reviews* 58:21–89.
- Jablonski, D., and J. J. Sepkoski Jr. 1996. Paleobiology, community ecology, and scales of ecological pattern. *Ecology* 77:1367–1378.
- Jablonski, D., S. Lidgard, and P. D. Taylor. 1997. Comparative ecology of bryozoan radiations: origin of novelties in cyclostomes and cheilostomes. *Palaios* 12:505–523.
- Jackson, J. B. C., and A. F. Budd. 1996. Evolution and environment: Introduction and overview. Pp. 1–20 in J. B. C. Jackson, A. F. Budd, and A. G. Coates, eds. *Evolution and environment in tropical America*. University of Chicago Press, Chicago.
- Jackson, J. B. C., and A. H. Cheetham. 1990. Evolutionary significance of morphospecies: a test with cheilostome Bryozoa. *Science* 248:579–583.
- . 1994. Phylogeny reconstruction and the tempo of speciation in cheilostome Bryozoa. *Paleobiology* 20:407–423.
- . 1999. Tempo and mode of speciation in the sea. *Trends in Ecology and Evolution* 14:72–77.
- Jackson, J. B. C., and T. P. Hughes. 1985. Adaptive strategies of coral-reef invertebrates. *American Scientist* 73:265–274.
- Jackson, S. T., and J. T. Overpeck. 2000. Responses of plant populations and communities to environmental changes of the Late Quaternary. *Paleobiology* 26:194–220.
- Jacobs, D. K. 1990. Selector genes and the Cambrian radiation of Bilateria. *Proceedings of the National Academy of Sciences USA* 87:4406–4410.
- Johnson, A. L. A. 1984. The paleobiology of the bivalve families Pectinidae and Propeamussidae in the Jurassic of Europe. *Zitteliana* 11:235 p.
- . 1985. The rate of evolutionary change in European Jurassic scallops. *Special Papers in Paleontology* 33:91–102.
- . 1993. Punctuated equilibria vs. phyletic gradualism in European Jurassic *Gryphaea* evolution. *Proceedings of the Geologists' Association* 104:209–222.
- . 1994. Evolution of European Lower Jurassic *Gryphaea* (*Gryphaea*) and contemporaneous bivalves. *Historical Biology* 7:167–186.
- Johnson, A. L. A., and C. D. Lennon. 1990. Evolution of gryphaeate oysters in the mid-Jurassic of western Europe. *Palaontology* 33:453–485.
- Johnson, J. G. 1982. Occurrence of phyletic gradualism and punctuated equilibria through time. *Journal of Paleontology* 56:1329–1331.
- Jones, D. S. 1988. Sclerochronology and the size versus age problem. Pp. 93–108 in M. L. McKinney, ed. *Heterochrony in evolution*. Plenum, New York.
- . 1998. Isotopic determination of growth and longevity in fossil and modern invertebrates. In R. D. Norris and R. M. Corfield, eds. *Isotope paleobiology and paleoecology*. *Paleontological Society Papers* 4:37–67. Paleontological Society, Knoxville, Tenn.
- Jones, D. S., and S. J. Gould. 1999. Direct measurement of age in fossil *Gryphaea*: the solution to a classic problem in heterochrony. *Paleobiology* 25:158–187.
- Judd, W. S., R. W. Sanders, and M. J. Donoghue. 1994. Angiosperm family pairs: preliminary phylogenetic analysis. *Harvard Papers in Botany* 5:1–51.

- Kammer, T. W., T. K. Baumiller, and W. I. Ausich. 1998. Evolutionary significance of differential species longevity in Osaegan–Meramecian (Mississippian) crinoid clades. *Paleobiology* 24:155–176.
- Keese, M. C. 1998. Performance of two monophagous leaf feeding beetles (Coleoptera: Chrysomelidae) on each other's host plant: do intrinsic factors determine host plant specialization? *Journal of Evolutionary Biology* 11:403–419.
- Kelley, P. H. 1989. Evolutionary trends within bivalve prey of Chesapeake Group naticid gastropods. *Historical Biology* 2: 139–156.
- . 1991. The effect of predation intensity on rate of evolution of five Miocene bivalves. *Historical Biology* 5:65–78.
- Kelley, P. H., A. Raymond, and C. B. Lutken. 1990. Carboniferous brachiopod migration and latitudinal diversity; a new palaeoclimatic method. Pp. 325–332 in W. S. McKerrow and C. R. Scotese, eds. *Palaeozoic palaeogeography and biogeography*. Geological Society of London Memoir 12.
- Kennish, M. J. 1980. Shell microgrowth analysis: *Mercenaria mercenaria* as a type example for research in population dynamics. Pp. 255–294 in D. C. Rhoads and R. A. Lutz, eds. *Skeletal growth of aquatic organisms*. Plenum, New York.
- Keys, D. N., D. L. Lewis, J. E. Selegue, B. J. Pearson, L. V. Goodrich, R. J. Johnson, J. Gates, M. P. Scott, and S. B. Carroll. 1999. Recruitment of a *hedgohg* regulatory circuit in butterfly eyespot evolution. *Science* 283:532–534.
- Kidwell, S. M., and T. A. Aigner. 1985. Sedimentary dynamics of complex shell beds: implications for ecologic and evolutionary patterns. Pp. 383–395 in U. Bayer and A. Seilacher, eds. *Sedimentary and evolutionary cycles*. Springer, Berlin.
- Kidwell, S. M., and K. W. Flessa. 1995. The quality of the fossil record: populations, species, and communities. *Annual Review of Ecology and Systematics* 26:269–299.
- Kirkpatrick, M. 1996. Genes and adaptation: a pocket guide to the theory. Pp. 125–146 in M. R. Rose and G. V. Lauder, eds. *Adaptation*. Academic Press, San Diego.
- Kirkpatrick, M., and M. Slatkin. 1993. Searching for evolutionary patterns in the shape of a phylogenetic tree. *Evolution* 47: 1171–1181.
- Kirschner, M., and J. Gerhart. 1997. *Cells, embryos, and evolution*. Blackwell Science, Malden, Mass.
- Kitazato, H., M. Tsuchiya, and K. Takahara. 2000. Recognition of breeding populations in foraminifera: an example using the genus *Glubratella*. *Paleontological Research* 4:1–15.
- Klingenberg, C. P. 1998. Heterochrony and allometry: the analysis of evolutionary change in ontogeny. *Biological Reviews* 73:79–123.
- Knoll, A. H., and S. B. Carroll. 1999. Early animal evolution: emerging views from comparative biology and geology. *Science* 284:2129–2137.
- Knowlton, N. 1993. Sibling species in the sea. *Annual Review of Ecology and Systematics* 24:189–216.
- Knowlton, N., and L. A. Weigt. 1997. Species of marine invertebrates: a comparison of the biological and phylogenetic species concepts. Pp. 199–219 in Claridge et al. 1997.
- Knowlton, N., J. Maté, H. M. Guzmán, R. Rowan, and J. Jara. 1997. Direct evidence for reproductive isolation among the three species of the *Montastraea annularis* complex in Central America (Panamá and Honduras). *Marine Biology* 127:705–711.
- Koch, P. L. 1986. Clinal geographic variation in mammals: implications for the study of chronoclines. *Paleobiology* 12:269–281.
- Kodric-Brown, A., and J. H. Brown. 1979. Competition between distantly related taxa and the co-evolution of plants and pollinators. *American Zoologist* 19:1115–1127.
- Kohn, A. J., and F. E. Perron. 1994. Life history and biogeography: patterns in *Conus*. Clarendon, Oxford.
- Kowalewski, M., E. Dyreson, J. D. Marcot, J. A. Vargas, K. W. Flessa, and D. P. Hallman. 1997. Phenetic discrimination of biometric simpletons: paleobiological implications of morphospecies in the lingulide brachiopod *Glottidia*. *Paleobiology* 23:444–469.
- Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30:314–334.
- . 1986. The dynamics of peak shifts and the pattern of morphological evolution. *Paleobiology* 12:343–354.
- Langan-Cranford, K. M., and J. S. Pearse. 1995. Breeding experiments confirm species status of two morphologically similar gastropods (*Lacuna* spp.) in central California. *Journal of Experimental Marine Biology and Ecology* 186:17–31.
- Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* 84: 177–192.
- Lawton-Rauh, A. L., E. R. Alvarez-Buylla, and M. D. Purugganan. 2000. Molecular evolution of flower development. *Trends in Ecology and Evolution* 15:144–149.
- Lazarus, D., H. Hilbrecht, C. Spencer-Cervas, and H. Thierstein. 1995. Sympatric speciation and phyletic change in *Globorotalia truncatulinoides*. *Paleobiology* 21:28–51.
- Leamy, L. J., E. J. Routman, and J. M. Cheverud. 1999. Quantitative trait loci for early- and late-developing skull characters in mice: a test of the genetic independence model of morphological integration. *American Naturalist* 153:201–214.
- Lerner, I. M. 1953. *Genetic homeostasis*. Wiley, New York.
- Levin, D. A. 1970. Developmental instability and evolution in peripheral populations. *American Naturalist* 104:343–353.
- Levin, S. A. 1999. *Fragile dominion: complexity and the commons*. Perseus Books, Reading, Mass.
- Levinton, J. 1988. *Genetics, paleontology, and macroevolution*. Cambridge University Press, New York.
- Lewontin, R. C. 1970. The units of selection. *Annual Review of Ecology and Systematics* 1:1–18.
- Li, X., and W. McGinnis. 1999. Activity regulation of Hox proteins, a mechanism for altering functional specificity in development and evolution. *Proceedings of the National Academy of Sciences USA* 96:6802–6807.
- Lidgard, S., F. K. McKinney, and P. D. Taylor. 1993. Competition, clade replacement, and a history of cyclostome and cheilostome diversity. *Paleobiology* 19:352–371.
- Lieberman, B. S., C. E. Brett, and N. Eldredge. 1994. Patterns and processes of stasis in two species lineages of brachiopods from the Middle Devonian of New York State. *American Museum Novitates* 3114:1–23.
- . 1995. A study of stasis and change in two species lineages of brachiopods from the Middle Devonian of New York State. *Paleobiology* 21:15–27.
- Lindberg, D. R. 1988. Heterochrony in gastropods: a neontological view. Pp. 197–216 in M. L. McKinney, ed. *Heterochrony in evolution*. Plenum, New York.
- Lister, A. M. 1989. Rapid dwarfing of red deer on Jersey in the last interglacial. *Nature* 342:539–542.
- Lloyd, E. A., and S. J. Gould. 1993. Species selection on variability. *Proceedings of the National Academy of Sciences USA* 90:595–599.
- Long, A. D., S. L. Mullaney, T. F. C. Mackay, and C. H. Langley. 1996. Genetic interactions between naturally occurring alleles at quantitative trait loci and mutant alleles at candidate loci affecting bristle number in *Drosophila melanogaster*. *Genetics* 144:1497–1510.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522–1536.
- Losos, J. B., K. I. Warheit, and T. W. Schoener. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature* 387:70–73.
- Luckow, M. 1995. Species concepts: assumptions, methods, and applications. *Systematic Botany* 20:589–605.

- Ludwig, M. Z., C. Bergman, N. H. Patel, and M. Kreitman. 2000. Evidence for stabilizing selection in a eukaryotic enhancer element. *Nature* 403:564–567.
- Lupia, R. 1999. Discordant morphological disparity and taxonomic diversity during the Cretaceous angiosperm radiation: North American pollen record. *Paleobiology* 25:1–28.
- Lynch, J. B. 1989. The gauge of speciation: on the frequencies of modes of speciation. Pp. 527–553 *in* Otte and Endler 1989.
- Lynch, M., and J. B. Walsh. 1998. *Genetics and analysis of quantitative traits*. Sinauer, Sunderland, Mass.
- Mackay, T. F. C. 1996. The nature of quantitative genetic variation revisited: lessons from *Drosophila* bristles. *BioEssays* 18: 113–121.
- MacLeod, N. 1991. Punctuated anagenesis and the importance of stratigraphy to paleobiology. *Paleobiology* 17:167–188.
- Marshall, C. R. 1991. Estimation of taxonomic ranges from the fossil record. *In* N. L. Gilinsky and P. W. Signor, eds. *Analytical paleobiology. Short Courses in Paleontology* 4:19–38. Paleontological Society, Knoxville, Tenn.
- . 1995. Stratigraphy, the true order of species originations and extinctions, and testing ancestor-descendant-hypotheses among Caribbean Neogene bryozoans. Pp. 208–235 *in* Erwin and Anstey 1995b.
- Martin, P. S., and D. W. Steadman. 1999. Prehistoric extinctions on islands and continents. Pp. 17–55 *in* R. D. E. MacPhee, ed. *Extinctions in near time*. Kluwer Academic/Plenum, New York.
- Martin, R. A. 1993. Patterns of variation and speciation in Quaternary rodents. Pp. 226–280 *in* R. A. Martin and A. D. Barnosky, eds. *Morphological change in Quaternary mammals of North America*. Cambridge University Press, Cambridge.
- Martin, R. E. 1999. *Taphonomy: a process approach*. Cambridge University Press, New York.
- Maurer, B. A., and M. P. Nott. 1998. Geographic range fragmentation and the evolution of biological diversity. Pp. 31–50 *in* McKinney and Drake 1998.
- Mayden, R. L. 1997. A hierarchy of species concepts: the denouement in the saga of the species problem. Pp. 381–424 *in* Claridge et al. 1997.
- Maynard Smith, J. 1989. The causes of extinction. *Philosophical Transactions of the Royal Society of London B* 325:241–252.
- Mayr, E. 1992. Controversies in retrospect. *Oxford Surveys in Evolutionary Biology* 8:1–34.
- McKenzie, J. A., and P. Batterham. 1994. The genetic, molecular and phenotypic consequences of selection for insecticide resistance. *Trends in Ecology and Evolution* 9:166–169.
- McKinney, F. K., S. Lidgard, J. J. Sepkoski Jr., and P. D. Taylor. 1998. Decoupled temporal patterns of evolution and ecology in two post-Paleozoic clades. *Science* 281:809–809.
- McKinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics* 28:495–516.
- . 1998. Biodiversity dynamics: Niche preemption and saturation in diversity equilibria. Pp. 1–16 *in* McKinney and Drake 1998.
- McKinney, M. L., and J. A. Drake, eds. 1998. *Biodiversity dynamics*. Columbia University Press, New York.
- McKinney, M. L., and J. L. Gittleman. 1995. Ontogeny and phylogeny: tinkering with covariation in life history, morphology and behaviour. Pp. 21–47 *in* K. J. McNamara, ed. *Evolutionary change and heterochrony*. Wiley, Chichester, England.
- McKinney, M. L., and K. J. McNamara. 1991. *Heterochrony: the evolution of ontogeny*. Plenum, New York.
- McNamara, K. J. 1983. Progenesis in trilobites. *Special Papers in Palaeontology* 30:59–68.
- McShea, D. W. 1994. Mechanisms of large-scale evolutionary trends. *Evolution* 48:1747–1763.
- Meyen, S. V. 1992. Geography of macroevolution in higher plants. *Soviet Scientific Reviews G (Geology)* 1:39–70.
- Michaux, B. 1987. An analysis of allozymic characters of four species of New Zealand *Amalda* (Gastropoda: Olividae: Ancillinae). *New Zealand Journal of Zoology* 14:359–366.
- . 1989. Morphological variation of species through time. *Biological Journal of the Linnean Society* 38:239–255.
- Miller, A. I. 1997a. Comparative diversification dynamics among palaeocontinents during the Ordovician radiation. *Geobios Mémoire Spécial* 20:397–406.
- . 1997b. Dissecting global diversity patterns: examples from the Ordovician Radiation. *Annual Review of Ecology and Systematics* 28:85–104.
- . 1998. Biotic transitions in global marine diversity. *Science* 281:1157–1160.
- Miller, A. I., and J. J. Sepkoski Jr. 1988. Modeling bivalve diversification: the effect of interaction on a macroevolutionary system. *Paleobiology* 14:364–369.
- Müller, G. B. 1990. Developmental mechanisms at the origin of morphological novelty: a side-effect hypothesis. Pp. 99–130 *in* M. H. Nitecki, ed. *Evolutionary innovations*. University of Chicago Press, Chicago.
- Nemeschkal, H. L. 1999. Morphometric correlation patterns of adult birds (Fringillidae: Passeriformes and Columbiformes) mirror the expression of developmental control genes. *Evolution* 53:899–918.
- Nevo, E., R. Ben-Shlomo, A. Beiles, C. P. Hart, and F. H. Ruddle. 1992. Homeobox DNA polymorphisms (RFLPs) in subterranean mammals of the *Spalax ehrenbergi* superspecies in Israel: patterns, correlates, and evolutionary significance. *Journal of Experimental Zoology* 263:430–441.
- Newell, N. D. 1956. Fossil populations. *In* A. C. Sylvester-Bradley, ed. *The species concept in palaeontology*. Systematics Association Publication 2:63–82.
- Nijhout, H. F., and D. J. Emlen. 1998. Competition among body parts in the development and evolution of insect morphology. *Proceedings of the National Academy of Sciences USA* 95: 3685–3689.
- Nijhout, H. F., and S. M. Paulsen. 1997. Developmental models and polygenic characters. *American Naturalist* 149:394–405.
- Niklas, K. J. 1997. *The evolutionary biology of plants*. University of Chicago Press, Chicago.
- Nixon, K. C., and Q. D. Wheeler. 1990. An amplification of the phylogenetic species concept. *Cladistics* 6:211–223.
- Norell, M. A. 1996. Ghost taxa, ancestors, and assumptions: a comment on Wagner. *Paleobiology* 22:453–455.
- Norris, R. D., R. M. Corfield, and J. E. Cartlidge. 1996. What is gradualism? Cryptic speciation in globorotaliid foraminifera. *Paleobiology* 22:386–405.
- Nunn, C. L., and K. K. Smith. 1998. Statistical analyses of developmental sequences: the craniofacial region in marsupial and placental mammals. *American Naturalist* 152:82–101.
- Nuzhdin, S. V., C. L. Dilda, and T. F. C. Mackay. 1999. The genetic architecture of selection response: inferences from fine-scale mapping of bristle number quantitative trait loci in *Drosophila melanogaster*. *Genetics* 153:1317–1331.
- Olson, E. C., and R. L. Miller. 1958. *Morphological integration*. University of Chicago Press, Chicago (reprinted 1999).
- Omland, K. E. 1997. Examining two standard assumptions of ancestral reconstructions: repeated loss of dichromatism in dabbling ducks (Anatini). *Evolution* 51:1636–1646.
- Orr, H. A. 1998. The population genetics of adaptation: the distribution of factors fixed during adaptive evolution. *Evolution* 52:935–949.
- Orr, H. A., and J. A. Coyne. 1992. The genetics of adaptation revisited. *American Naturalist* 140:725–742.
- Otte, D., and J. A. Endler. 1989. *Speciation and its consequences*. Sinauer, Sunderland, Mass.

- Page, K. N. 1996. Mesozoic ammonoids in time and space. Pp. 755–794 in N. H. Landman, K. Tanabe, and R. A. Davis, eds. *Ammonoid paleobiology*. Plenum, New York.
- Palmer, A. R. 1985. Quantum changes in gastropod shell morphology need not reflect speciation. *Evolution* 39:699–705.
- Palopoli, M. F., and N. H. Patel. 1996. Neo-Darwinian developmental evolution: Can we bridge the gap between pattern and process? *Current Opinion in Genetics and Development* 6: 502–508.
- Palumbi, S. R. 1996. Macrospatial genetic structure and speciation in marine taxa with high dispersal abilities. Pp. 101–117 in J. Ferraris and S. R. Palumbi, eds. *Molecular zoology*. Wiley, New York.
- Palumbi, S. R., G. Grabowsky, T. Duda, L. Geyer, and N. Tachino. 1997. Speciation and population genetic structure in tropical Pacific sea urchins. *Evolution* 51:1506–1517.
- Paradis, E. 1998. Detecting shifts in diversification rates without fossils. *American Naturalist* 152:176–187.
- Parsons, P. A. 1993. Stress, extinctions and evolutionary change: from living organisms to fossils. *Biological Reviews* 68:313–333.
- . 1994. Habitats, stress, and evolutionary rates. *Journal of Evolutionary Biology* 7:387–397.
- Paterson, A. H., Y.-R. Lin, Z. Li, K. F. Schertz, J. F. Doebley, S. R. M. Pinson, S.-C. Liu, J. W. Stansel, and J. E. Irvine. 1997. Convergent domestication of cereal crops by independent mutation at corresponding genetic loci. *Science* 269:1714–1718.
- Patzkowsky, M. E. 1995. A hierarchical branching model of evolutionary radiations. *Paleobiology* 21:440–460.
- Paul, C. R. C. 1992. The recognition of ancestors. *Historical Biology* 6:239–250.
- Pearson, P. N. 1995. Investigating age-dependency of species extinction rates using dynamic survivorship analysis. *Historical Biology* 10:119–136.
- Pechenik, J. A. 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Marine Ecology Progress Series* 177:269–297.
- Peterson, A. T., J. Soberon, and V. Sanchez-Cordero. 1999. Conservatism of ecological niches in evolutionary time. *Science* 285:1265–1267.
- Potts, D. C., A. F. Budd, and R. L. Garthwaite. 1993. Soft tissue vs. skeletal approaches to species recognition and phylogeny reconstruction in corals. *Courier Forschungsinstitut Senckenberg* 16:221–231.
- Povel, G. D. E. 1993. The main branch of Miocene *Gyraulus* (Gastropoda; Planorbidae) of Steinheim (southern Germany): a reconsideration of Mensink's data set. *Scripta Geologica Special Issue* 3:371–386.
- Price, T. D., A. J. Helbig, and A. D. Richman. 1997. Evolution of breeding distributions in the Old World leaf warblers (genus *Phylloscopus*). *Evolution* 51:552–561.
- Prothero, D. R., and T. H. Heaton. 1996. Faunal stability during the Early Oligocene climatic crash. *Palaeogeography, Palaeoclimatology, Palaeoecology* 127:257–283.
- Prothero, D. R., and N. Shubin. 1989. The evolution of Oligocene horses. Pp. 142–175 in D. R. Prothero and R. M. Schoch, eds. *The evolution of perissodactyls*. Oxford University Press, New York.
- Purugganan, M. D. 1998. The molecular evolution of development. *BioEssays* 20:700–711.
- . 2000. The molecular population genetics of regulatory genes. *Molecular Ecology* (in press).
- Quinn, J. C., J. D. West, and R. E. Hill. 1996. Multiple functions for Pax6 in mouse eye and nasal development. *Genes and Development* 10:435–446.
- Rabinowitz, D. 1981. Seven forms of rarity. Pp. 205–217 in H. Syngé, ed. *The biological aspects of rare plant conservation*. Wiley, New York.
- Rabinowitz, D., S. Cairns, and T. Dillon. 1986. Seven forms of rarity and their frequency in the flora of the British Isles. Pp. 182–204 in M. E. Soulé, ed. *Conservation biology*. Sinauer, Sunderland, Mass.
- Rachootin, S. P., and K. S. Thomson. 1981. Epigenetics, paleontology, and evolution. Pp. 181–193 in G. G. E. Scudder and J. L. Reveal, eds. *Evolution today*. Proceedings of the second international congress of systematic and evolutionary biology. Hunt Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburgh, Penn.
- Raff, R. A. 1996. *The shape of life: genes, development, and the evolution of animal form*. University of Chicago Press, Chicago.
- Raff, R. A., and T. C. Kaufman. 1983. *Embryos, genes, and evolution*. Macmillan, New York (reprinted 1991, Indiana University Press, Bloomington).
- Raff, R. A., and G. A. Wray. 1989. Heterochrony: developmental mechanisms and evolutionary results. *Journal of Evolutionary Biology* 2:409–434.
- Raup, D. M. 1983. On the early origins of major biologic groups. *Paleobiology* 9:107–115.
- . 1991. A kill curve for Phanerozoic marine species. *Paleobiology* 17:37–48.
- . 1994. The role of extinction in evolution. *Proceedings of the National Academy of Sciences USA* 91:6758–6763.
- Relaix, F., and M. Buckingham. 1999. From insect eye to vertebrate muscle: redeployment of a regulatory network. *Genes and Development* 13:3171–3178.
- Rice, S. H. 1995. A genetical theory of species selection. *Journal of Theoretical Biology* 177:237–245.
- . 1998. The evolution of canalization and the breaking of von Baer's laws: modeling the evolution of development with epistasis. *Evolution* 52:647–656.
- Ricklefs, R. E., and R. E. Latham. 1992. Intercontinental correlation of geographic ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. *American Naturalist* 139:1305–1321.
- Riedl, R. 1978. *Order in living organisms*. Wiley, Chichester, England.
- Robertson, F. W. 1959. *Studies in quantitative inheritance*. XIII. Interrelations between genetic behavior and development in the cellular constitution in the *Drosophila* wing. *Genetics* 44: 1113–1130.
- Rogers, B. T., M. D. Peterson, and T. C. Kaufman. 1997. Evolution of the insect body plan as revealed by the Sex combs reduced expression pattern. *Development* 124:149–157.
- Roopnarine, P. D., G. Byars, and P. Fitzgerald. 1999. Anagenetic evolution, stratophenetic patterns, and random walk models. *Paleobiology* 25:41–57.
- Rosenzweig, M. L., and R. D. McCord. 1991. Incumbent replacement: evidence for long-term evolutionary progress. *Paleobiology* 17:202–213.
- Routman, E. J., and J. M. Cheverud. 1997. Gene effects on a quantitative trait: two-locus epistatic effects measured at microsatellite markers and at estimated QTL. *Evolution* 51:1654–1662.
- Roy, K. 1996. The roles of mass extinction and biotic interaction in large-scale replacements: a reexamination using the fossil record of stromboidean gastropods. *Paleobiology* 22:436–452.
- Roy, K., J. W. Valentine, D. Jablonski, and S. M. Kidwell. 1996. Scales of climatic variability and time averaging in Pleistocene biotas: implications for ecology and evolution. *Trends in Ecology and Evolution* 11:458–463.
- Rugh, N. S. 1997. Differences in shell morphology between the sibling species *Littorina scutulata* and *Littorina plena* (Gastropoda: Prosobranchia). *Veliger* 40:350–357.
- Rumrill, S. S. 1990. Natural mortality of marine invertebrate larvae. *Ophelia* 32:163–198.

- Rutherford, S. L., and S. Lindquist. 1998. Hsp 90 as a capacitor for morphological evolution. *Nature* 396:336–342.
- Salmon, W. C. 1971. Statistical explanation and statistical relevance. University of Pittsburgh Press, Pittsburgh, Penn.
- Sanderson, M. J., and M. J. Donoghue. 1996. Reconstructing shifts in diversification rates on phylogenetic trees. *Trends in Ecology and Evolution* 11:15–20.
- Sato, S. 1995. Spawning periodicity and shell microgrowth patterns of the venerid bivalve *Phacosoma japonicum* (Reeve, 1850). *Veliger* 38:61–72.
- . 1999. Temporal change of life-history traits in fossil bivalves: an example of *Phacosoma japonicum* from the Pleistocene of Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 154:313–323.
- Saunders, W. B., D. M. Work, and S. V. Nikolaeva. 1999. Evolution of complexity in Paleozoic ammonoid sutures. *Science* 286:760–763.
- Schankler, D. M. 1981. Local extinction and ecological re-entry of early Eocene mammals. *Nature* 293:135–138.
- Scheltema, R. S. 1989. Planktonic and non-planktonic development among prosobranch gastropods and its relationship to the geographic range of species. Pp. 183–188 in J. S. Ryland and P. A. Tyler, eds. *Reproduction, genetics and distribution of marine organisms*. Olsen and Olsen, Fredensborg, Denmark.
- . 1992. Passive dispersal of planktonic larvae and the biogeography of tropical sublittoral invertebrate species. Pp. 195–202 in G. Colombo et al., eds. *Marine eutrophication and population dynamics*. Olsen and Olsen, Fredensborg, Denmark.
- Schemske, D. W., and H. D. Bradshaw. 1999. Pollinator preference and the evolution of floral traits in monkeyflowers (*Mimulus*). *Proceedings of the National Academy of Sciences USA* 96:11910–11915.
- Schlichting, C. D., and M. Pigliucci. 1998. Phenotypic evolution: a reaction norm perspective. Sinauer, Sunderland, Mass.
- Schluter, D. 1986. Character displacement between distantly related taxa? Finches and bees in the Galapagos. *American Naturalist* 127:95–102.
- . 1996. Adaptive radiation along genetic lines of least resistance. *Evolution* 50:1766–1774.
- Schneider, J. A. 1995. Phylogenetic relationships of transisthmian Cardiidae (Bivalvia) and the usage of fossils in reinterpreting the geminate species concept. *Geological Society of America Abstracts with Programs* 27(6):A-52.
- Sepkoski, J. J., Jr. 1996. Competition in macroevolution: the double wedge revisited. Pp. 211–255 in D. Jablonski, D. H. Erwin, and J. H. Lipps, eds. *Evolutionary paleobiology*. University of Chicago Press, Chicago.
- . 1998. Rates of speciation in the fossil record. *Philosophical Transactions of the Royal Society of London B* 353:315–326.
- Sepkoski, J. J., Jr., F. K. McKinney, and S. Lidgard. 2000. Competitive displacement among post-Paleozoic cyclostome and cheilostome bryozoans. *Paleobiology* 26:7–18.
- Shackleton, N. J., I. N. McCave, and G. P. Weedon, eds. 1999. Astronomical (Milankovitch) calibration of the geological time-scale. *Philosophical Transactions of the Royal Society of London A* 357:1733–2007.
- Shaffer, H. B. 1984. Evolution in a paedomorphic lineage. I. An electrophoretic analysis of the Mexican ambystomatid salamanders. *Evolution* 38:1194–1206.
- Shaw, F. H., R. G. Shaw, G. S. Wilkinson, and M. Turelli. 1995. Changes in genetic variances and covariances: G whiz! *Evolution* 49:1260–1267.
- Sheldon, P. R. 1987. Parallel gradualistic evolution in Ordovician trilobites. *Nature* 330:561–563.
- . 1988. Trilobite size-frequency distributions, recognition of instars, and phyletic size change. *Lethaia* 21:293–306.
- . 1993. Making sense of microevolutionary patterns. Pp. 19–31 in D. R. Lees and D. Edwards, eds. *Evolutionary patterns and processes*. Academic Press, London.
- . 1996. Plus ça change—a model for stasis and evolution in different environments. *Palaeogeography, Palaeoclimatology, Palaeoecology* 127:209–227.
- Shubin, N., C. Tabin, and S. Carroll. 1997. Fossil, genes and the evolution of animal limbs. *Nature* 388:639–648.
- Signor, P. W., III, and C. E. Brett. 1984. The mid-Paleozoic precursor to the Mesozoic marine revolution. *Paleobiology* 10:229–245.
- Simms, M. J. 1988a. The role of heterochrony in the evolution of post-Paleozoic crinoids. Pp. 97–102 in R. D. Burke, P. V. Mladenov, P. Lambert, and R. L. Parsley, eds. *Echinoderm biology*. Balkema, Rotterdam.
- . 1988b. The phylogeny of post-Paleozoic crinoids. Pp. 269–284 in C. R. C. Paul and A. B. Smith, eds. *Echinoderm phylogeny and evolution*. Clarendon, Oxford.
- . 1994. Crinoids from the Chambara Formation, Pucara Group, central Peru. *Palaeontographica, Abteilung A* 233:169–175.
- Simpson, G. G. 1961. *Principles of animal taxonomy*. Columbia University Press, New York.
- Sinervo, B., and L. R. McEdward. 1988. Developmental consequences of an evolutionary change in egg size: an experimental test. *Evolution* 42:885–899.
- Slatkin, M. 1981. A diffusion model of species selection. *Paleobiology* 7:421–425.
- Slowinski, J. B., and C. Guyer. 1993. Testing whether certain traits have caused amplified diversification: an improved method based on a model of random speciation and extinction. *American Naturalist* 142:1019–1024.
- Smith, A. B. 1994. *Systematics and the fossil record*. Blackwell Scientific, Oxford.
- Smith, G. R. 1992. Introgression in fishes: significance for paleontology, cladistics, and evolutionary rates. *Systematic Biology* 41:41–57.
- Smith, K. K. 1996. Integration of craniofacial structures during development in mammals. *American Zoologist* 36:70–79.
- . 1997. Comparative patterns of craniofacial development in eutherian and metatherian mammals. *Evolution* 51:1663–1678.
- Sneppan, K., P. Bak, H. Flybjerg, and M. H. Jensen. 1995. Evolution as a self-organized critical phenomenon. *Proceedings of the National Academy of Sciences USA* 92:5209–5213.
- Sober, E. 1984. *The nature of selection*. MIT Press, Cambridge.
- . 1999. The multiple realizability argument against reductionism. *Philosophy of Science* 66:542–564.
- Solé, R. V., S. C. Manrubia, M. Benton, S. Kauffman, and P. Bak. 1999. Criticality and scaling in evolutionary ecology. *Trends in Ecology and Evolution* 14:156–160.
- Spencer-Cervato, C., H. R. Thierstein, D. B. Lazarus, and J.-P. Beckmann. 1994. How synchronous are Neogene marine plankton events? *Paleoceanography* 9:739–763.
- Stanley, S. M. 1973. An explanation for Cope's Rule. *Evolution* 27:1–26.
- . 1979. *Macroevolution*. W. H. Freeman, San Francisco.
- . 1982. Macroevolution and the fossil record. *Evolution* 36:460–473.
- . 1990. The general correlation between rate of speciation and rate of extinction: fortuitous causal linkages. Pp. 103–127 in R. M. Ross and W. D. Allmon, eds. *Causes of evolution*. University of Chicago Press, Chicago.
- Stanley, S. M., and X. Yang. 1987. Approximate evolutionary stasis for bivalve morphology over millions of years: a multivariate, multilinesage study. *Paleobiology* 13:113–139.

- Stanley, S. M., K. L. Wetmore, and J. P. Kennett. 1988. Macroevolutionary differences between two major clades of Neogene planktonic Foraminifera. *Paleobiology* 14:235–249.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford.
- Stebbins, G. L. 1982. Perspectives in evolutionary theory. *Evolution* 36:1109–1119.
- Stehli, F. G., R. G. Douglas, and N. D. Newell. 1969. Generation and maintenance of gradients in taxonomic diversity. *Science* 164:947–949.
- Steppan, S. J. 1998. Phylogenetic relationships and species limits within *Phyllotis* (Rodentia: Sigmodontinae): concordance between mtDNA sequence and morphology. *Journal of Mammalogy* 79:573–593.
- Stereley, K., and P. E. Griffiths. 1999. *Sex and death: an introduction to philosophy of biology*. University of Chicago Press, Chicago.
- Stevenson, R. D., M. F. Hill, and P. J. Bryant. 1995. Organ and cell allometry in Hawaiian *Drosophila*: how to make a big fly. *Proceedings of the Royal Society of London B* 259:105–110.
- Stidd, B. M., and D. L. Wade. 1995. Is species selection dependent upon emergent characters? *Biology and Philosophy* 10: 55–76.
- Tabachnick, R. E., and F. L. Bookstein. 1990. The structure of individual variation in Miocene *Globorotalia*. *Paleobiology* 44: 416–434.
- Templeton, A. R. 1989. The meaning of species and speciation: a genetic perspective. Pp. 3–27 in Otte and Endler 1989.
- . 1998. Species and speciation: Geography, population structure, ecology, and gene trees. Pp. 32–43 in Howard and Berlocher 1998.
- Theissen, G., A. Becker, A. Di Rosa, A. Kanno, J. T. Kim, T. Münster, K.-U. Winter, and H. Saedler. 2000. A short history of MADS-box genes in plants. *Plant Molecular Biology* 42:115–149.
- Theriot, E. 1992. Clusters, species concepts, and morphological evolution of diatoms. *Systematic Biology* 41:141–157.
- Thomas, R. D. K., R. M. Shearman, and G. W. Stewart. 2000. Evolutionary exploitation of design options by the first animals with hard skeletons. *Science* 288:1239–1242.
- Thomson, K. S. 1988. *Morphogenesis and evolution*. Oxford University Press, New York.
- Trussell, G. C., and L. D. Smith. 2000. Induced defenses in response to an invading crab predator: an explanation of historical and geographic phenotypic change. *Proceedings of the National Academy of Sciences USA* 97:2123–2127.
- Turelli, M. 1988. Phenotypic evolution, constant covariances, and the maintenance of additive variance. *Evolution* 42:1342–1347.
- Valentine, J. W. 1969. Taxonomic and ecological structure of the shelf benthos during Phanerozoic time. *Palaeontology* 12: 684–709.
- . 1973. *Evolutionary paleoecology of the marine biosphere*. Prentice-Hall, Englewood Cliffs, N.J.
- . 1980. Determinants of diversity in higher taxonomic categories. *Paleobiology* 6:444–450.
- . 1990. The fossil record: a sampler of life's diversity. *Philosophical Transactions of the Royal Society of London B* 330: 251–268.
- . 1995. Why no new phyla after the Cambrian? *Genome and ecospace hypotheses revisited*. *Palaios* 10:190–194.
- . 2000. Two paths to complexity in metazoan evolution. *Paleobiology* 26:513–519.
- Valentine, J. W., and D. Jablonski. 1983. Speciation in the shallow sea: General patterns and biogeographic controls. In R. W. Sims, J. H. Price, and P. E. S. Whalley, eds. *Evolution, time and space*. Systematics Association Special Volume 23:201–226. Academic Press, London.
- . 1993. Fossil communities: compositional variation at many time scales. Pp. 341–349 in R. E. Ricklefs and D. Schlüter, eds. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago.
- Valentine, J. W., D. Jablonski, and D. H. Erwin. 1999. Fossils, molecules and embryos: new perspectives on the Cambrian explosion. *Development* 126:851–859.
- Van Valen, L. 1976. Ecological species, multispecies, and oaks. *Taxon* 25:233–239.
- Vermeij, G. J. 1987. *Evolution and escalation*. Princeton University Press, Princeton, N.J.
- . 1991. When biotas meet: understanding biotic interchange. *Science* 253:1099–1104.
- . 1994. The evolutionary interaction among species: selection, escalation, and coevolution. *Annual Review of Ecology and Systematics* 25:219–236.
- Via, S., and D. J. Hawthorne. 1998. The genetics of speciation: promises and prospects of Quantitative Trait Locus mapping. Pp. 352–354 in Howard and Berlocher 1998.
- Via, S., and A. J. Shaw. 1996. Short-term evolution in size and shape of pea aphids. *Evolution* 50:163–173.
- Voss, S. R., and H. B. Shaffer. 1997. Adaptive evolution via a major gene effect: paedomorphosis in the Mexican axolotl. *Proceedings of the National Academy of Sciences USA* 94:14185–14189.
- Vrba, E. S. 1984. What is species selection? *Systematic Zoology* 33:318–328.
- . 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 in Evolutionary Biology* 6:111–168.
- 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.
- Wagner, G. P. 1996. Homologues, natural kinds and the evolution of modularity. *American Zoologist* 36:36–43.
- Wagner, G. P., G. Booth, and H. Bagheri-Chaichian. 1997. A population genetic theory of canalization. *Evolution* 51:329–347.
- Wagner, G. P., C. H. Chiu, and T. H. Hansen. 1999. Is Hsp 90 a regulator of evolvability? *Journal of Experimental Zoology (Molecular and Developmental Evolution)* 285:116–118.
- Wagner, P. J. 1995. Testing evolutionary constraint hypotheses: examples with early Paleozoic gastropods. *Paleobiology* 21: 248–272.
- . 1996a. Ghost taxa, ancestors, and assumptions: A reply to Norell. *Paleobiology* 22:456–460.
- . 1996b. Contrasting the underlying patterns of active trends in morphological evolution. *Evolution* 50:990–1007.
- . 1998. A likelihood approach for evaluating estimates of phylogenetic relationships among fossil taxa. *Paleobiology* 24:430–449.
- Wagner, P. J., and D. H. Erwin. 1995. Phylogenetic patterns as tests of speciation models. Pp. 87–122 in Erwin and Anstey 1995b.
- Walsh, J. A. 1996. No second chances? New perspectives on biotic interactions in post-Paleozoic brachiopod history. Pp. 281–288 in P. Copper and J. Jin, eds. *Brachiopods*. Balkema, Rotterdam.
- Watts, P. C., J. P. Thorpe, and P. D. Taylor. 1998. Natural and anthropogenic dispersal mechanisms in the marine environment: a study using cheilostome Bryozoa. *Philosophical Transactions of the Royal Society of London B* 353:453–464.

- Wayne, R. K. 1986. Cranial morphology of domestic and wild canids: the influence of development on morphological change. *Evolution* 40:243–261.
- Wayne, R. K., and E. A. Ostrander. 1999. Origin, genetic diversity, and genome structure of the domestic dog. *BioEssays* 21: 247–257.
- Weatherbee, S. D., H. F. Nijhout, L. W. Grunert, G. Halder, R. Galant, J. Selegue, and S. Carroll. 1999. *Ultrabithorax* function in butterfly wings and the evolution of insect wing patterns. *Current Biology* 9:109–115.
- Wei, K.-Y., and J. P. Kennett. 1986. Taxonomic evolution of Neogene planktonic Foraminifera and paleoceanographic relations. *Paleoceanography* 1:67–84.
- Weil, E., and N. Knowlton. 1994. A multi-character analysis of the Caribbean coral *Montastraea annularis* (Ellis and Solander, 1786) and its two sibling species, *M. faveolata* (Ellis and Solander, 1786) and *M. franksi* (Gregory, 1895). *Bulletin of Marine Science* 55:151–175.
- Wen, J. 1999. Evolution of the eastern Asian and eastern North American disjunct distributions in flowering plants. *Annual Review of Ecology and Systematics* 30:421–455.
- Wiley, E. O. 1981. *Phylogenetics*. Wiley, New York.
- Williams, G. C. 1992. *Natural selection: domains, levels, and challenges*. Oxford University Press, New York.
- Williamson, M. 1996. *Biological invasions*. Chapman and Hall, London.
- Wilson, A. C., G. L. Bush, S. M. Case, and M.-C. King. 1975. Social structuring of mammalian populations and rate of chromosomal evolution. *Proceedings of the National Academy of Sciences USA* 72:5061–5065.
- Wing, S. L., and L. D. Boucher. 1998. Ecological aspects of the Cretaceous flowering plant radiation. *Annual Review of Earth and Planetary Sciences* 26:379–421.
- Wright, S. 1982a. Character change, speciation and higher taxa. *Evolution* 36:427–443.
- . 1982b. The shifting balance theory and macroevolution. *Annual Review of Genetics* 16:1–19.
- Zakany, J., C. Fromental-Ramain, X. Wartot, and D. Duboule. 1997. Regulation of number and size of digits by posterior Hox genes: a dose-dependent mechanism with potential evolutionary implications. *Proceedings of the National Academy of Sciences USA* 94:13695–13700.
- Zelditch, M. L., and W. L. Fink. 1996. Heterochrony and heterotopy: stability and innovation in the evolution of form. *Paleobiology* 22:241–254.