Chapter 17

Paleontological Perspectives on Morphological Evolution

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The fossil record documents over three billion years of evolution. Darwin considered the general succession of morphologies in the fossil record to corroborate the basic idea of evolution by natural selection. However, he also recognized aspects of the fossil record that challenged his ideas. For example, did the sudden appearance of higher taxa reflect a different underlying model of evolution or the imperfections of the fossil record? In the 150 years since the publication of *The Origin of Species*, paleontologists have used fossil data to challenge, corroborate, and augment elements of Darwin's basic model. Here, I will focus particularly on work from the last 40 years. In that time, paleontologists have taken advantage of advances in biological theory and quantitative methods to predictably and quantitatively summarize patterns that Darwin could only describe verbally and to articulate predictions for Darwin's models that Darwin himself was unable to derive. Paleontologists also have devised tools for assessing sampling levels, thus testing whether geology or biology might be responsible for patterns. Fossil data contradict some of Darwin's ideas, such as the idea that differences among higher taxa reflect the unsampled, long-term accumulation of changes. However, fossil data strongly corroborate Darwin's idea that natural selection is the major force for fixing novelties once they do appear.

Morphospace and Related Concepts

Throughout this paper, I frequently discuss concepts and patterns in terms of morphospace. A morphospace describes the distribution and range of observed and potential morphologies. Although the word is relatively new, the basic concept obviously is not: for example, Darwin's (1845: 379–380) summary of the range of forms among Galapagos finches represents a crude verbal description of a morphospace. Similarly, Sewall Wright's (1932) adaptive landscapes tacitly refer to morphospaces as potential selective points for adaptive peaks and valleys (Simpson 1944; Lande 1986).

However, use of the concept of repeatable, quantified morphospaces is relatively new. There are in three basic varieties of morphospaces. Theoretical morphospaces use predetermined characters, such as mathematical descriptions of mollusk shell coiling (Raup 1966; McGhee 1991). Empirical morphospaces use multivariate summaries of morphometric data (Foote 1990). Character-based morphospaces represents a hybrid involving multivariate summaries of predetermined characters (Foote 1992b). All three morphospaces permit repeatable quantitative summaries of what Darwin and other workers of his era could only verbally describe. More importantly, morphospaces enable workers to make calculations and assessments, such as illustrate similarities as well as differences among classes of morphotypes and provide insights into *possible* but unobserved morphotypes that were more difficult to make with simple verbal descriptions.

Morphospaces are a useful device for describing important aspects of morphological evolution that paleontologists measure. Disparity describes the breadth and range of taxon distributions within morphospace (Gould 1991; Foote 1993b; Wills et al. 1994). Intrinsic constraints and/or ecological restrictions can make regions of morphospace difficult to occupy, evolve, or re-evolve, or simply may slow rates of change. Trends reflect shifts in morphospace occupancy over time (McShea 1994). Finally, rates represent the size of "steps" that phylogenies take through morphospace over either time or speciation events. These concepts all are related: disparity, constraint/restrictions, and trends not only all affect one another (Ciampaglio et al. 2001), but they can all be described or modeled in terms of rates (McShea 1994; Foote 1996b). Therefore, I will review disparity, constraints/restrictions, and trends in turn, with particular regard to rates, and emphasize areas in which paleontological research has corroborated, contradicted, or augmented Darwin's ideas.

Morphological Disparity

Overview

Workers throughout evolutionary biology commonly discuss constraints, ecological restrictions, trends, and rates, but until fairly recently only paleontologists studied disparity in great detail. Therefore, I will review disparity in the most detail. The paleontological literature of the 1980s uses the word "disparity" for a variety of related concepts. However, Gould's (1991) definition of disparity as the diversity of morphological types, in contrast to "diversity" as numbers of taxa (i.e., richness) is now the standard definition, and the one that I will use here.
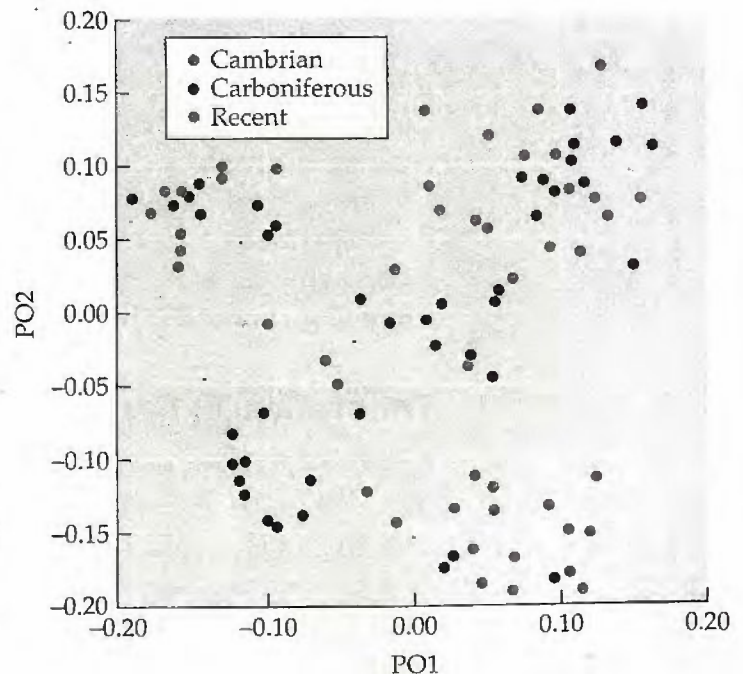
Obviously, the concept of disparity is quite old, and Darwin implicitly referred to what is now called disparity in a number of ways. However, morphological disparity studies require a battery of tools, including numerical taxonomy, morphometrics, and multivariate analysis, which requires computer data to be easily analyzed and expressed. Thus, it was not until

the 1990s that Foote (1990, 1991b, 1991c, 1992a, 1992b, 1993a, 1993b, 1994, 1996a, 1996b) and others (Wills et al. 1994; Ciampaglio 2002) built upon frameworks established in the 1960s to advance morphological disparity both methodologically and theoretically to the point where disparity studies offered objective summaries of evolutionary history.

Historical disparity studies based upon extant taxa are becoming common. Such studies use ancestral reconstructions over molecular phylogenies to infer disparity in the past (e.g., Harmon et al. 2003; Ricklefs 2004; Sidlauskas 2007; Adams et al. 2009). Paleontological studies differ fundamentally from these in that they use observed taxa from different time intervals rather than from inferred taxa at inferred time intervals. Thus, paleontological disparity studies do not depend on particular ideas of phylogeny, even if a phylogenetic context is invaluable for corroborating theoretical implications of those studies (see below). More importantly, paleontological disparity studies use extinct taxa that cannot be inferred from modern phylogenies. Arthropods exemplify this issue (Figure 17.1): the great disparity among extant arthropods concentrates largely in regions of morphospace unoccupied during the Cambrian, whereas the nearly equal disparity among Cambrian arthropods concentrates largely in regions unoccupied by extant taxa (Briggs et al. 1992; Wills et al. 1994). Carboniferous arthropods not only link the Cambrian and Recent morphospaces, but also add their own disparity (Stockmeyer Lofgren et al. 2003).

There are a variety of ways in which paleontologists evaluate disparity. Typical disparity metrics summarize the average differences among taxa, such as average pairwise dissimilarity or variance. Ciampaglio et al. (2001) and Wills (2001) provide excellent summaries of different disparity metrics. Consider a simple hypothetical example (Figure 17.2A): in its first stage, a clade has four species distributed evenly in morphospace. The clade then adds new species at a similar underlying rate of morphologic evolution as it did in the first stage. Given either pairwise dissimilarity or variance along the morphological axes 1 and 2, the expansion in morphospace accompanies an increase in disparity (Figure 17.2B).

Figure 17.1 Principal Coordinate Summary of Arthropod Morphospace Occupancy within Three Geological Intervals PO1 and PO2 represent the first two principal coordinate axes. (Based on data from Wills et al. 1994 and Stockmeyer Lofgren et al. 2003.)
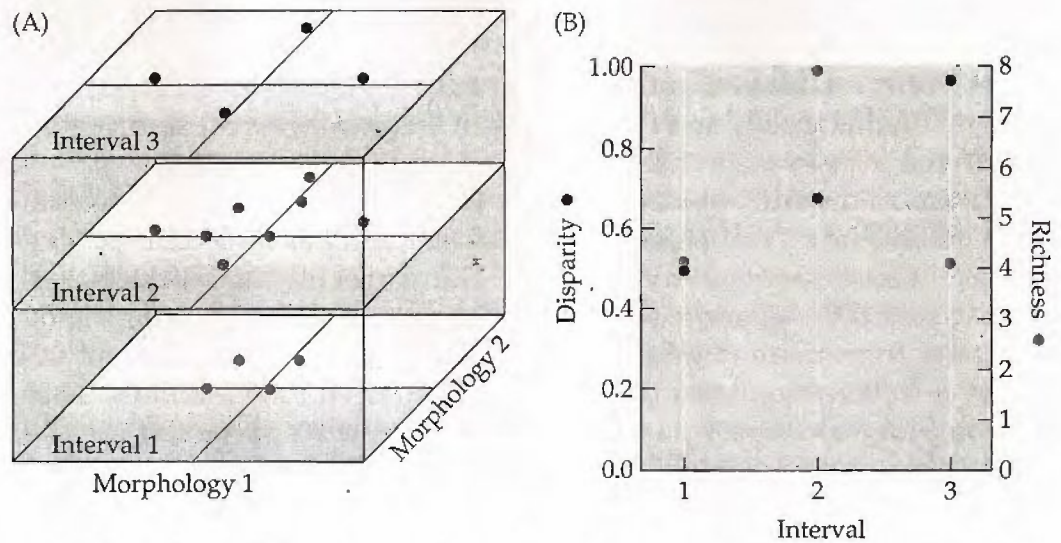
Figure 17.2 Morphologic Disparity: A Simple Example (A) Morphospace distributions of a hypothetical clade. Morphology might represent either measurements of a predefined theoretical character or multivariate summaries of discrete or morphometric characters. (B) Disparity through time (see red circles) is based on the pairwise dissimilarities among the taxa in each interval. Note that summed variances yield the same general pattern. Initially, disparity increases as richness increases (see green circles in B). However, the extinction of the middle of the morphospace strengthens disparity without altering the size of the occupied morphospace and thus increases disparity, while richness declines.

If the primitive morphologies become extinct after Interval 2 with no additions to morphospace (see Interval 3), then the sparser occupation of morphospace increases average pairwise dissimilarities and variances along morphological axes, despite the fact that the size of the morphospace is unchanged. Disparity measured in this manner is conceptually akin to ecological diversity (Hurlbert 1971), that is, it is a product both of the size (richness/total range) and the distributions (evenness/patchiness). These disparity metrics have the added advantage of being fairly robust to sampling, whereas metrics, such as the total range, are very sensitive to sampling (e.g., Foote 1991a; Roy and Foote 1997; Ciampaglio et al. 2001).

Theoretical Expectations of Disparity and Empircal Tests

Figure 17.2B shows high disparity accompanying low richness *after* selective extinction. However, the fossil record seems to offer many examples of high morphological disparity accompanying lower richness at the *outset* of clade history. Darwin describes this phenomenon in general terms when discussing the sudden appearance of a wide variety of metazoans in the Cambrian and also in reference to the sudden appearance of major taxa,

such as teleost fishes. Darwin attributes such patterns to geology rather than biology, and I will return to how paleontologists test this sort of idea in the following discussion. Valentine (1969, 1980; Valentine and Campbell 1975; Erwin et al. 1987) as well as Gould (1989, 1991) and others argued that this pattern reflects evolution rather than geology: they invoked models of increasing intrinsic constraints and/or ecological restrictions as representative of slowing rates of morphological evolution.

Foote (1991b, 1993a, 1996b) used simulations to go beyond first-principle arguments and examined the expected relationship between diversification and disparity. He contrasted a wide variety of models, but I will focus on just a few important ones. Given constant step size (i.e., rate of morphological change between ancestors and descendents), Foote showed that we expect disparity to increase linearly as diversity increases exponentially (Figure 17.3A). Given a Valentine–Gould model of elevated early step-size, disparity begins at very high levels despite low richness and does not increase markedly as richness increases (Figure 17.3B). Adding constraints to morphospace will yield somewhat similar patterns; even if step-sizes do not decrease over time (Figure 17.3C), the size of the morphospace cannot continue to increase, resulting in a crowded, less disparate morphospace.

Foote's distinctions are not just theoretical experiments, as the majority of relevant disparity studies show high disparity early in clade histories (Table 17.1). This finding might not be *the* typical pattern, although paleontologists no doubt have been drawn to examples for which simple observation
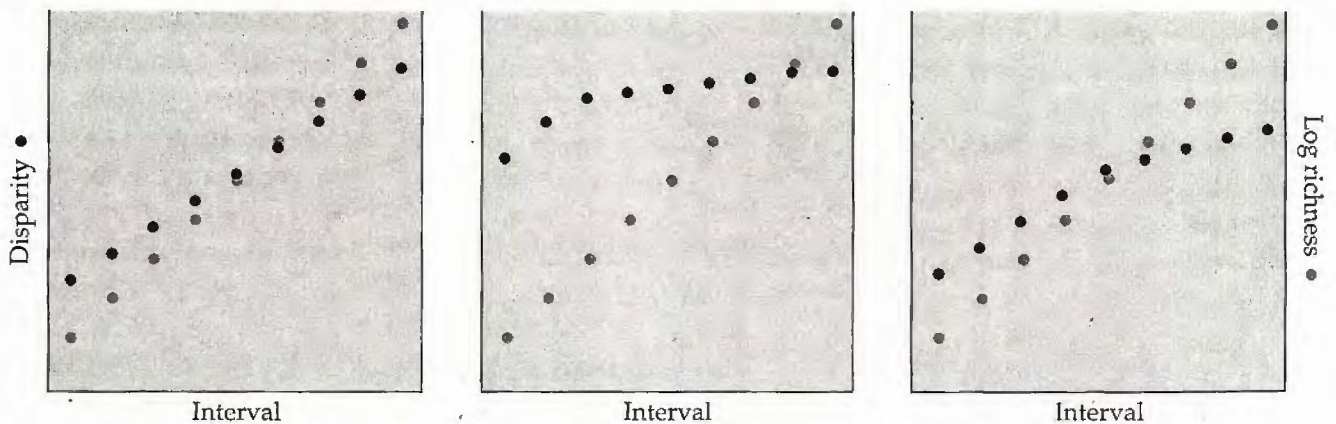

Figure 17.3 Disparity (Red Circles) and Richness (Green Circles) Under Three Models of Morphological Evolution with Exponential Diversification (A) Constant rates of morphologic change over time. (B) Elevated rates of morphologic change early, decreasing markedly after the early intervals. Although peak disparity does not change greatly from constant rates of morphologic change, the clade approaches peak disparity much more rapidly. (C) Constant rates of morphologic change, but with constraints/restrictions on the range of possible designs. Now the same initial start leads to much lower morphologic disparity. (Adapted from Foote 1993a: Figure 1 and Wesley-Hunt 2005: Figure 1.)

TABLE 17.1 DISPARITY PATTERNS

TAXON	STUDY
HIGH EARLY DISPARITY	
Proterozoic–Cambrian acritarchs	Huntley et al. (2006)
Angiosperm pollen	Lupia (1999)
Paleozoic gastropods	Wagner (1995)
Rostroconchs	Wagner (1997)
Ammonites	Saunders et al. (2008)
Ordovician bryozoans	Anstey and Pachut (1995)
Mesozoic articulate brachiopods	Ciampaglio (2004)
Paleozoic crinoids	Foote (1994, 1995)
Mesozoic crinoids	Foote (1996a)
Blastozoans	Foote (1992b)
Stylophorans	Lefebvre et al. (2006)
Holasteroid echinoids	Eble (2000)
Spatangoid echinoids	Eble (2000)
Arthropods	Briggs et al. (1992), Wills et al. (1994)
Crustacea	Wills (1998b)
Insects	Labandeira and Eble (2008)
Tetrapods	Ruta et al. (2006)
Archosaurs	Brusatte et al. (2008)
LOW EARLY DISPARITY	
Trilobites	Foote (1991c)
Olenelloid trilobites	Smith & Lieberman (1999)
Ptychoparioid trilobites	Cotton (2001)
Blastoids	Foote (1991b)
Atelostomate echinoids	Eble (2000)
Aporrhaid gastropods	Roy (1994)
Inarticulate brachiopods	Smith & Bunge (1999)
Paleozoic articulate brachiopods	Ciampaglio (2004)
Priapulids	Wills (1998a)
Carnivore mammals	Wesley-Hunt (2005)
Ungulate mammals	Jernvall (1996)

Source: Adapted from Erwin 2007: Table 1.
Note: Many clades with high disparity retain it late in their histories.

suggests this sort of pattern. Nevertheless, Figure 17.3B is common enough that the issue of whether disparity patterns predict rates of change (and shifts in those rates of change) across the empirical phylogenies, as Foote's simulations indicate that they should, must be addressed. When the necessary phylogenetic context is available, disparity patterns predict rate patterns accurately (Table 17.2). Taxa with relatively low early disparity do

TABLE 17.2	STUDIES EXAMINING RATE SHIFTS ASSOCIATED WITH DISPARITY PATTERN
TAXON	**STUDY**
HIGH EARLY RATES	
Paleozoic gastropods	Wagner (1995)
Rostroconchs	Wagner (1997)
Blastozoans	Smith (1988) & Foote (1992b)
Bryozoans	Anstey and Pachut (1995)
Coelacanths	Cloutier (1991)
Tetrapods	Ruta et al. (2006)
Archosaurs	Brusatte et al. (2008)
NO SHIFT	
Synapsids	Sidor and Hopson (1998)
Sauropod dinosaurs	Sereno et al. (1999)
Olenelloid trilobites	Smith and Lieberman (1999)
Ptychoparioid trilobites	Cotton (2001)

not show high early rates of change. For example, neither olenelloid nor ptychoparioid trilobites show any major shifts in rates (Smith and Lieberman 1999; Cotton 2001), and trilobites as a whole, show peak disparity reasonably late in clade history (Foote 1991c, 1993a). Among taxa with high early disparity, there are variations on elevated early rates. Tetrapods show a continuous decrease in rates over the middle-late Paleozoic (Ruta et al. 2006), whereas Paleozoic gastropods and Triassic archosaurs show very high rates in the earliest intervals, followed by lower rates in subsequent intervals (Wagner 1995; Brusatte et al. 2008). Within rostroconch mollusks, one derived subclade shows lower rates of change than does the stem-group and other subclades (Wagner 1997). However, that derived subclade is essentially the sole survivor of the end-Ordovician extinction, which thus concentrates the high rates in the first third of rostroconch history.

Elevated Rates of Change as Artifacts of an Imperfect Fossil

Record: Testing Darwin's Geological Hypothesis

Darwin (1859) suggested that the appearance of major groups, such as teleost fishes or trilobites, reflects the poor quality of the fossil record early in clade histories. Darwin (1859) went so far as to posit that the Silurian through the Recent represents half or less of the evolution of metazoans (note that Darwin's definition of Silurian included the Ordovician and workers had only just begun to recognize the Cambrian). Thus, the sediments containing much (if not most) of metazoan evolution are lost or

undiscovered. Darwin (1859) also offered a perfectly plausible first-principles argument for how limited biogeographic distribution might hide the early history of teleosts from the fossil record. Therefore, we should ask whether Darwin's non-preservation hypothesis might explain high early disparity and high early measured rates.

For Paleozoic gastropods, Wagner (1995) showed that both the average samples per species and the number of sampling opportunities per time interval are *greater* in the latest Cambrian and Early Ordovician, when rates are high, and that sampling actually is substantially lower in the Middle Ordovician, when rates are moderate. Similarly, Wagner (1997) showed that sampling intensity is greater among Cambro–Ordovician rostroconchs than among post-Ordovician rostroconchs. In both cases, the relationship between sampling and reconstructed rates contradicts Darwin's expectations.

One might counter that Wagner does not actually test Darwin's hypothesis, as Darwin actually proposes long unsampled records *prior to* major taxa first appearing in the fossil record. Ruta et al. (2006) consider this approach for early tetrapods. Although Darwin does not mention tetrapods, they represent a good possible example of his non-preservation hypothesis. The major innovations of tetrapods correspond to high early disparity, and rates of change seem to decrease through their early history (Ruta et al. 2006; Figure 17.4). Although workers scrutinize the early
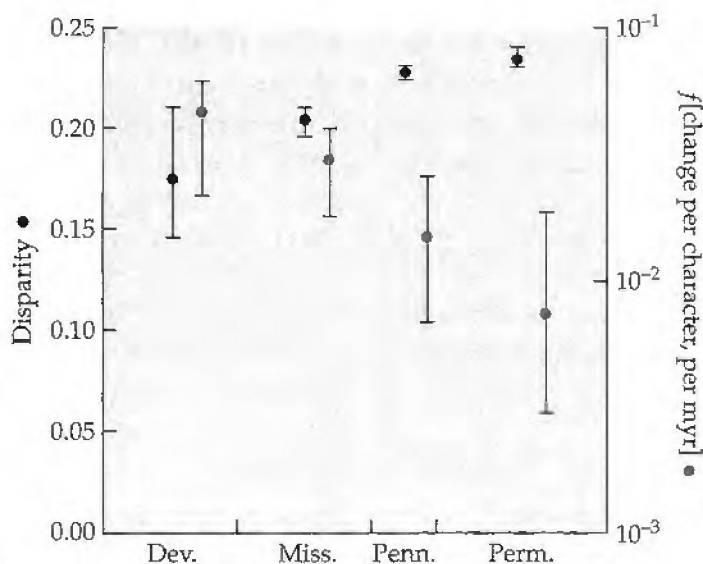

Figure 17.4 Disparity and Average Per-Branch Rates (*f*) of Character Change among Early Tetrapods Red circles denote disparity; green circles denote average per-branch rates of character change. Brackets for disparity represent 95% error bars from 500 bootstrap replications (Foote 1992b). Brackets for rates reflect 25th and 75th percentiles. The Devonian (Dev.)/Mississippian (Miss.) boundary is approximately 359 millions years ago (Ma). The Mississippian / Pennsylvanian (Penn.) boundary is approximately 318 Ma, and the Pennsylvanian/Permian (Perm.) boundary is approximately 299 Ma (Gradstein et al. 2005). "Myr" denotes millions of years. (Adapted from Ruta et al. 2006.)

tetrapod record keenly, that record clearly is not an outstanding record when compared to the marine mollusk record. For example, Niedzwiedzki et al. (2010) document tetrapod tracks from the Eifelian, approximately 12 million years prior to the origin of "tetrapodomorphs" (i.e., the red taxa in Figure 17.5), as assumed by Ruta et al. (2006). Thus, an extrapolation of Darwin's suggestion, that is, that high rates of early evolution in the middle Devonian–Early Carboniferous reflect unsampled evolution from the Early Devonian and earlier, might seem plausible in this case. Here, I will recast the first-principles argument of Ruta et al. quantitatively to illustrate how paleontologists can test and potentially refute Darwin's non-preservation hypothesis.

A phylogenetic context is critical to this argument. Tetrapods are a derived group of sarcopterygian fish, with sister taxa that also appear in the Middle to Late Devonian (see Figure 17.5). Thus, extending the origins of tetrapods to the earliest Devonian (i.e., when lungfish first appear) requires positing range extensions for at least six sarcopterygian fish taxa also (Smith 1988, 1994). If we lump the relatively short Lockhovian and Pragian
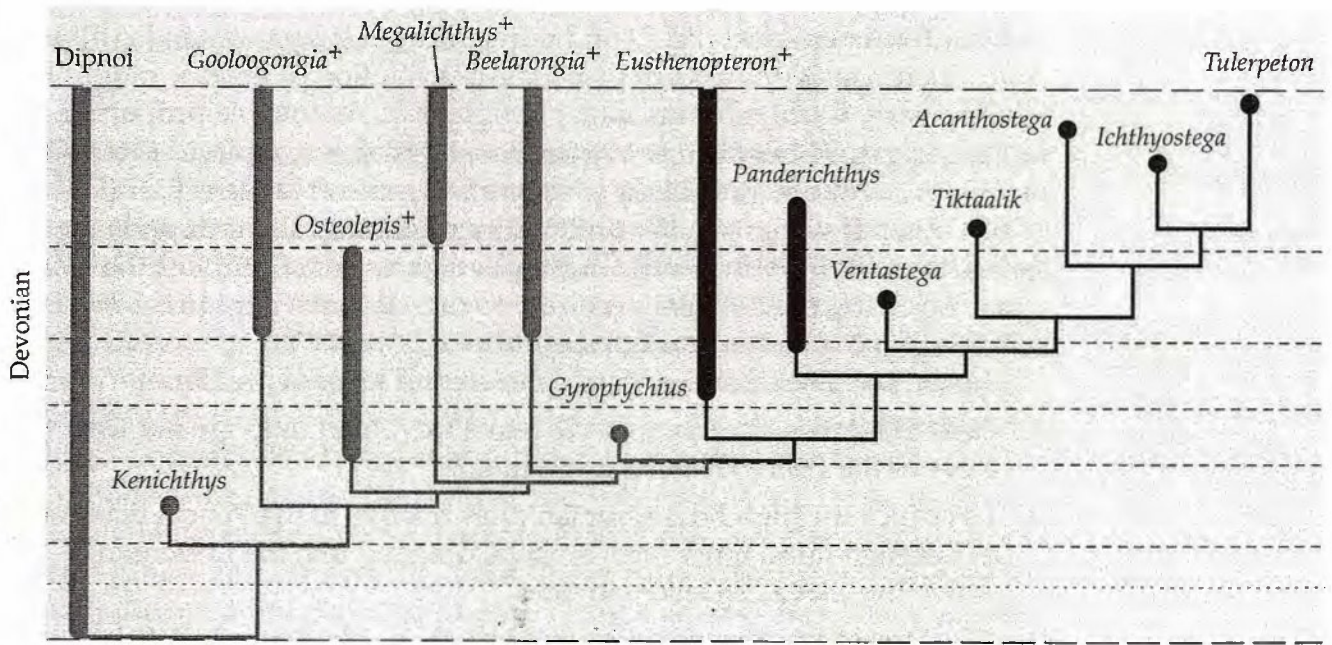

Figure 17.5 Sarcopterygian Phylogeny Divergence times for tetrapods using the analysis by Ruta et al. (2006) that optimizes estimated rates (see red). Divergence times for other sarcopterygians (see blue) reflect general appearance times in the fossil record as given. "+" denotes clade, including named genus. Dashed lines denote stages (see Gradstein et al. 2005). Faint dashed line denotes short stages, lumped with prior stages for preservation rate analyses. Note that a long unsampled record of tetrapods requires a long unsampled record of their closest fish relatives as well. (Graph based on consensus of data from Johanson and Ahlberg 2001, Ruta et al. 2003, Daeschler et al. 2006, Friedman 2007a, and Ruta and Coates 2007.)

stages into a single stage, an earliest Devonian tetrapod origin now requires an additional 11 stages of unsampled sarcopterygian fish record.

An estimate of the probability of these sampling gaps must now be made. The optimal approach involves using numbers of fossiliferous localities and the proportion of times that individual taxa are found in those localities (Strauss and Sadler 1989; Marshall 1990). Such a database is not yet available for early sarcopterygians. An alternative is to estimate R, or the average preservation potential per stage. The exact probability of an early Devonian diversification of tetrapods, given just the sarcopterygian fish record, then, is $(1 - R)$. We can estimate R using distributions of stratigraphic ranges. Although earlier workers use ranges to estimate extinction rates (Simpson 1953; Van Valen 1973), Sepkoski (1975) notes that imperfect preservation truncates stratigraphic ranges and thus affects "survivorship curves." Foote and Raup (1996) further note that as preservation becomes worse, the proportion of taxa sampled from a single time interval increases relative to the true (but unknown) survivorship curve. Numerous taxa known from two or more stages thus reflect (in part) good enough preservation for paleontologists to find taxa in two or more stages. Foote (1997) formalizes this idea to estimate the joint likelihood of average extinction and preservation rates given stratigraphic ranges.

Data from Sepkoski (2002) and other sources (Johanson and Ahlberg 2001; Friedman 2007a, 2007b) provide a distribution of generic ranges for Silurian-early Carboniferous sarcopterygians. A reasonable proportion of sarcopterygian fishes have stratigraphic ranges of two or more stages (Figure 17.6A), and the most likely preservation rate per stage is 0.23 (Figure 17.6B). Even if we ignore the probability of missing the tetrapods themselves, then $P < 0.06$ (in which P is [implied gaps | data]) for just the fishes alone. Thus, it is not the fossil record of tetrapods that contradicts Darwin's solution, but the fossil record of their near-relatives.

This unlikely solution leaves and/or creates its own problems:

1. Early Devonian divergences still leave Devonian rates greater than those of the Pennsylvanian or Permian.

2. To reduce the high Mississippian rates relative to the Pennsylvanian or Permian rates, those rates must be dragged into the Devonian, which (re-)elevates Devonian rates.

3. All of the sarcopterygian morphologic change between lungfishes and tetrapods now must be squeezed into the very beginning of the Devonian.

Accommodating all three problems by pushing the divergences of sarcopterygians still deeper in time simply pushes the problems elsewhere. Moreover, such action requires additional (and increasingly unlikely) gaps in the records not just of sarcopterygians, but also of basal osteichthyans, chondrichthyans, and placoderms. New "oldest evidence of" finds, such as those reported by Niedzwiedzki et al. (2010), still might alter ideas about
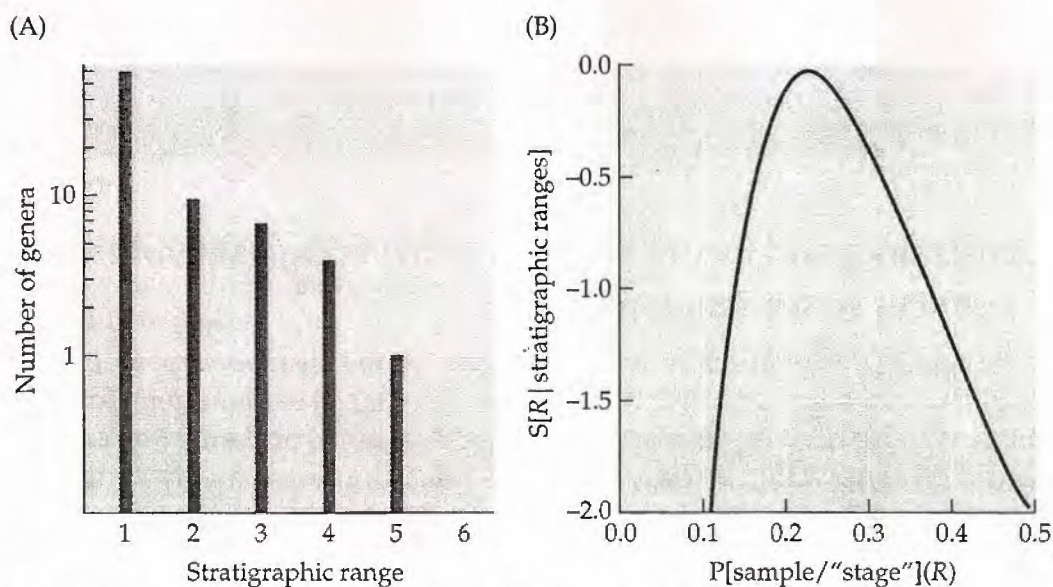
(A)

(B)

FIGURE 17.6 Stratigraphic Ranges and Preservation Rates (A) Distribution of generic ranges in stages. Note that the Ludlow + Pridoli and the Lockhovian + Pragian both are considered single stages here to make stage lengths roughly comparable in millions of years. (B) Support curves for preservation rates integrating over extinction rates (Foote 1997). Support rescales the log-likelihood to the maximum log-likelihood (Edwards 1992).

ecological correlates of the diversification of major clades. However, much more radical "oldest" finds are necessary to alter ideas about basic rates of morphological evolution in this case.

Obviously, this sort of analysis must be repeated for other taxa. In the case of gastropods, the Paleobiology Database (PBDB; http://pbdb.org as of 1 December 2009) records 1760 occurrences of Cambrian mollusks from 678 localities and 181 formations. These mollusks show shell mineralogies with similar preservation potential as the shell mineralogies of early gastropods (Vendrasco et al. 2010), which means that the absence of gastropods is meaningful (see Bottjer and Jablonski 1988). These mollusks also are phylogenetically very basal to gastropods and are sampled from much of the Cambrian world. Thus, there is no missing record here to explain the apparent elevated rates of change among the earliest known gastropods (Wagner 1995). Even the so-called missing Precambrian record is fairly well known and increasingly well sampled. The PBDB currently is far sparser for Ediacaran data than for Phanerozoic data, but as of December 1 2009, it includes 530 occurrences from 149 localities and 49 formations. These localities preserve both soft-bodied and calcitic fossils and thus should be able to preserve the arthropod and molluscan synapomorphies that Darwin's non-preservation hypothesis predicts existed then. However, although there are possible examples of stem-group members of modern phyla (Fedonkin and Waggoner 1997), none of them clearly nest within

subclades of metazoan phyla. Indeed, many Ediacaran taxa are so different from Cambrian metazoans (typically lacking even bilateral symmetry) that workers have questioned the affinity of the Vendobionts to metazoans (Seilacher 1992). So, we now have the sediments: but they do not yield what Darwin predicts they should yield.

Constraints and Restrictions on Morphological Evolution
Constraints Versus Restrictions

If we reject preservation as an explanation for the sudden appearance of disparity in the fossil record, then we need biological explanations for rate shifts. We also need explanations for the general limits on forms that are observed (Wagner 2000). Broadly, two ideas exist. One is essentially a complement to Darwin's explanation for the diversity of forms among Galapagos finches: some clades have great numbers of ecological opportunities early in their history or following mass extinctions (see Losos and Mahler, Chapter 15). The intense resulting selection creates high rates of morphological change (Valentine 1980, 1986; Conway Morris 1989). However, selection afterwards is a *deterrent* to change: incumbent species with adaptations for particular habitats present selection against adaptations for those same habits in other species.

The second idea focuses on changes in intrinsic constraints, such as canalization, increased regulatory networks, refractory gene networks (Valentine and Campbell 1975; Campbell and Marshall 1987; Erwin 1993; Wallace 2000; Davidson and Erwin 2006; see Kirkpatrick, Chapter 7; G. Wagner, Chapter 8). The basic premise is that the evolution of general regulatory systems has made it more difficult for many anatomical features to change, reducing rates of change.

In many cases, paleontologists can document only changes in rates and/or morphospace occupancy. However, in some cases they can distinguish between restrictions and constraints (Table 17.3). Post-extinction rebounds offer good testing grounds, because intrinsic constraint hypotheses predict that it should be difficult for clades to recover disparity, whereas ecological restriction hypotheses predict that newly opened ecospace should encourage high rates of change and thus high levels of disparity. The Permo-Triassic is a particularly good system, because many surviving clades likely bottlenecked at that time (Erwin et al. 1987). Brachiopods and cephalopods suffered major losses at the end-Permian. However, both rapidly re-acquired high disparity in the Triassic (Ciampaglio 2002, 2004; McGowan 2004). The surviving brachiopod clades radiate into morphospace previously occupied by extinct clades, which strongly corroborates the idea that the surviving clades were not constrained in morphospace, but instead restricted by casualties of the end-Permian extinction.

Other clades show evidence of both restrictions and constraints. After the end-Permian extinction, the surviving crinoids do radiate into previously

TABLE 17.3 STUDIES CORROBORATING CHANGES IN ECOLOGICAL RESTRICTIONS AND INTRINSIC CONSTRAINTS

TAXON	STUDY
ECOLOGICAL RESTRICTIONS	
Ordovician–Silurian gastropods	Wagner (1995)
Triassic ammonites	McGowan (2004)
Triassic brachiopods	Ciampaglio (2004)
Carboniferous blastozoans	Ciampaglio (2002)
Triassic crinoids	Foote (1996a, 1999)
Amniotes	Wagner et al. (2006)
INTRINSIC CONSTRAINTS	
Ordovician–Silurian gastropods	Wagner (1995)
Triassic crinoids	Foote (1999)
Lissamphibians	Wagner et al. (2006)
Amniotes	Wagner et al. (2006)

Note: Some studies show evidence of both changing ecological restrictions and intrinsic constraints.

occupied morphospace, but they do not achieve the levels of disparity seen in the early Paleozoic (Foote 1999). Given the absence of ecological analogs to crinoids (e.g., other stalked echinoderms) after the end-Permian, Foote suggests that intrinsic constraints tempered the opportunities offered by ecology. Wagner (1995) partitions general gastropod shell characters into those associated with general differences in internal anatomy from those associated with differences in basic shell functional type. Among modern gastropods, the basic anatomical groups exploit all of the basic gastropod ecological strategies. As ecology does not seem to restrict soft-tissue anatomy among gastropods, increasing restrictions are an unlikely explanation for decreases in step size changes that seem to reflect differences in soft-tissue. The different functional shell types (and thus differences in those types) occur in all major anatomical groups among extant gastropods. As these shell features appear unconstrained among modern gastropods, increasing constraints are an unlikely explanation for decreases in step size among these shell features. Although step size decreases for both types of differences, the decrease is much greater for steps associated with difference in internal anatomy than for steps associated with shell function.

The radiation of tetrapods also corroborates both constraints and restrictions. Wagner et al. (2006) use distributions of changes to examine the number of evolving characters in lissamphibians, amniotes, and stem tetrapods. Lissamphibians occupy the same general habitats as the stem

tetrapods and rapidly become the only amphibian-grade tetrapods. If ecological opportunity allowed the appearance of high numbers of characters among amphibian-grade tetrapods, then the same ecological opportunities should have allowed a similar number of characters among lissamphibians. Instead, lissamphibians show a highly restricted character space relative to stem tetrapods. Even if lissamphibians had some sort of "Swiss army knife" character allowing them to exploit habitats that their predecessors exploited with a variety of characters, one still would expect only decreased rates rather than freezing of those other characters. This strongly implicates constraints as the limiting factor. On the other side of the tetrapod tree, amniotes exhibit approximately the same size character space as stem tetrapods. However, both stem tetrapods and amniotes occupy far less than the total tetrapod morphospace, which requires amniotes to gain as well as lose characters. The locking in of old characters for amniotes implicates intrinsic constraints, because amphibian grade tetrapods should not have excluded the increasingly terrestrial amniotes from ecomorphological grades. Conversely, the addition of new characters accompanies the invasion of fully terrestrial habits and thus corroborates the empty ecospace model.

This idea brings us back to Darwin's suggestions that the sudden appearances in the fossil record of teleosts, trilobites, and other major groups require either that his model be incorrect or that the fossil record be highly incomplete. One hundred fifty years later, it is clear that this was predicated on incorrect assumptions, in part, because Darwin himself underestimated natural selection in two ways. One, theoretical (Garcia-Ramos and Kirkpatrick 1997; see Kirkpatrick, Chapter 7) and empirical (Losos et al. 1997) studies indicate that selection operates far more quickly than Darwin seems to have thought possible (Hendry and Kinnison 1999). Two, the idea that ecological restrictions slowed rates of evolution is simply a logical compliment to Darwin's model that he failed to consider explicitly: if ecological opportunity plus natural selection permits radiations, such as those seen in Galapagos finches, then ecological incumbency plus natural selection will restrict morphological change. However, this theory also reflects Amundson's (2005) point that natural selection describes only whether novelties are inherited and not how they are generated. Darwin offers no model for this phenomenon: at best, Darwin's frequent citation of (what is now termed) the Principle of Uniformitarianism (Lyell 1830) indicates that Darwin thought that the same mechanisms existed in the past as exist today—whatever those mechanisms might be. The possibility of changing constraints provides a mechanism for very different amounts of variation over time that is totally lacking from Darwin's model. This possibility also undermines Darwin's supposition that taxa, such as trilobites, teleosts, and others, require extensive time to acquire their distinctive morphologies. Thus, the fossil data contradict Darwin's (at best) vaguely formulated ideas about how morphological variation arises rather than contradicting the

idea of natural selection being the primary arbiter by which changes are inherited.

Trends

Overview

Trends offer some of the strongest evidence of natural selection that the fossil record can provide. Curiously, however, Darwin never explicitly refers to trends *among* lineages, as most of his discussion focused on trends *within* lineages. Large-scale trends are a corollary of his theory, only if one supposes that the same (or very similar) selective forces affect numerous related lineages and that the same morphological options would appear for those lineages. The closest Darwin comes to discussing this idea is in his suggestion that Eocene organisms would fare poorly in the modern world (Darwin 1859) or that Paleozoic organisms would fare poorly in the Mesozoic (i.e., Secondary) world. This statement implies that related lineages would undergo parallel improvement over time, leading to morphologies that are better adapted than their predecessors. This idea is essentially a more general version of later paleontological ones, such as Van Valen's (1973) Red Queen hypothesis and Vermeij's (1977, 1987) Predator–Prey Escalation hypothesis. However, Darwin himself does not suggest that the parallel improvements would lead to repeated evolution of the same morphologies: indeed, Darwin confesses that he knows of no way to test this idea! The idea of massive parallel evolution in response to similar general selective pressures, as Vermeij and so many others have suggested, apparently did not occur to Darwin.

Paleontologists were well aware of trends in the nineteenth and early twentieth centuries, which led them to posit mechanisms for deriving the same features repeatedly. Cope (1868) presented early definitions of parallelism that are now equated with general homoplasy. Cope focused particularly on the idea that ontogenetic recapitulation causes homoplasy. Scott (1896) and Osborn (1902, 1935) took this a step further by formally defining parallelism as separate achievements of "latent" homologous features. On one hand, this was a recognition and solution to the problem that Amundson (2005) details: Darwin's model explains what happens to variants, but not what causes variation (see G. Wagner, Chapter 8). Such models, coupled with natural selection, offered the predictions Darwin was unable to derive for features, such as escalation over time. However, some researchers in this school allow only that natural selection accounts for differences among closely related lineages (Osborn 1934, 1935). Otherwise, they largely reject natural selection as an important factor in historical trends and instead invoke orthogenetic models to explain paleontological patterns! Recent works by paleontologists on trends theory (hopefully) have much greater utility and generally augment or complement Darwinian ideas well.

Driven Trends

Let us assume that similar selective forces on closely related species could fix parallel morphological change. Natural selection now offers a mechanism for driven trends (McShea 1994), that is, frequent parallel changes across a phylogeny. It bears noting that driven trends do not necessarily demonstrate selection; for example, driven trends toward decreasing complexity might indicate that transitions from complex to simple character states are easier (and thus more probable) than simple to complex transitions (Strathmann 1978). However, in most cases, similar selective forces represent a good explanation for paleontological trends. Corollary predictions of driven trends include: (1) active displacement of distributions over time, with ancestral regions of morphospace becoming vacant (e.g., loss of minimum sizes; Jablonski 1997) and (2) parallel patterns of skewness in distributions for single characters among subclades of a larger clade (McShea 1994; Wang 2001). Indeed, discredited mechanisms, such as orthogenesis, would generate driven trends if they existed. However, in most cases, similar selective forces represent a good explanation for driven trends.

Numerous paleontological studies document driven trends (Table 17.4). Sophisticated likelihood methods sometimes can identify driven trends with only extant taxa (Hibbet 2006). However, fossil data usually are crucial for easily identifying driven trends. In part, this finding reflects the fact that historical data improve ancestral reconstructions in general (Donoghue et al. 1989; Huelsenbeck 1991). Historical data simply become even more important when driven trends are pervasive (Cunningham 1999). For example, Finarelli and Flynn (2006) show that modern carnivores alone imply larger common ancestors than do modern + fossil carnivores, as methods confound parallel increases in body size for ancestral conditions. Thus, this arena is one in which paleontological data are the most useful for testing hypotheses stemming from Darwin's model, even if Darwin himself did not devise these hypotheses.

Trends as Artifacts

Frequently investigators use the word "trend" simply to describe directionality in distributions without satisfying the criteria listed above. Constraints become important here. Stanley (1973) notes that the classic explanation for increasing body size within clades (termed "Cope's Rule," after Cope 1887) might not be necessary, because clades, such as mammals, begin at small body size and can get much larger but not much smaller, a simple increase in variance will increase the proportion of large animals. Complexity offers a similar example (McShea 1994, 2005) in that organisms cannot have fewer than zero or one parts, but there often is no obvious upper limit on the number of parts. Passive trends (Fisher 1986; Gould 1988) of this sort exist in many systems (McShea 1994; Marcot and McShea 2007; Novack-Gottshall 2008) and augment Darwin's ideas, as they would be expected to exist independently of selection. However, Gould (1988) correctly stresses

TABLE 17.4 CLADES SHOWING EVIDENCE OF DRIVEN TRENDS

TAXON	TRAIT	STUDY
Metazoans*	Decreased complexity	Marcot and McShea (2007)
Crustacea	Increased complexity	Adamowicz et al. (2008)
Paleozoic brachiopods	Muscle geometry	Carlson (1992)
Devonian shelly invertebrates	Increased defensive features	Signor and Brett (1984)
Early gastropods	Decreased shell sinus	Wagner (1996)
Trochonematoid gastropods	Increased shell ornament	Wagner (2001)
Muricid gastropods	Increased defensive features .	Vermeij and Carlson (2000)
Plesiosaurs	Size, locomotion	O'Keefe and Carrano (2005)
Pterosaurs*	Increased size	Hone and Benton (2007)
Dinosaurs	Hindlimb dimensions	Carrano (2000)
Dinosaurs*	Increased size	Hone et al. (2005); Carrano (2006)
Synapsids	Decreased skull complexity	Sidor (2001)
Synapsids	Decreased jaw complexity	Sidor (2003)
Mammals*	Increased size	Alroy (1998)
Horses*	Increased size	MacFadden (1986)
Carnivores*	Increased size	Finarelli (2008)

*Denotes studies for which some subclades either showed contrary trends or no trends at all.

that passive trends must be rejected before invoking selective scenarios. McShea (1994) and others (Wagner 1996; Alroy 2000; Wang 2001) put forward several tests for distinguishing passive and driven or active trends based on skewness and related aspects of distributions.

Phylogenetic autocorrelation also can create trends in morphospace. In an early simulation study, Raup and Gould (1974) show that strong clusters in morphospace and temporal shifts in morphospace distributions happen simply because of the chance success and failure of clades. Wagner (1996) reverses Raup and Gould's approach to show that this sort of "phylogenetic hitchhiking" can cause weak but statistically significant active trends without any bias in morphological change. Although this is not a possibility that Darwin considered, it is a necessary corollary to his idea that all taxa are joined by a single phylogeny. Indeed, evolutionary biologists now consider the theoretical removal of phylogenetic autocorrelation to be an important approach to testing hypotheses about adaptations (Felsenstein 1985). Like passive trends, phylogenetic hitchhiking simply augments Darwin's views.

Multimodal Trends

We often describe trends as having single optima. However, there is no reason why this should be true, and it certainly does not follow from Darwin's ideas about natural selection. Although there almost certainly is a

passive component to body-size evolution in mammals (Stanley 1973), Alroy (1998) demonstrates that there is also a driven trend towards increasing size. Moreover, Alroy also shows that there appear to be *two* body size optima for mammals, which results in a so-called hole in mammalian size distributions. More importantly, it also indicates a tendency for overlarge or smallish-medium–sized mammals to show driven trends towards *smaller* rather than larger size. Thus, there are minority trends along the same continuum.

Several other studies extend Alroy's point that trends are not homogeneous within clades. For example, although some metazoan clades show driven trends towards decreasing complexity, most simply exhibit passive trends (Marcot and McShea 2007). For both pterosaurs and carnivores, some subclades ignore general trends in body size (Hone and Benton 2007; Finarelli 2008). Among horses, the trend towards large size does not become prominent until the second half of the clade's history (MacFadden 1986). Findings such as these do not contradict Darwin's model; as previously noted, he did not seem to consider driven trends to be an expectation of selection. Instead, such patterns indicate that selective forces and/or the results of selective forces are not homogeneous across time, space, or phylogeny.

Multivariate trends in morphospace might obfuscate patterns along single axes (Cheetham 1987). Wagner and Erwin (2006) demonstrate that several regions of morphospace for Cambro-Devonian gastropods become occupied many more times than expected, given the changes along the individual characters comprising that morphospace and the assumed underlying phylogenetic topology. Notably, the frequently-evolved regions of morphospace match functional models of optimal ecomorphological types (Linsley 1977, 1978). Similarly, marine invertebrates often show trends towards increased protective morphologies (Vermeij 1977; Signor and Brett 1984; Vermeij and Carlson 2000). However, because some morphological adaptations either preclude the necessity or even feasibility of others, trends along any one possible morphological axis are not as strong as are the general trends in morphospace. These examples broaden traditional definitions of trend, but they still corroborate the idea that general selective forces strongly affect morphological evolution.

Species Selection and Punctuated Change: Threats to the Darwinian Paradigm?

Darwin's model of change is anagenetic, envisioning continuous change within lineages. However, Eldredge and Gould (1972) argued that substantial anagenetic change is rare and that change is both pulsed and between lineages. Following this theme, Stanley (1975) and others (Wright 1967; Eldredge and Gould 1972) present a model of differential diversification based on position in morphospace or other characters. Like a driven trend, this would cause active loss of the ancestral condition but (potentially!)

without frequent parallel changes between ancestors and descendants. Species selection has evolved so that current definitions bear little resemblance to Stanley's original idea (Lieberman and Vrba 2005). However, the idea that major trends reflect differential success of species within clades, rather than the differential survival of individuals within species, begs the question of whether traditional depictions of Darwin's model can explain major evolutionary patterns (Gould 1980, 1985).

In assessing whether species selection *sensu* Stanley occurs, one must understand Stanley's challenge of Darwin's model, which requires detailing the assumptions of Stanley's original idea. The first assumption is that change typically is pulsed rather than continuous. The most detailed and sophisticated meta-analysis of trends within lineages to date (Hunt 2007) shows that only a small proportion of published examples best fit directional change models (Figure 17.7). Instead, the vast majority best fit either random walk models (especially for size) or stasis (especially for shape characters).

A second assumption of Stanley's model involves Wright's Rule: evolution in morphospace follows an unbiased, Brownian motion at the species level (Gould and Eldredge 1977; Wright 1967). Contrary to Stanley's
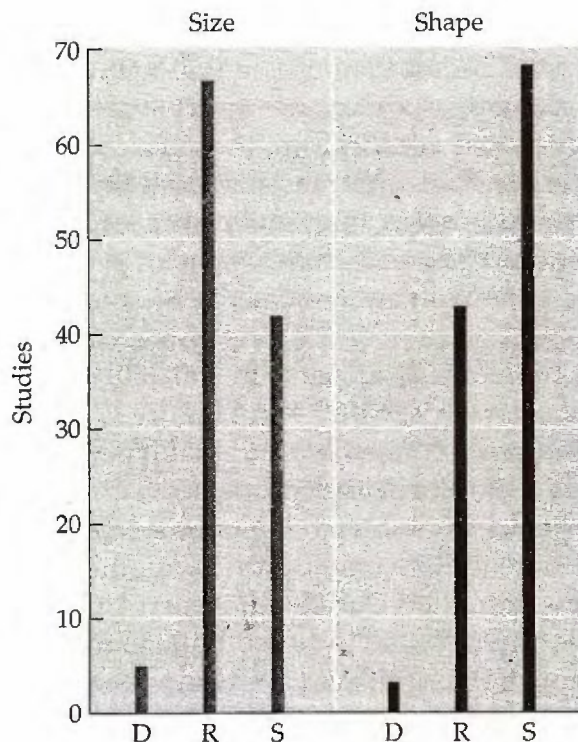

Figure 17.7 Distribution of Most-Likely Models of Character Evolution within Lineages for Size and Shape Characters within Lineages Gould's (2002) definition of stasis includes both random walks and strictly static lineages, but here static lineages show "pull" to a mean morphology, whereas random walks show no demonstrable pull. "D" denotes directional trends, "R," random walks, and "S," static lineages. (Adapted from Hunt 2007: Table 1.)

expectations, clades shown to have driven trends (see Table 17.4) include lineages having random walks and stasis, rather than the individual lineages showing trends. Driven trends also exist in clades for which phylogenetic evidence indicates stasis and pulsed change (Wagner and Erwin 1995). Thus, movement in morphospace can be both punctuated and directional.

A third assumption is that there is too little change within lineages to account for trends. In the same year that Stanley published his model, Lande (1975) made the opposite observation: large scale trends are too *weak* to be products of continuous directional anagenesis. (Haldane (1949) came to a similar conclusion.) Lande estimated that the mortality rates needed for long-term trends in horses amounts to selection culling only one horse in 500,000 per generation. Lande arrived at similar extremely weak selection coefficients for trends in other fossil mammals. Thus, the rare anagenetic trends reported by Hunt (2007) would produce far stronger trends over millions of years than we actually see in the fossil record.

The reconciliation of punctuated equilibrium with natural selection provides explanations for why punctuated change and driven trends are compatible. Ultimately, Gould (2002) favors an extension of Futuyma's (1987) model in which speciation *facilitates* rather than induces change. Here, speciation permits local selective forces to permanently fix novel morphologies that otherwise would be lost to interbreeding with conspecific populations (Lande 1975). Although such ideas clearly are important for reconciling the debate over punctuated equilibrium, they also have two major implications for the question of whether stasis necessitates species selection. First, if some selective forces recur frequently over long periods of time, then even periodic fixation can create driven trends. Second, periodic fixation of change by natural selection in reproductively isolated populations means that the *relevant* selection responsible for, say, increasing body size in horses is much greater than one dead horse in 500,000. These two implications combined with the data in Table 17.4 and Figure 17.7 indicate both that stasis and driven trends are compatible and that it is very possible for natural selection to be the major force underlying pulsed driven trends.

Although stasis does not demand species selection, we cannot dismiss the concept of differential diversification as another major trend that augments rather than contradicts Darwinian theory. Unfortunately, adequately documenting this phenomenon is difficult due to the large amounts of data required to demonstrate significant shifts in speciation and/or extinction rates and because parallel shifts associated with position in morphospace among 2+ subclades are really required to separate Stanley's species selection from classic adaptive radiation models. Liow (2006) demonstrates that deviant trachyleberidid ostracodes have lower extinction rates than do normal trachyleberidids. If origination rates per unit time are the same for deviants and normals, then one would expect the deviants to leave more descendant taxa and thus create trends in trachyleberidid morphospace.

However, Liow (2004) also shows the opposite for crinoids; long-lived genera tend to come from the middle of crinoid morphospace. This presents the intriguing possibility of "stabilizing species selection" (Gilinsky 1981).

Summary

Although workers periodically portray paleontological data as contradicting Darwin's basic ideas, fossil data strongly contradict only the idea that rates of change have been uniform through time. High early disparity in fossil clades and sudden appearances of higher taxa likely do not reflect the imperfections of the geological record. Instead, they probably reflect elevated rates of morphological evolution early in clade histories or following mass extinctions. In some cases, rate shifts apparently reflect changes in intrinsic constraints and thus involve mechanisms that were unknown in Darwin's time. In other cases, they likely reflect changes in ecological restrictions, and thus suggest both that natural selection operates far more quickly than Darwin seems to have supposed and also that selection is a more powerful limiting force than he apparently recognized. Fossil data also provide ample evidence of driven trends or differential acquisition of particular traits, which provide strong evidence of common selective forces frequently affecting related lineages in similar ways. Paleontologists have augmented Darwinian explanations for trends with other ideas that necessarily follow from ideas about constraints (e.g., passive trends) as well as Darwin's basic idea of common ancestry among taxa (i.e., phylogenetic hitchhiking). Ultimately, the most important point to stress is that although fossil data refute Darwin's uniformitarianist notions, these same data build upon, modify, and perhaps even enhance Darwin's most important idea: the importance of natural selection on long-term patterns of morphological evolution.

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