

Figure 7.4 Changes in the number of known (A) families of insects, (B) species of vascular land plants, and (C) families of nonmarine tetrapod vertebrates. (A after Labandeira and Sepkoski 1993; B and C after Benton 1990.)

and of birds and mammals account for dramatic increases in the diversity of vascular plants (Figure 7.4B) and terrestrial vertebrates (Figure 7.4C) after the mid-Cretaceous.

Rates of origination and extinction

Since the Triassic, the rate of origination of marine animal taxa has been greater than the rate of extinction, resulting in the increase in diversity during the Mesozoic and Cenozoic, but both rates have fluctuated throughout Phanerozoic history. The rate of origination of new families was highest early in recorded animal evolution, in the Cambrian and Ordovician, and in the early Triassic, after the great end-Permian extinction (Figure 7.5). Extinction rates have varied dramatically. A distinction is often made between episodes during which exceptionally high numbers of taxa became extinct, the so-called **mass extinctions**, and periods of so-called “normal” or **background extinction** (Figure 7.6). Five mass extinctions are generally recognized: at the end of the Ordovician, in the late Devonian, at the Permian/Triassic (P/Tr) boundary (the end-Permian extinction), at the end of the Triassic, and at the Cretaceous/Tertiary (K/T) boundary (the K/T extinction), but several other episodes of heightened extinction occurred as well.

In both plants and animals, taxa with high rates of origination (speciation) also have high rates of extinction (Niklas et al. 1983; Stanley 1990). That is, they have high rates of **turnover**. For example, both *S* and *E* were higher in ammonoids and trilobites than in gastropods or bivalves. Several possible reasons for this correlation between extinction and origination rates have been suggested (Stanley 1990; see also Chapter 16):

1. *Degree of ecological specialization.* Ecologically specialized species are likely to be more vulnerable than generalized species to changes in their environment (Jackson 1974). They may also be more likely to speciate be-

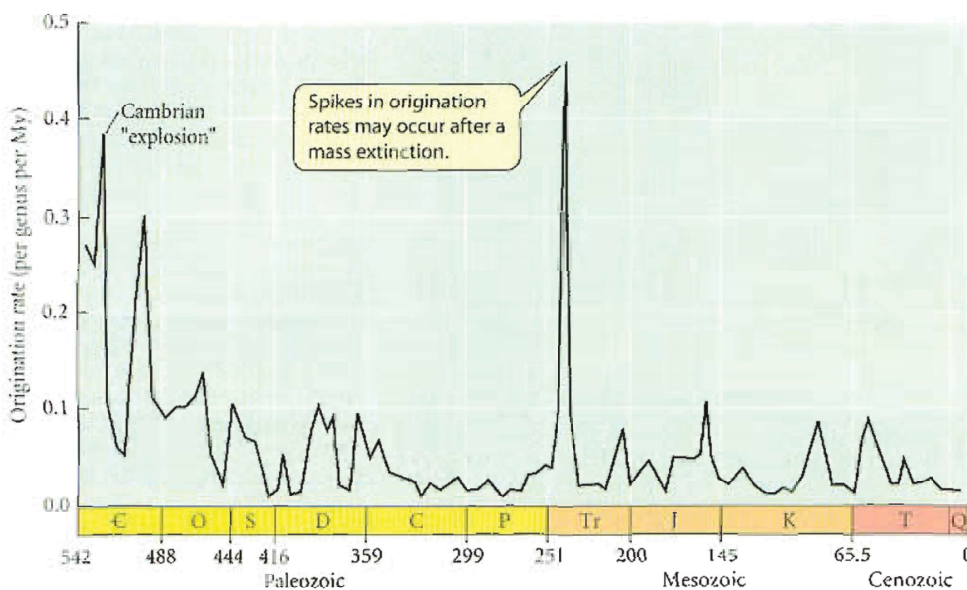


Figure 7.5 Rates of origination of marine animal genera in 107 stages of the Phanerozoic, expressed as the number of new genera per capita per million years. Only taxa that cross boundaries between stages are counted. (After Foote 2000a.)

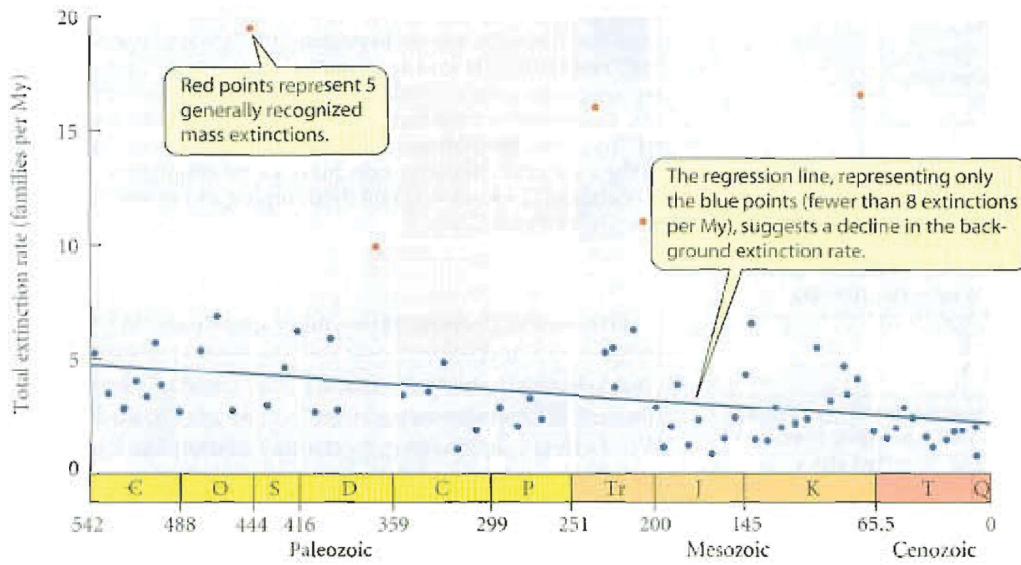


Figure 7.6 Extinction rates of marine animal families during the Phanerozoic, expressed as the number of families per million years. The solid regression line fits the blue points, which represent fewer than 8 extinctions per million years. The red points, which deviate significantly from the background cluster, mark the five major mass extinction events at the ends of the (1) Ordovician, (2) Devonian, (3) Permian (the end-Permian event), (4) Triassic, and (5) Cretaceous (the K/T extinction). (After Raup and Sepkoski 1982.)

cause of their more patchy distribution, and newly formed species may be more likely to persist by specializing on different resources and thus avoiding competition with other species.

2. *Population dynamics.* Species with low or fluctuating population sizes are especially susceptible to extinction. Some authors believe that speciation is also enhanced by small or fluctuating population sizes, although this hypothesis is controversial.
3. *Geographic range.* Species with broad geographic ranges tend to have a lower risk of extinction because they are not extinguished by local environmental changes. They also have lower rates of speciation (Jablonski and Roy 2003), probably because they have a high capacity for dispersal.

Taxa whose component species have high rates of origination and extinction are quite “volatile,” fluctuating greatly in diversity—and are prone to extinction. The early extinction of many such groups may contribute to an observation that has not been fully explained: a long-term decline in origination and extinction rates throughout the Phanerozoic (Foote 2000b; see Figures 7.5 and 7.6).

Origination and extinction rates are one source of evidence that interactions among species have tended to stabilize diversity. Mike Foote (2000b) examined changes in marine animal diversity within each of 107 stages of the Phanerozoic record in relation to the change in per capita rates of origination (*S*) and extinction (*E*) from one stage to the next. He found that diversity increased more when *S* increased, and decreased more when *E* increased. More interestingly, extinction had a stronger effect on changes in diversity than did origination during the Paleozoic, but origination had a stronger effect during the Mesozoic and Cenozoic.

Foote then examined the correlation between the diversity at the start of each time interval and the change in the origination and extinction rates between that interval and the previous one. If changes in these rates were diversity-dependent, one would expect diversity to be negatively correlated with origination rate and positively correlated with extinction rate. The expected relationships were found, strongly supporting the hypothesis that diversity-dependent factors, such as competition among species, tend to stabilize diversity around an equilibrium (Figure 7.7).

In the same vein, Sepkoski (1984) statistically distinguished three major, taxonomically different “evolutionary faunas” that dominated the seas during the Phanerozoic (Figure 7.8). By modeling competition among these faunas as if they were three species populations, he found that the rise and fall of family diversity in each of the three faunas could be explained by diversity-dependent competition.

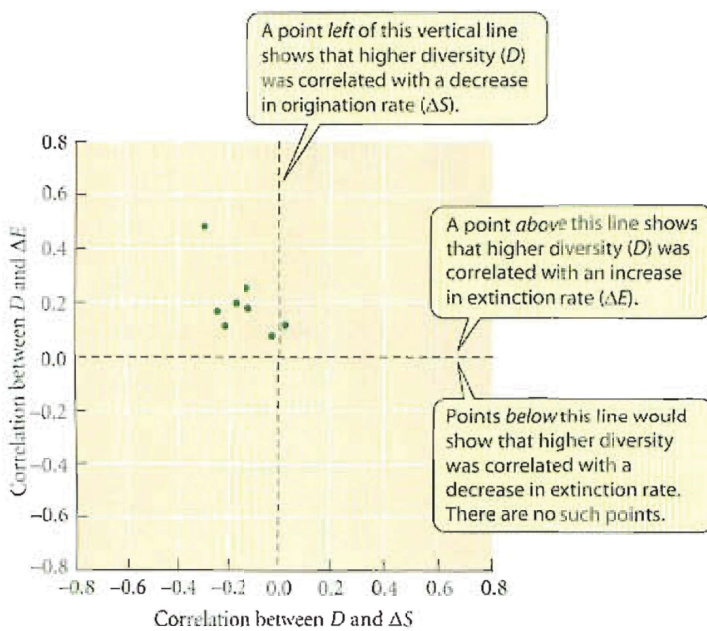


Figure 7.7 The correlation between diversity (D) in a geological stage and changes in origination (ΔS) and extinction (ΔE) rates from the mid-Jurassic to the Cenozoic. Each point represents two correlations, each of which may be either positive (a “direct” correlation, > 0) or negative (an “inverse” correlation, < 0). High diversity was associated with an increase in the extinction rate and a decrease in the origination rate—evidence of diversity-dependent damping of growth in diversity. (After Foote 2000b.)

These observations raise many questions: Why might origination and extinction rates decline over time? How could diversity increase steadily after the end-Permian extinction if diversity-dependent factors tend to stabilize it? What effects did mass extinctions have on the history of life? A closer look at extinction and origination may help to answer these questions.

Causes of extinction

Extinction has been the fate of almost all the species that have ever lived, but little is known of its specific causes. Biologists agree that extinction is caused by failure to adapt

to changes in the environment. Ecological studies of contemporary populations and species point to habitat destruction as the most frequent cause of extinction by far, and some cases of extinction due to introduced predators, diseases, and competitors have been documented (Lawton and May 1995).

When a species’ environment deteriorates, some populations may become extinct, and the geographic range of the species contracts, unless formerly unsuitable sites become suitable for colonists to establish new populations. If environmental changes cause populations to decline, the survival of those populations—and perhaps of the entire species—depends on adaptive genetic change. Whether or not this suffices to prevent extinction depends on how rapidly the environment (and hence the optimum phenotype) changes relative to the rate at which a character evolves. The rate of evolution may depend on the rate at which mutation supplies genetic variation and on population size, because smaller populations experience fewer mutations. Thus an environmental change that reduces population size also reduces the chance of adapting to it (Lynch and Lande 1993). Because a change in one environmental factor, such as temperature, may bring about changes in other factors, such as the species composition of a community, the survival of a species may require evolutionary change in several or many features.

Both abiotic and biotic changes have doubtless caused extinction. For example, during the Pliocene, the rate of extinction of bivalves and gastropods increased, chiefly in northern seas. This increase coincided with a decrease in temperature, a likely cause of the extinctions (Sepkoski 1996b). We will discuss the role of competition in extinction later in this chapter.

Declining extinction rates

It would seem reasonable to expect lineages of organisms to become more resistant to extinction over the course of time as they become better adapted. Evolutionary theory does not necessarily predict this, however, because natural selection, having no foresight, cannot prepare species for changes in the environment. If the environmental changes that threaten extinction are numerous in kind, we should not expect much carryover of “extinction resistance” from one change to the next. Consequently, we should expect that at any time t , the probability of extinction of a species (or higher taxon) would be the same, whether it is old (i.e., arose long before time t) or young (i.e., arose shortly before time t).

Extinctions of taxa in the fossil record can be analyzed by plotting the fraction that survive for different lengths of time (i.e., their age at extinction). If the probability of extinc-

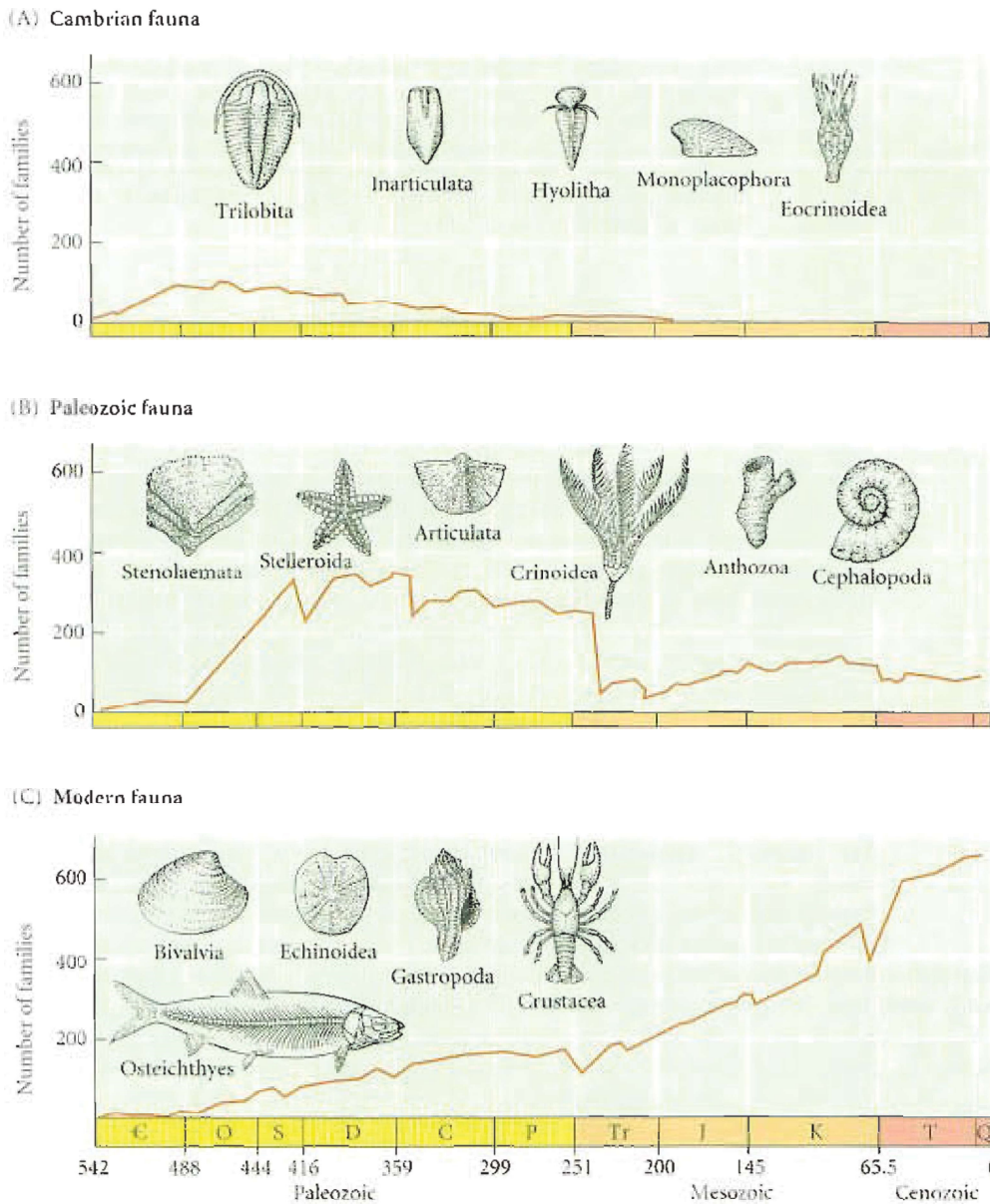


Figure 7.8 The history of diversity of the three “evolutionary faunas” in the marine fossil record, with illustrations of major forms. (The three diversity profiles add up to yield the overall diversity profile of Figure 7.3A.) (After Sepkoski 1984.)

tion is independent of age, the proportion of taxa surviving to increasingly greater ages should decline exponentially (just like the proportion of “surviving” parent atoms in radioactive decay; see Figure 4.2). Plotted logarithmically, the curve would become a straight line. If taxa evolve increasing resistance to causes of extinction as they age, the logarithmic plot should be concave upward, with a long tail (Figure 7.9A).

When Leigh Van Valen (1973) analyzed taxon survivorship in this way, he obtained rather straight curves, suggesting that the probability of extinction is roughly constant (Figure 7.9B). This is what we would expect if organisms are continually assaulted by new environmental changes, each carrying a risk of extinction. One possibility, Van Valen suggested, is that the environment of a taxon is continually deteriorating because of the evolution of other taxa. He proposed the **Red Queen hypothesis**, which states that, like the Red Queen in Lewis Carroll’s *Through the Looking-Glass*, each species has to run (i.e., evolve) as fast as possible just to stay in the same place (i.e., survive), because its competitors, predators, and parasites also continue to evolve. There is always a roughly constant chance that it will fail to do so.

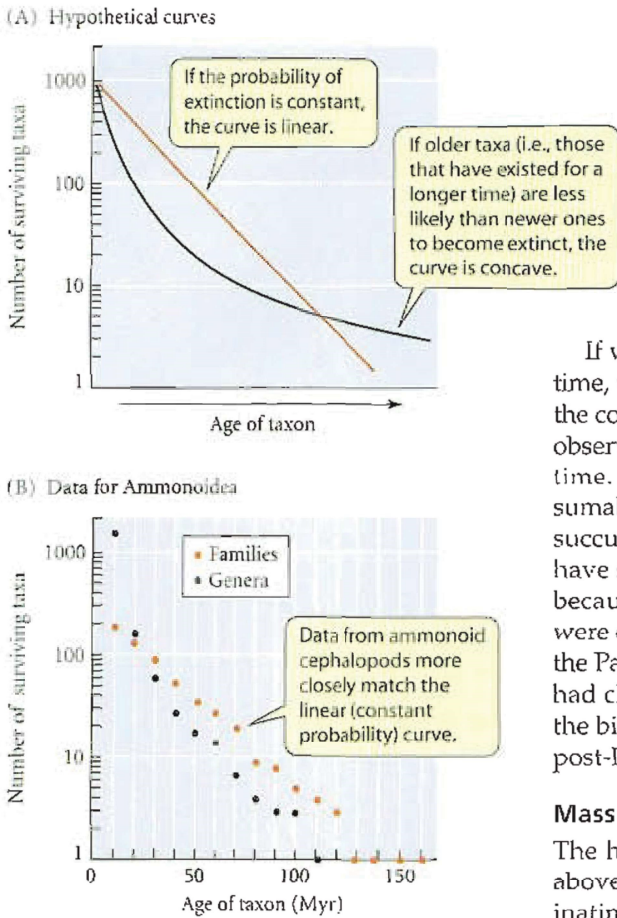


Figure 7.9 Taxonomic survivorship curves. Each curve or series of points represents the number of taxa that persisted in the fossil record for a given duration, irrespective of when they originated during geological time. (A) Hypothetical survivorship curves. In a semilogarithmic plot, the curve is linear if the probability of extinction is constant. It is concave if the probability of extinction declines as a taxon ages, as it might if adaptation lowered the long-term probability of extinction. (B) Taxonomic survivorship curves for families and genera of ammonoids. (B after Van Valen 1973.)

If we do not expect resistance to extinction to evolve progressively over time, what might explain the decline in the rate of background extinction over the course of the Phanerozoic (see Figure 7.6)? One hypothesis is based on the observation that the average number of species per family has increased over time. This increase would lower the extinction rate because it would presumably take longer for all the species of a large family than a small family to succumb to extinction (Flessa and Jablonski 1985). Another possibility, as we have seen, is that higher taxa that are intrinsically more prone to extinction because of their characteristic features (such as dispersal ability or habitat) were eliminated early in the Phanerozoic. Most of the groups that dominated the Paleozoic fauna, such as crinoids (sea lilies) and brachiopods (lamp shells), had characteristically high rates of extinction and turnover compared with the bivalves (clams), gastropods (snails), and other taxa that dominated the post-Paleozoic (Erwin et al. 1987).

Mass extinctions

The history of extinction is dominated by the five mass extinctions listed above. The end-Permian extinction was the most drastic (Figure 7.10), eliminating about 54 percent of marine families, 84 percent of genera, and 80–90 percent of species (Erwin 1993). On land, major changes in plant assemblages occurred, several orders of insects became extinct, and the dominant amphibians and therapsids were replaced by new groups of therapsids (including the ancestors of mammals) and diapsids (including the ancestors of dinosaurs). The second most severe mass extinction, in terms of the proportion of taxa affected, occurred at the end of the Ordovician. Less severe, but much more famous, was the K/T, or end-Cretaceous, extinction, which marked the demise of many marine and terrestrial plants and animals, including the dinosaurs (except for birds).

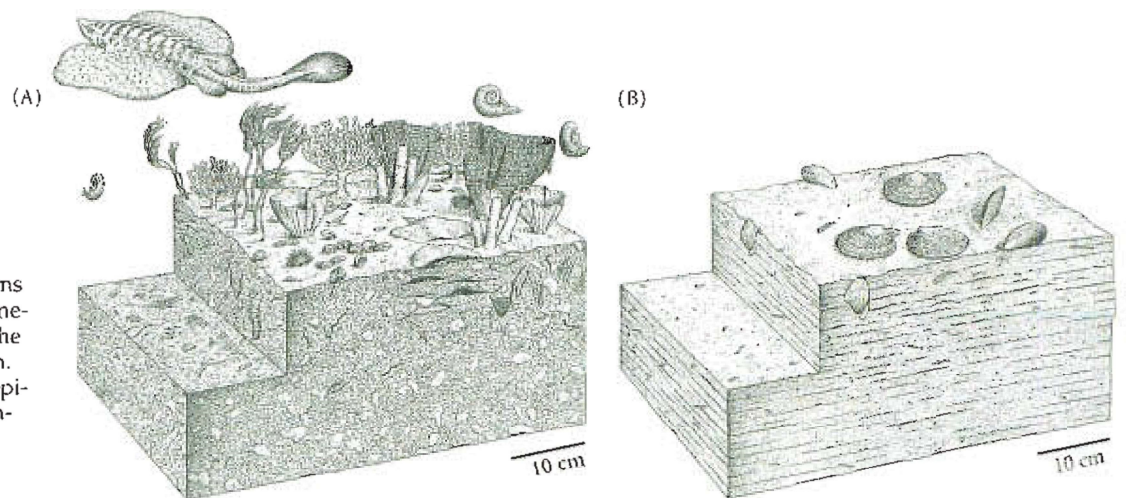


Figure 7.10 Reconstructions of an ancient seabed (A) immediately before and (B) after the end-Permian mass extinction. A rich fauna of burrowing, epifaunal, and swimming organisms was almost completely extinguished. (Artwork © J. Sibbick.)

CAUSES OF MASS EXTINCTIONS. The K/T extinction is famous because of the truly dramatic hypothesis, first suggested by Walter Alvarez and his colleagues (1980), that the dinosaurs were extinguished by the impact of an extraterrestrial body—an asteroid or large meteorite. Alvarez et al. postulated that this object struck the Earth with a force great enough to throw a pall of dust into the atmosphere, darkening the sky and lowering temperatures, thus reducing photosynthesis. Geologists now agree that such an impact occurred; its site, the Chicxulub crater, has been discovered off the coast of the Yucatán Peninsula of Mexico. Most paleontologists agree that this impact caused the mass extinction at the K/T boundary, although some argue that extinctions of various taxa were too spread out in time to have all been caused by this catastrophe, and that the impact was only one of several environmental changes that interacted to cause the K/T extinction (MacLeod 1996).

The most drastic mass extinction by far was the end-Permian extinction. Many possible causes have been suggested. Recently, the hypothesis that massive volcanic eruption was responsible has become popular (Benton and Twitchett 2003). The end-Permian extinction was almost instantaneous, and it coincides with volcanic eruptions that produced enough lava to cover an area of eastern Russia equivalent to all of Europe (the formation called the Siberian traps). It is postulated that the global warming caused by these eruptions altered oceanic circulation, resulting in almost complete loss of oxygen in the deeper waters. Global warming may also have caused the release of vast quantities of methane, which further enhanced warming in a positive feedback spiral that brought life on Earth “close to complete annihilation 251 Mya” (Benton and Twitchett 2003).

VICTIMS, SURVIVORS, AND CONSEQUENCES. Mass extinctions were “selective” in that some taxa were more likely than others to survive. Survival of gastropods through the end-Permian extinction was greater for species with wide geographic and ecological distributions and for genera consisting of many species (Erwin 1993). Extinction appears to have been random with respect to other characteristics, such as mode of feeding. The pattern of selectivity was much the same as during periods of background extinction, when gastropods and other taxa with broad geographic distributions have had lower rates of extinction than narrowly distributed taxa (Boucot 1975). Patterns of survival through the end-Cretaceous mass extinction, however, differed from those during “normal” times (Jablonski 1995). During times of background extinction, survivorship of late Cretaceous bivalves and gastropods was greater for taxa with planktonic development (larvae dispersed by currents) and for genera consisting of numerous species, especially if those genera had broad geographic ranges. In contrast, during the end-Cretaceous mass extinction, planktonic and nonplanktonic taxa had the same extinction rates, and the survival of genera, although enhanced by broad distribution, was not influenced by their species richness. Thus the characteristics that were correlated with survival seem to have differed from those during “normal” times.

During mass extinction events, taxa with otherwise superb adaptive qualities succumbed because they happened not to have some critical feature that might have saved them from extinction under those circumstances. Evolutionary trends initiated in “normal” times were cut off at an early stage. For example, the ability to drill through bivalve shells and feed on the animals inside evolved in a Triassic gastropod lineage, but was lost when this lineage became extinct in the late Triassic mass extinction (Fürsich and Jablonski 1984). The same feature evolved again 120 My later, in a different lineage that gave rise to diverse oyster drills. A new adaptation that might have led to a major adaptive radiation in the Triassic was strangled in its cradle, so to speak.

Both physical and biotic environmental conditions were probably very different after mass extinctions than before. Perhaps for this reason, many taxa continued to dwindle long after the main extinction events (Jablonski 2002), while others, often members of previously subdominant groups, diversified. Full recovery of diversity took millions of years—as much as 100 million years after the end-Permian disaster.

The mass extinction events, especially the end-Permian and K/T extinctions, had an enormous effect on the subsequent history of life because, to a great extent, they wiped the slate clean. Stephen Jay Gould (1985) suggested, in fact, that there are “tiers” of evo-

lutionary change, each of which must be understood in order to comprehend the full history of evolution. The first tier is microevolutionary change *within populations and species*. The second tier is “species selection,” the *differential proliferation and extinction of species* during “normal” geological times, which affects the relative diversity of lineages with different characteristics (see Chapter 11). The third tier is the *shaping of the biota by mass extinctions*, which can extinguish diverse taxa and reset the stage for new evolutionary radiations, initiating evolutionary histories that are largely decoupled from earlier ones.

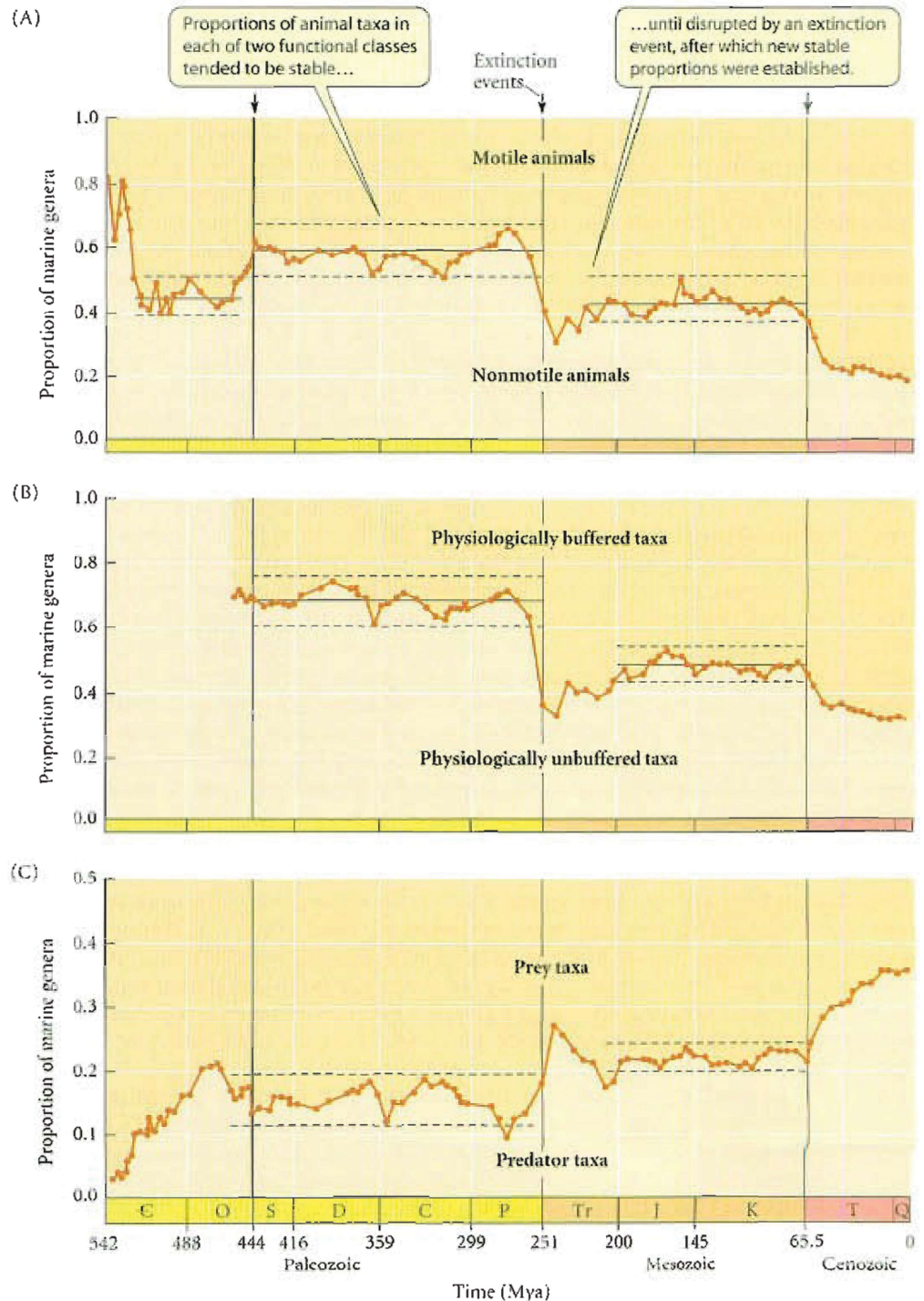


Figure 7.11 Changes in the proportions of marine animal genera classified by three functional criteria during the Phanerozoic. The proportions were roughly stable (dashed lines) between mass extinctions, but changed abruptly to a new stable state after mass extinction events at the end of the Ordovician, Permian, and Cretaceous (black lines). (A) Motile versus nonmotile animals. (B) Physiologically buffered versus unbuffered animals. “Buffered” taxa are those whose physiological systems (e.g., gills and circulatory systems) allow greater homeostatic control. (C) Predators versus nonpredators. (After Bambach et al. 2002.)

The results of a study by Bambach et al. (2002) lent some support to Gould's idea. Bambach and colleagues classified Phanerozoic marine animal genera by three functional criteria: whether they were passive (nonmotile, such as barnacles) or active (motile), whether they were physiologically "buffered" (with well-developed gills and circulatory system, such as crustaceans) or not (such as echinoderms), and whether or not they were predatory. With respect to all three kinds of functional groupings, the proportions of taxa with alternative characteristics remained stable over intervals as long as 200 My, even though the total diversity and the taxonomic composition of the marine fauna changed greatly (Figure 7.11). Shifts from one stable configuration to another are associated with the mass extinctions at the end of the Ordovician, Permian, and Cretaceous, suggesting that the extinction of long-prevalent (incumbent) taxa permitted the emergence of new community structures.

This observation—that extinction of one group permitted the efflorescence of others—describes one of the most important effects of mass extinction events and is a major theme in analyses of origination and diversification.

Origination and diversification

We turn now to the question of why increases in diversity have been greater in some lineages than in others and at some times than at others, and why diversity has tended to increase ever since the end-Permian extinction. Among the major factors that have fostered diversification are release from competition, ecological divergence, coevolution, and provinciality (Signor 1990; Benton 1990).

RELEASE FROM COMPETITION. Studies of both living and extinct organisms have shown that lineages often have diversified most rapidly when presented with ecological opportunity: what is often called "ecological space" or "vacant niches" not occupied by other species. In many isolated islands and bodies of water, descendants of just a few original colonizing species have diversified and filled ecological niches that are occupied in other places by unrelated organisms. Such adaptive radiations include the cichlid fishes in the Great Lakes of eastern Africa, the honeycreepers in the Hawaiian Islands, and Darwin's finches in the Galápagos Islands (see Figure 3.22). Islands and other habitats with taxonomically depauperate biotas typically harbor organisms that have evolved unusual new ways of life. For example, the larvae of almost all moths and butterflies are herbivorous, but in the Hawaiian Islands, the larvae of the moth genus *Eupithecia* are specialized for predation (Figure 7.12; Montgomery 1982). Probably such unusual forms are more prevalent where species diversity is reduced because they are not faced with as many predators or superior competitors in their early, relatively inefficient, stages of adaptation to new ways of life.

The fossil record provides many instances in which the reduction or extinction of one group of organisms has been followed or accompanied by the proliferation of an ecologically similar group. For example, conifers and other gymnosperms declined as angiosperms (flowering plants) diversified, and mammals radiated after the late Cretaceous extinction of the nonavian dinosaurs.

Several hypotheses can account for these patterns (Benton 1996; Sepkoski 1996a). Two of these hypotheses involve competition between species in the two clades. On one hand, the later group may have *caused* the extinction of the earlier group



Figure 7.12 A predatory moth caterpillar (*Eupithecia*) in the Hawaiian islands, holding a *Drosophila* that it has captured with its unusually long legs. Predatory behavior is extremely unusual in the order Lepidoptera. (Photo by W. P. Mull, courtesy of W. P. Mull and S. L. Montgomery.)