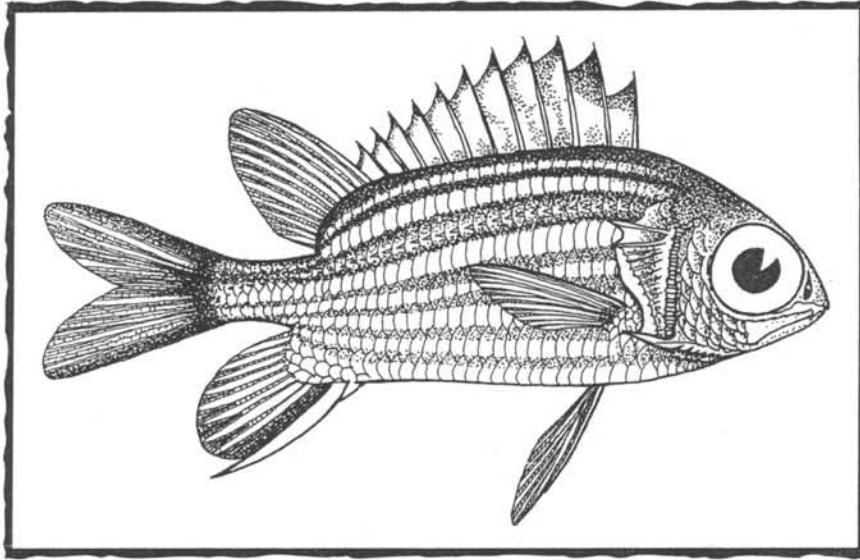


## ADAPTIVE RADIATION



The soldier fish (*Holocentrus rubrum*), a species from Indo-Pacific Oceans that colonized the Mediterranean Sea after construction of the Suez Canal was completed in 1869. (Illustration by Stephen Price)

- 8.1 Adaptive Radiation and Progressive Occupation
- 8.2 Generalizations
- 8.3 Examples of Radiations from the Fossil Record
- 8.4 Are Radiations Predictable?

- 8.5 Types of Adaptive Radiation
- 8.6 Beyond the Adaptive Model of Radiation
- 8.7 Sources of Radiation in Dominant Groups
- Summary

## 8.1 ADAPTIVE RADIATION AND PROGRESSIVE OCCUPATION

Mayr (1963, 663) defined **adaptive radiation** as "evolutionary divergence of members of a single phyletic line into a series of rather different niches or adaptive zones." An adaptive zone is simply a set of similar ecological niches (Futuyma 1986). Earlier, Simpson (1953, 223) had made an admittedly vague distinction between adaptive radiation and **progressive occupation**:

So far as adaptive radiation can be distinguished from progressive occupation of numerous [adaptive] zones, a phenomenon with which it intergrades, the distinction is that adaptive radiation strictly speaking refers to more or less simultaneous divergence of numerous lines all from much the same ancestral adaptive type in different, also diverging adaptive zones [Figure 8-1]. Progressive occupation of such zones is not simultaneous and usually involves in any one period of time the change of only one or a few lines from one zone to another, with each transition involving a distinctly different ancestral type. Theoretically, at least, the whole of the diversity of life is

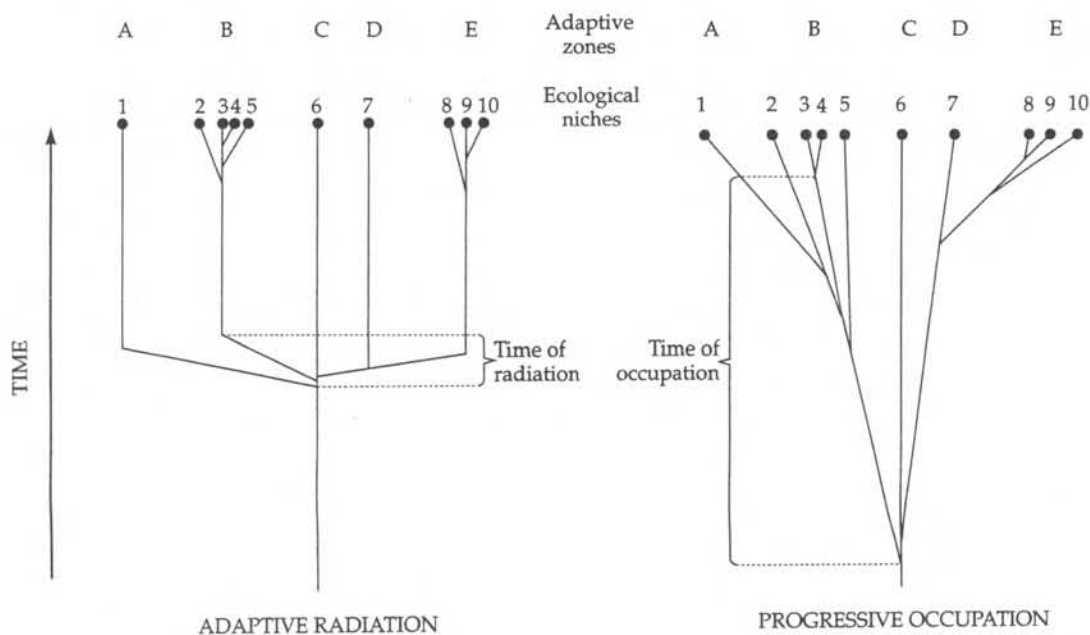
explicable by these two not sharply distinct processes plus the factor of geographic isolation which may permit essential duplication of adaptive types by different organisms in different regions.

Therefore, after speciation, the processes of adaptive radiation and progressive occupation are fundamental to our understanding of the increase in organismal diversity and are central to our knowledge of the mechanisms resulting in the richness of life on earth.

Simpson was right in asserting that adaptive radiation and progressive occupation are not clearly distinct processes. In fact, they result largely from scientists' attempts to pigeonhole parts of nature's continuum of change. On what scale do we measure "more or less simultaneous divergence"? Does progressive occupation in real time come to look like adaptive radiation when we collapse the record into geological strata? Questions of rapid or slow rates of change are always debated (as Chapter 18 will discuss). In this chapter, then, while we concentrate on the more celebrated cases of adaptive radiation, keep in mind that similar processes on the continuum from adaptive radiation to progressive occupation have resulted in the rich species assemblages around

FIGURE 8-1

The concepts of adaptive radiation and progressive occupation, representing the extremes of a continuum of patterns occurring in nature. Both processes can result in the same ultimate diversity—in this example, ten species in five adaptive zones—but in adaptive radiation from a recent common ancestor, evolution into these zones is rapid, whereas in progressive occupation with common ancestors much more distant in the phylogeny, evolution into the zones is gradual. Adaptive zones may represent major differences in food resources, such as nectar, seeds, fruits, and insects for birds. The ecological niches occupied by single species may subdivide an adaptive zone on the basis of food size (such as large, medium, or small seeds), accessibility (such as insects under bark, on leaves, or flying), food location (such as seeds on plants versus seeds on the ground), or combinations of these.



this globe. In addition, although studies of archipelagoes have dominated the literature on adaptive radiation, much more diversification of life has occurred on mainlands and continental shelves, albeit with some habitats distributed in island-like patches.

## 8.2 GENERALIZATIONS

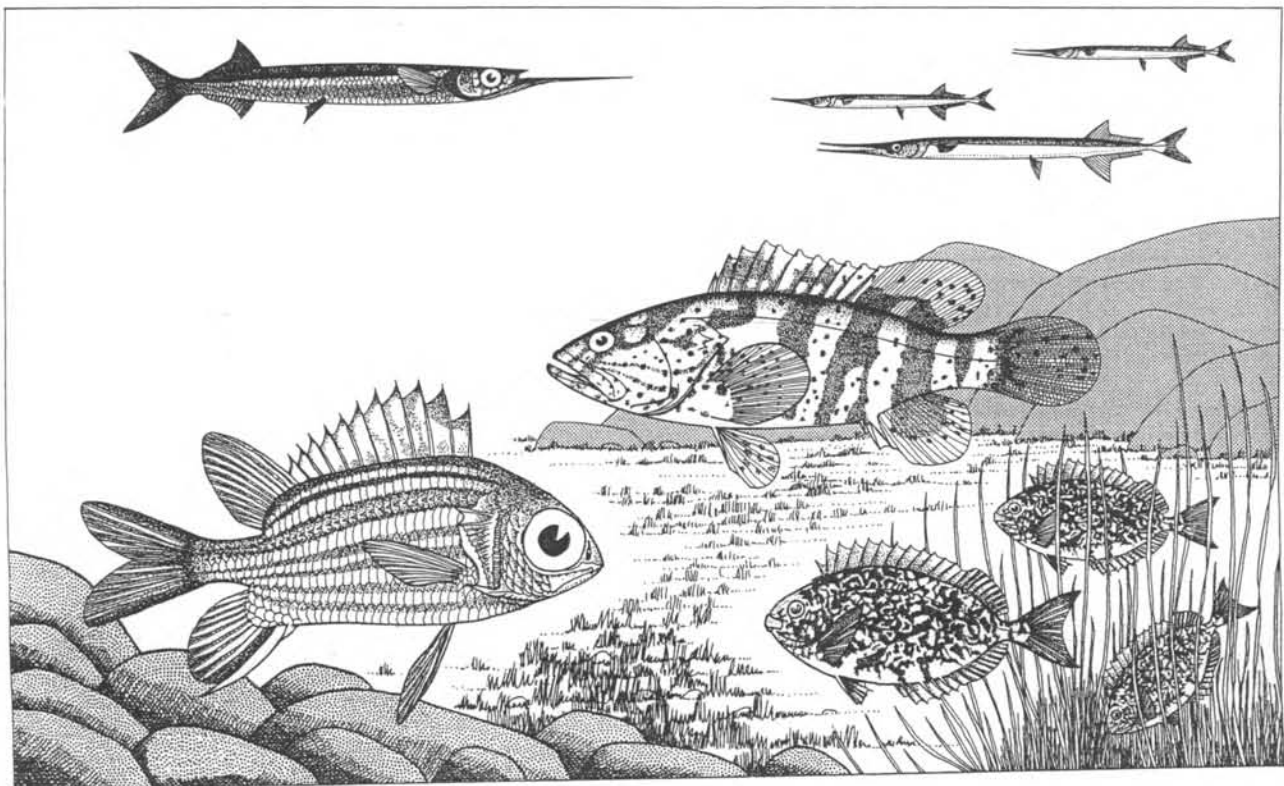
By 1963 Mayr could present a general consensus on aspects of adaptive radiation:

1. A shift into a new ecological niche is most likely at the edge of the species range because of the increased chances of genetic reconstruction in peripheral populations. Also, in these suboptimal habitats, a shift in ecology may match the needs of new genotypes better than those of old ones.
2. Lack of competitors facilitates adaptive radiation. A population finds it difficult or impossible to enter a new niche if that niche is already occupied

by another species. Even on continents and in seas, however, there is evidence of vacant niches in rich biotas. The impressive success of transfers of animals and plants affirms this point (Elton 1958, Drake et al. 1989). The destruction of faunal barriers also indicates the presence of empty niches. After the Suez Canal was opened in 1869, Red Sea fish species colonized the Mediterranean, and some became abundant—presumably filling vacant niches, because decreases in abundance of Mediterranean species were not evident. No Mediterranean fish colonized the Red Sea (Kosswig 1950). By 1971, the number of fish species along the Mediterranean coast of Israel that were derived from Red Sea species had increased to 30, or 10.6 percent of the fauna (Ben-Tuvia 1971) (Figure 8-2). For radiations to be extensive, then, it appears that not only must empty niches be available, but extensive sets of adaptive zones must be free for colonization.

FIGURE 8-2

Some fish species that have invaded the Mediterranean Sea from the Red Sea via the Suez Canal, listed in Ben-Tuvia (1971): *Hemirhamphus far* (top left), *Tylosurus choram* (top right), *Siganus rivulatus* (bottom right), *Holocentrus rubrum* (bottom left), and *Epinephelus tauvina* (background center). What has made these species successful colonizers? Did they occupy vacant niches in the Mediterranean? If so, why did Mediterranean groups not radiate into these niches before the Suez Canal was opened? Is competition really an important force preventing radiation, if so, how many vacant niches persist in communities? (Illustration by Stephen Price)

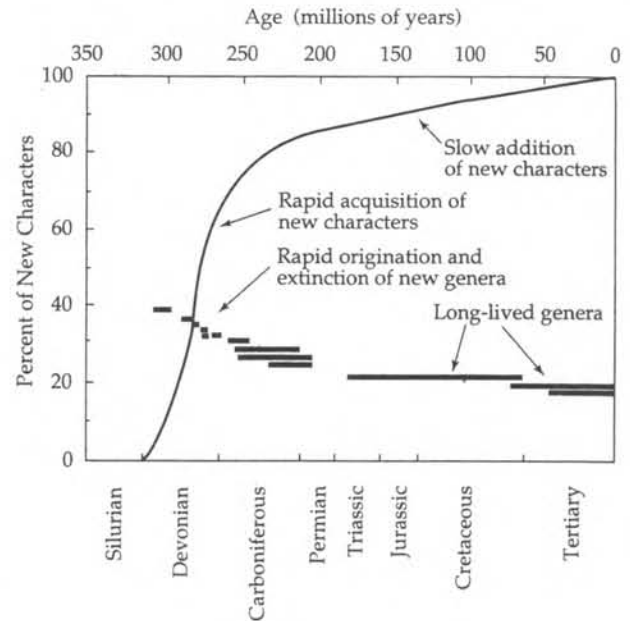


3. Islands provide many empty niches, but continents provide few. Empty niches are particularly numerous on islands with much habitat heterogeneity. The Hawaiian honeycreepers (*Drepanididae*) were early colonists of the Hawaiian Islands and evolved into rather varied adaptive zones that on the mainland would typically have been occupied by finches, honey-eaters, creepers, and woodpeckers (Amadon 1950). Later colonists such as thrushes, flycatchers, and honey-eaters did not radiate to the same extent even though they were preadapted for exploiting ecological niches occupied by drepaniids—presumably because of competitive exclusion in evolutionary time. Mayr noted that insects on the Hawaiian Islands have patterns similar to those of the drepaniids (Zimmerman 1948), as do Darwin's finches on the Galapagos Islands (Lack 1947).
4. Predators may prevent radiation; specifically, they may prevent colonization of empty niches by maladapted colonists. The frequency of successful shifts into radically new niches on oceanic archipelagoes (such as the Galapagos and the Hawaiian Islands) in the absence of predators supports this generalization.
5. The occupation of a new adaptive zone, which Mayr (1963, 617) considered to be a "break-through," is followed by two events. (A) The rate of evolution and speciation increases radically, and a period of adaptive radiation, which in retrospect appears to be synchronous, ensues. (B) Some major types develop, many minor evolutionary pathways are exploited. Examples of event A include the evolution of bats (*Chiroptera*) in the Paleocene, but the first fossils were basically modern-style bats. Also, the lungfishes in the middle and late Devonian evolved more than twice as much in about 30 million years as they did in the following 250 million years (Westoll 1949) (Figure 8-3). About 75 percent of new characteristics in the lungfishes had been expressed by the end of the Devonian, and only about 20 percent of new characteristics have evolved in the last 250 million years. Tertiary birds are all of modern lineages, and so most of their radiation must have taken place in the late Jurassic to early Cretaceous.
6. Speciation and opportunities for adaptive radiation define the size of taxonomic categories.

If a group speciates actively . . . , without much adaptive radiation, it will have many species per genus. If a group radiates actively . . . without much speciation, it will develop many monotypic genera and even families. The independence of these two processes is the main reason for the so-called "hollow curve" of taxonomists. (Mayr 1963, 619)

FIGURE 8-3

The rate of change in characteristics of lungfishes, and the rate of change in genera from the early Devonian to the present. Note the rapid origination and extinction of new genera (bars indicate the time ranges of main genera) that accompanied the rapid acquisition of new characteristics (sigmoid curve) from 300 to 280 million years ago, followed by 250 million years of long-lived genera and the development of relatively few new characteristics. (After Westoll 1949)



If Mayr's analysis is correct, then perhaps we can glimpse the relative contributions of adaptive radiation and progressive occupation. At the left of the hollow curve, much diversification may result from progressive occupation, whereas much of the taxonomic diversity in the right-hand tail of the distribution may be a consequence of adaptive radiation (Figure 8-4). Alternatively, patterns in lineage diversification, if assumed to be generated by chance events of speciation and extinction, would yield similar ranges of taxon size (see Chapter 11, Sections 11.1 and 11.2).

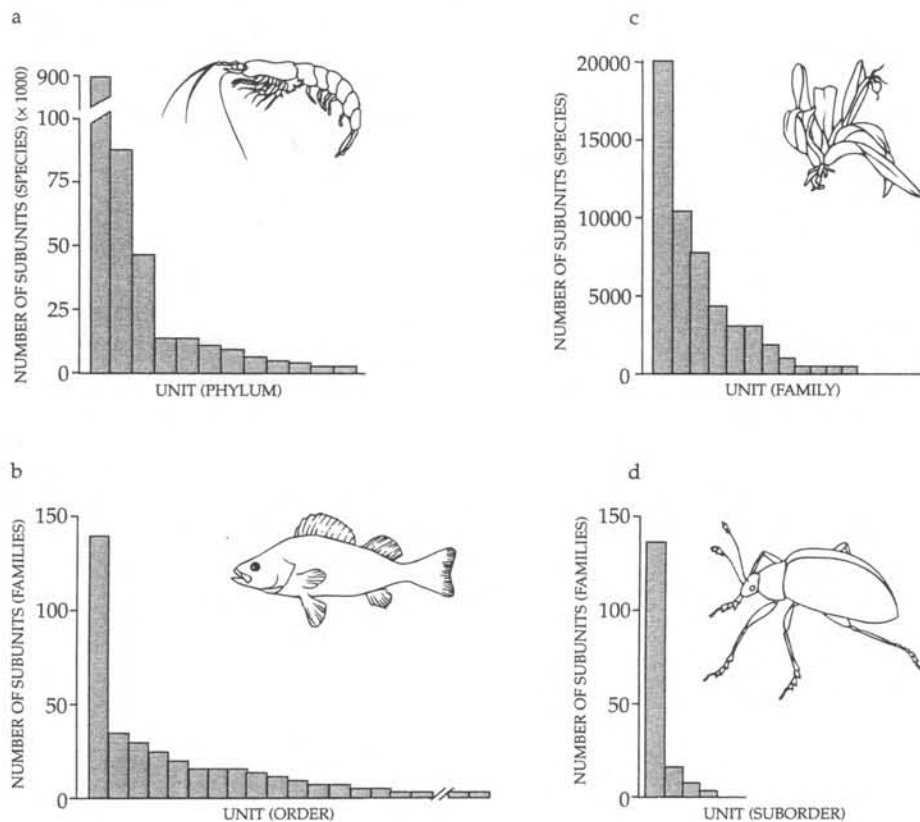
### 8.3 EXAMPLES OF RADIATIONS FROM THE FOSSIL RECORD

#### Ammonite Phylogeny and Radiation

The empirical data from the fossil record certainly support the patterns Mayr (1963) recognized, but whether the mechanisms are essentially correct is

FIGURE 8-4

The commonly observed hollow curve of distribution of lower taxa in a higher taxon. Note that the concave, or hollow, distribution always results from high taxon riches in a small number of the largest groups followed by a rapid decline to more numerous taxa with low taxonomic richness. These examples illustrate the number of species per phylum with the kingdom Animalia (top left), in which the arthropods are the largest taxon; the number of families per order within the fishes (bottom left), in which the perches predominate; the number of species per family within the Monocotyledonae (top right), with orchids as the largest group; and the number of families per suborder within the Australian beetles (bottom right), in which the Polyphaga is the largest group. The organism depicted in each distribution is a member of the largest taxon in the higher taxonomic unit. (From Dial and Marzluff 1989)



open to some debate. Let us explore ammonite phylogeny and radiation (Lehmann 1981) as an example. The ammonites were a group of extremely numerous shelled cephalopod molluscs; Chapter 9 discusses their extinctions. Ammonite shells have fossilized well, leaving a rich record of adaptive radiation and, eventually, complete extinction. The class Cephalopoda is divided into two infraclasses, Ectocochlia and Endocochlia. The subclasses within the Ectocochlia include the following:

*Subclasses:*

1. Nautiloidea
2. Endoceratoidea
3. Actinoceratoidea
4. Bactritoidea
5. Ammonoidea

*Orders:*

- |                    |   |                    |
|--------------------|---|--------------------|
| (a) Anarcestida    | } | "Goniatites"       |
| (b) Clymeniida     |   | "Palaeoammonoidea" |
| (c) Goniatitida    |   |                    |
| (d) Prolecanitida  | } | "Ceratites"        |
| (e) Ceratitida     |   | "Mesoammonoidea"   |
| (f) Phylloceratida | } |                    |
| (g) Lytoceritida   |   | "Ammonites"        |
| (h) Ammonitida     |   | "Neoammonoidea"    |
| (i) Ancyloceratida |   |                    |

The phylogeny of Ammonoidea shows that, during each radiation after a major extinction episode, it was often a new order that radiated from a rather small, unimpressive representation of species in an earlier period (Figure 8-5). In the Devonian, the Goniatitida radiated extensively while the Prolecanitida

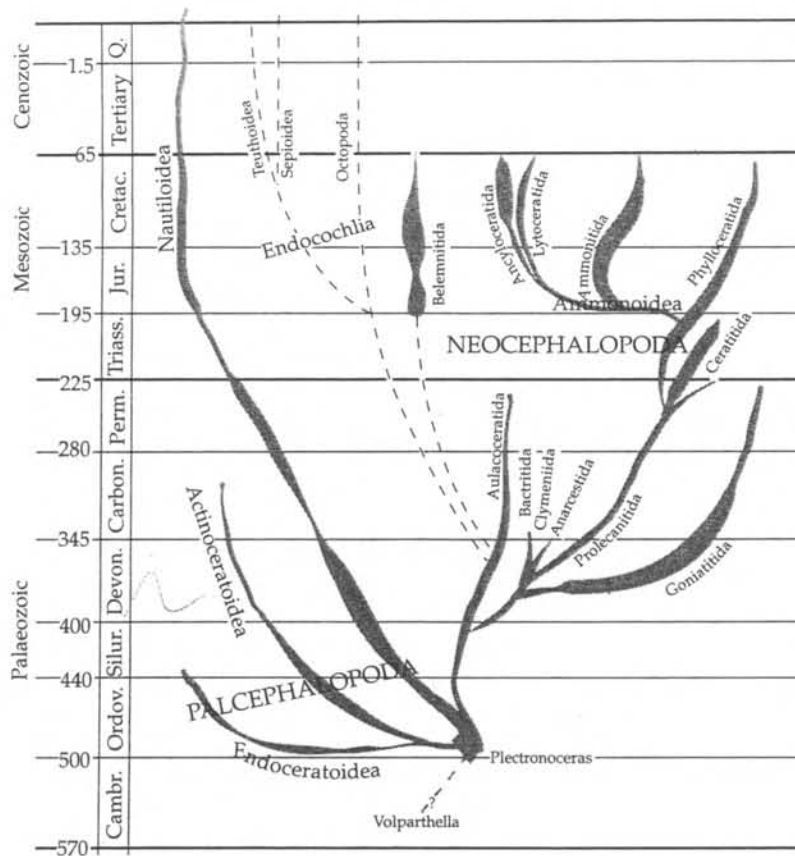


FIGURE 8-5

Adaptive radiation of ammonites, showing successive radiation events from rather unimpressive lineages. The thickness of the line indicates the relative richness of taxa in each lineage through time. Note, for example, that the Goniatitida was the richest taxon in the Devonian, but the comparatively poor relatives in the Prolecanitida provided the stock for major radiations in the Jurassic. (After Lehmann 1981 and Moore 1957)

remained a relatively small group. At the end of the Permian, it was the Prolecanitida that radiated while the Goniatitida went extinct. Then the Ceratitida radiated in the Triassic but went extinct, and another lineage underwent a massive and rapid radiation in the early Jurassic to produce the four orders of the Neoammonitida.

One might easily infer from this pattern that the radiation of one group precludes the radiation of another, just as Mayr explained. Competitive interactions set a carrying capacity on taxa and limit radiations to a small subset of their potential expansions. But this argument is hard to reconcile with the pattern of abundance of ammonoid genera from the Devonian to the Cretaceous (Figure 8-6). There is no sign of any equilibrium number of genera being reached, and about 60-plus genera were extant for continuous periods of millions of years. Thus, the following questions arise. (1) Why did no new radiations occur in the Carboniferous when 30 or fewer genera were present? (2) If 100 genera can be supported for periods of time, why did only one taxon, the Ammonitida, radiate extensively in the early Jurassic, when fewer than ten genera survived the Triassic–Jurassic extinc-

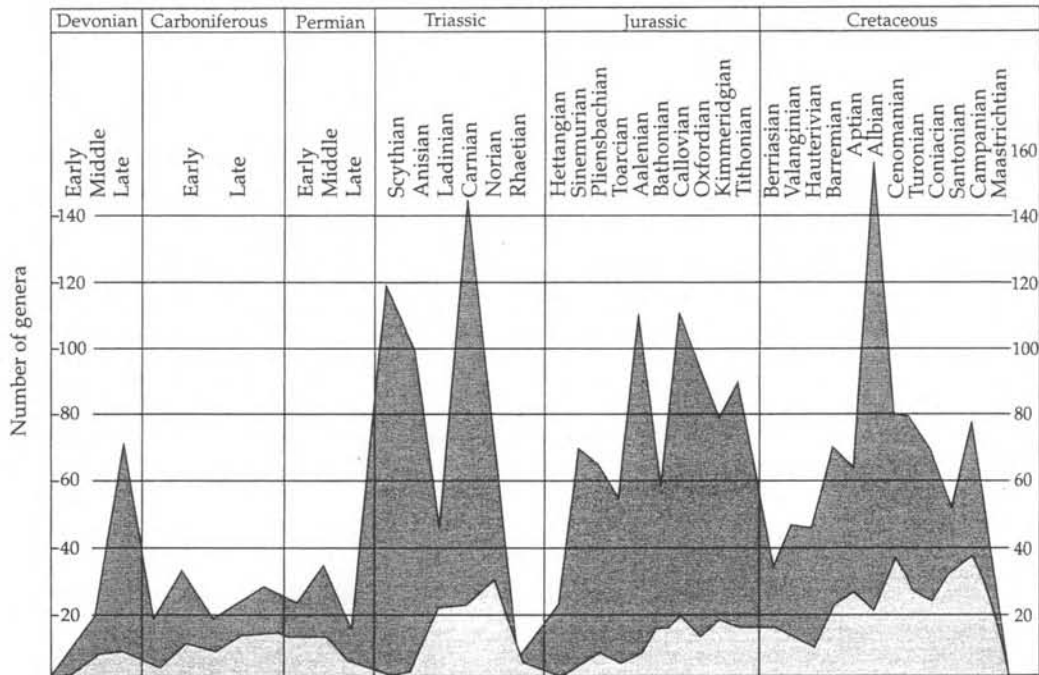
tions? (3) How could the Ammonitida suppress radiation of other groups when diversity of genera was below 100 for most of the Jurassic and yet 140 to 160 genera coexisted at other times? (4) How could new genera reach a peak of almost 160 in the Albian, just when continuous genera were at their maximum of about 35? If one considers only the ammonoids, the evidence for some kind of carrying capacity for genera is not impressive. The record for the ammonoids appears to exhibit a strongly stochastic element involved with radiation and extinction events. Alternatively, we must consider the role of other taxa in competition for habitat and resources, the role of extinction of other groups (Chapter 9), the nature of survival through extinction episodes (Chapter 10), and insights about chance or stochastic events in the fossil record gleaned from models (Chapter 11).

Other patterns in the ammonites agree with Mayr's generalizations.

1. At any one time, a small number of large taxonomic groupings and a large group of smaller taxa are producing the hollow-curve distribution of taxa (Figure 8-5).

FIGURE 8-6

The number of genera of ammonoids through the fossil record. Note that all extant ammonites went extinct at the end of the Cretaceous. Hatching indicates continuous genera, and the more erratic stippling represents the record of new genera. (From Lehmann 1981 and Moore 1957)



- Adaptive radiation was rapid after an extinction episode, as seen in the heteromorph ammonites after the Jurassic–Cretaceous and Albian extinctions (Figure 8-7).
- The opportunities for radiation coincided with the availability of vast new expanses of continental shelf for colonization.

Wiedmann (1973) argued that, as sea level rose and fell, up onto and then off continental shelves, the taxa of ammonites also waxed and waned (Figure 8-8). Deep-water species with smooth shells were largely responsible for maintaining the continuity of the ammonites. When continental shelves became available again, during transgression of seas, species radiated from the deep-basin forms, became progressively more ribbed, and went extinct during the next regression of seas.

**Echinoid Radiation**

Other taxa exhibit patterns similar to those of the ammonites, with large radiations from a single lineage and usually with no obvious superiority over other lineages, which either remain small or go extinct. For example, the echinoids (including sea urchins and sand dollars)

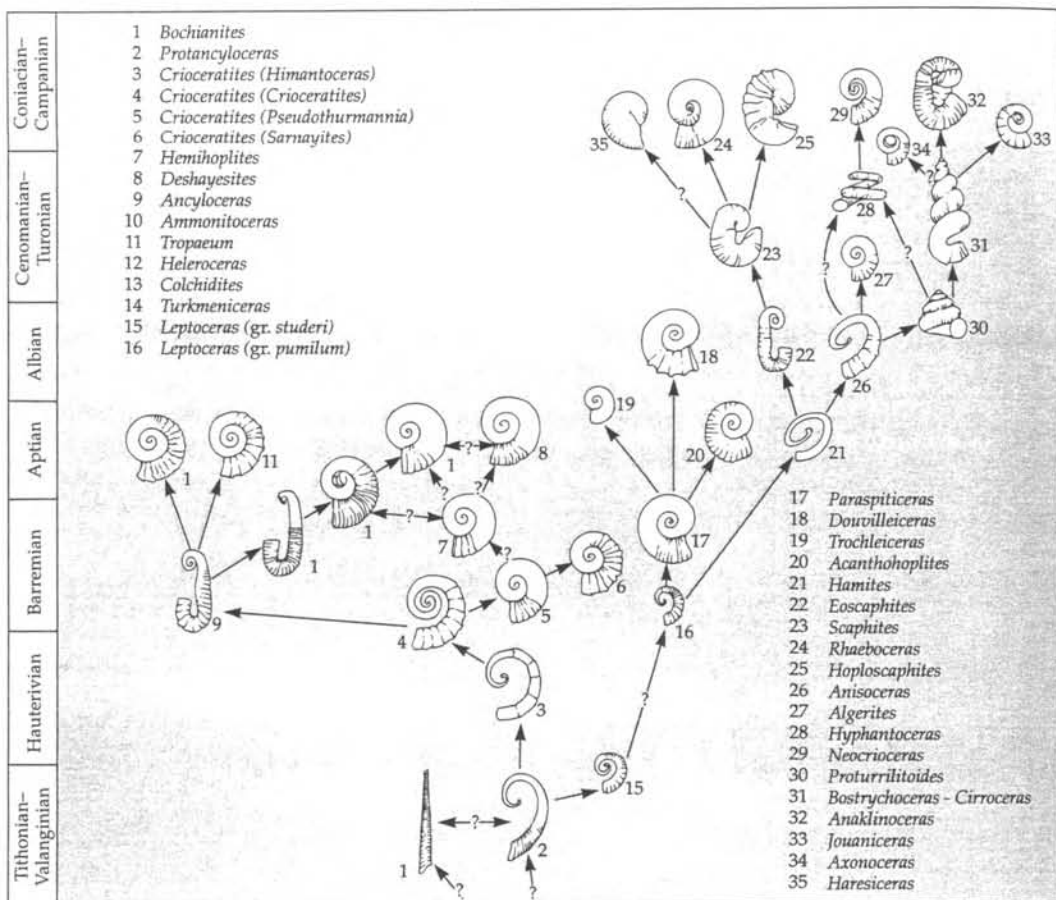
originated in the Ordovician and underwent a small radiation through the Silurian and Devonian, but all except one lineage went extinct by the end of the Permian (Smith 1984) (Figure 8-9). The major echinoid groups radiated rapidly in the Triassic and early Jurassic and have largely persisted into the present with no further radiation equivalent in magnitude to the Triassic–Jurassic radiation. In the echinoids there is an apparent plateau in the number of species per million years; about 900 species are extant (Smith 1984). In total, there have been 124 Paleozoic species, 3,672 Mesozoic species, and 3,250 Cenozoic species. It is interesting to note the relative stability of the echinoids after the Jurassic in contrast with the wide fluctuations of the ammonoids (Figure 8-10).

**Radiation of Brachiopods and Foraminiferans**

The brachiopods, or “lampshells” (like early Roman oil lamps), also exhibit patterns of one lineage radiating while others are almost static (e.g., early Devonian mutationellinid brachiopods; Boucot 1975). Foraminiferans are protozoans, related to the amebas, that secrete a shell-like calcareous test. They have left a

FIGURE 8-7

Rapid adaptive radiation of heteromorph ammonites (those with unconventional coiling) after the extensive extinctions around the Jurassic-Cretaceous boundary. (From Lehmann 1981 and Wiedmann 1969)



very rich fossil record of tests, usually made of calcium carbonate. In the Foraminifera, two genera, *Globigerina* and *Globorotalia*, radiated rapidly into several subgenera in the Late Oligocene and Early Miocene while others, such as *Cassigerinella* and *Globoquadrina* (Figure 8-11), did not radiate at all (Kennett and Srinivasan 1983). The fossil record of these groups reinforces the perception that survival through episodes of extinction and subsequent radiation contain a strong element of either chance or as-yet-undetected governing forces.

#### 8.4 ARE RADIATIONS PREDICTABLE?

Gould (1986) broached the question of whether there is anything predictable in the kinds of taxa that radiate and the kinds that do not. If we rewind the tape of life and played it again, would the results be the same? If they were, we would deduce a strongly de-

terministic evolutionary sequence and would find ourselves in our present shape once again. But what if the replay produced a totally different assemblage? From this result we could assume one of two alternatives to determinism: (1) chaotic evolutionary sequences or lineages, i.e., a random series of radiations and extinctions, or (2) evolutionary sequences that are unpredictable but, in retrospect, rational. Alternative pathways to dominant groups were not clearly inferior to the lineages that radiated. Life could have evolved, at any phase in adaptive radiation, in several alternative directions.

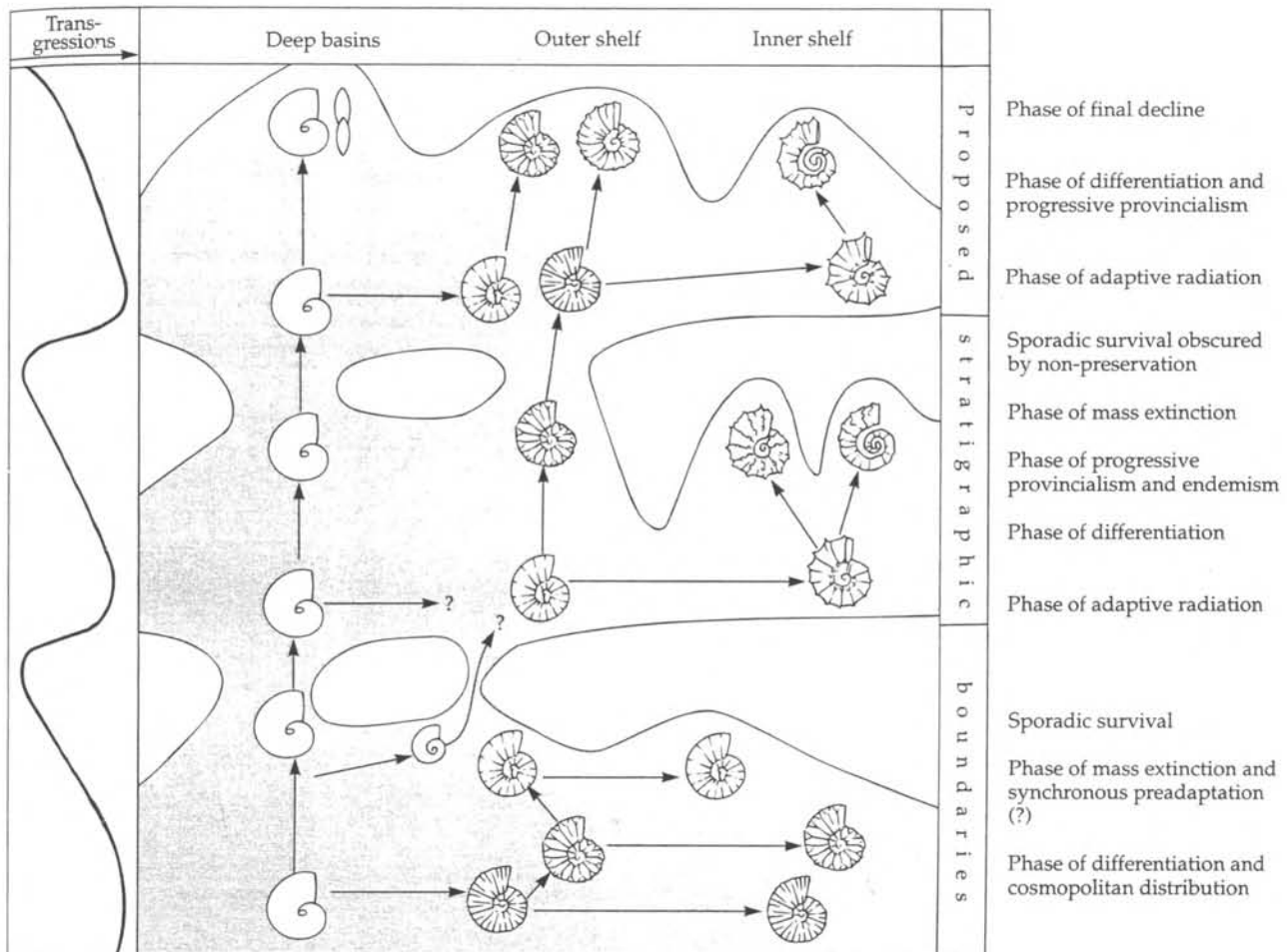
#### The Burgess Shale Fauna: Wiwaxiids and Clams

Gould used three scenarios to support the last-mentioned possibility: unpredictable results with rational explanations. During the great Cambrian explosion of early metazoans more than 500 million years ago,



FIGURE 8-8

The movement of seas over continental shelves (transgressions) and the corresponding adaptive radiation of ammonites derived from long-lived deep-basin species, followed by lowering of sea levels, regression of seas off the continental shelves, and extinction of all but the deep-basin species. In each phase of radiation, the newly available shelf must be similar to a remote archipelago on which many vacant niches are available to new colonists. Shading indicates the marine environment that is continuous in the deep basins but increasingly interrupted from the outer to the inner continental shelf. (From Wiedmann 1973)



some extraordinary creatures were present that ended up preserved in the Burgess Shale (Whittington 1985). *Wiwaxia* was a genus of worm-like organisms covered with plates, or sclerites, and two rows of spines (Figure 8-12) (Conway Morris 1985, Gould 1985, 1989). *Opabinia* had five large, stalked eyes and, extending beyond them, a highly mobile tube fringed at its end by vicious teeth (Figure 8-12). To modern eyes, *Hallucigenia* is a strange misfit; at first sight it seems to have walked on seven pairs of spines and had tentacles on its upper surface; but perhaps it stood the other way up (Figure 8-12) (see also Briggs and Whittington 1985)? (Such might be the hallucination of a tired paleontologist sifting through piles of

rock.) Further examination of these fossils indicates locomotory function of the paired "tentacles" and presumably a defensive role for the spines, as depicted in Figure 8-12 (Ramsköld and Xianguang 1991, Ramsköld 1992). These authors have proposed a possible affinity with the onychophorans.

Some taxa present in the Cambrian are readily linked to modern forms, such as the clams and snails. However, whereas *wiwaxiids* may have had six genera in the Cambrian, there were only two genera of small clams. Therefore, had we been able to observe the Burgess community and predict the future radiations of animals, we would almost certainly have expected *wiwaxiids* to radiate and clams to remain

FIGURE 8-9

The pattern of echinoid radiations and extinctions. (From Smith 1984)

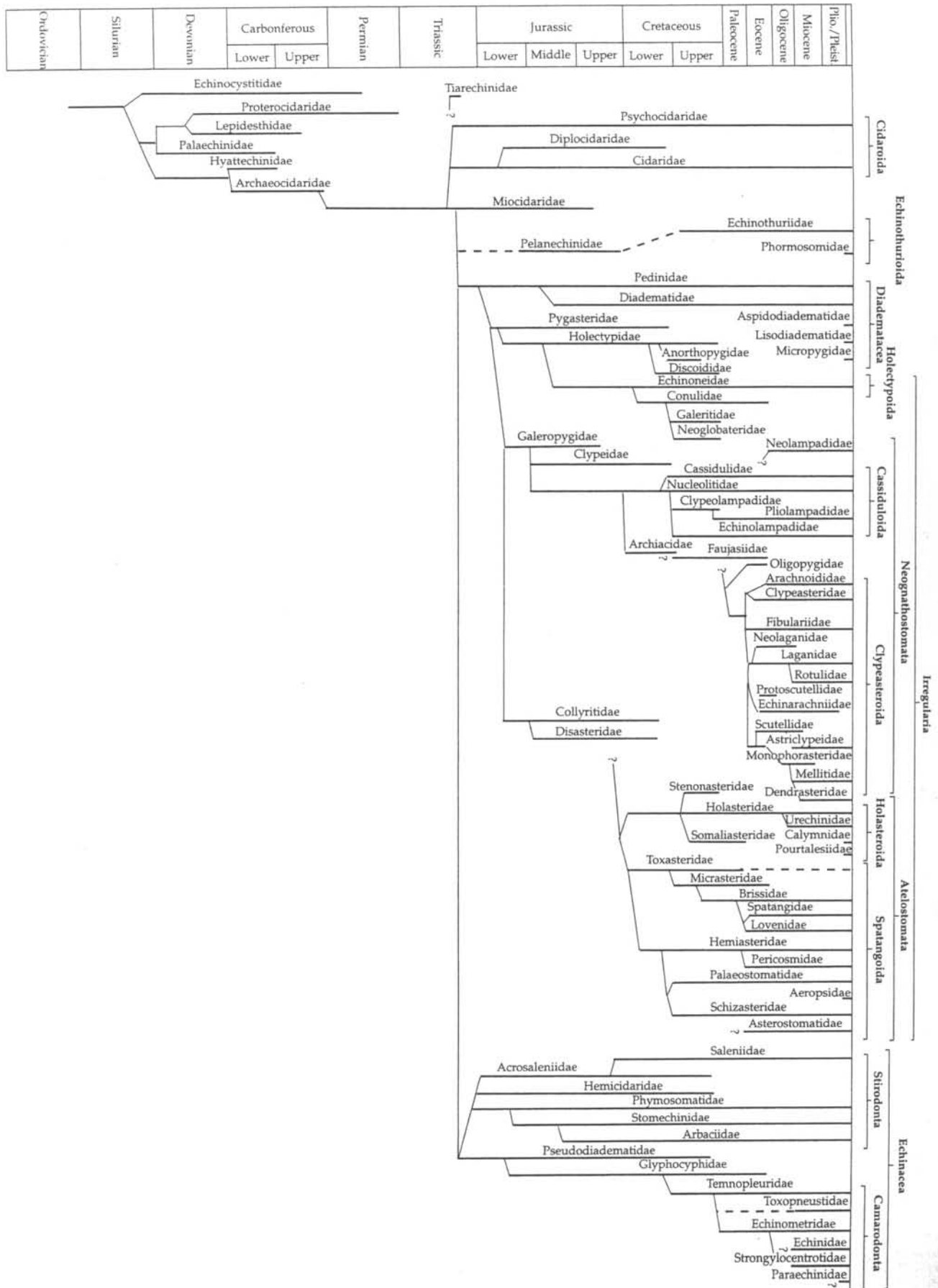
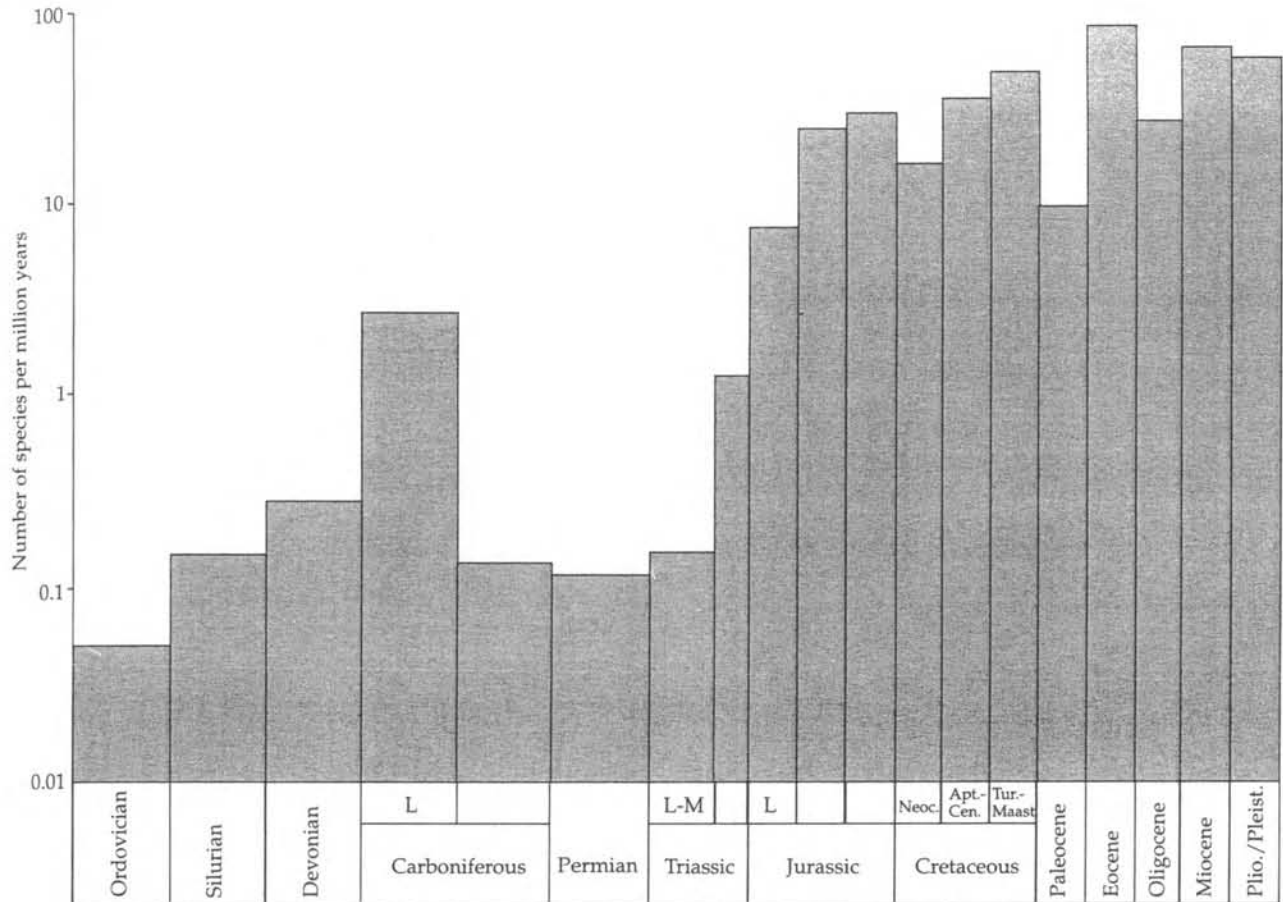


FIGURE 8-10

The number of species of echinoids per million years. (From Smith 1984)



depauperate in species or go extinct. Quite the reverse took place, for clams underwent a major radiation (although very much later, in the Triassic), and the wiwaxiids went extinct without leaving evidence for a rational explanation.

### The Burgess Shale Fauna: Priapulids and Polychaetes

Gould's second scenario concerning Burgess Shale organisms compares the polychaete worms and the priapulids, or "little penis worms." In the Burgess fauna the two were equally represented in number of genera, but the priapulids were abundant and the polychaetes were rare (Table 8-1). And yet it was the polychaetes that radiated spectacularly, while priapulids became a very insignificant component of any fauna. No convincing reason for this turn of events is available.

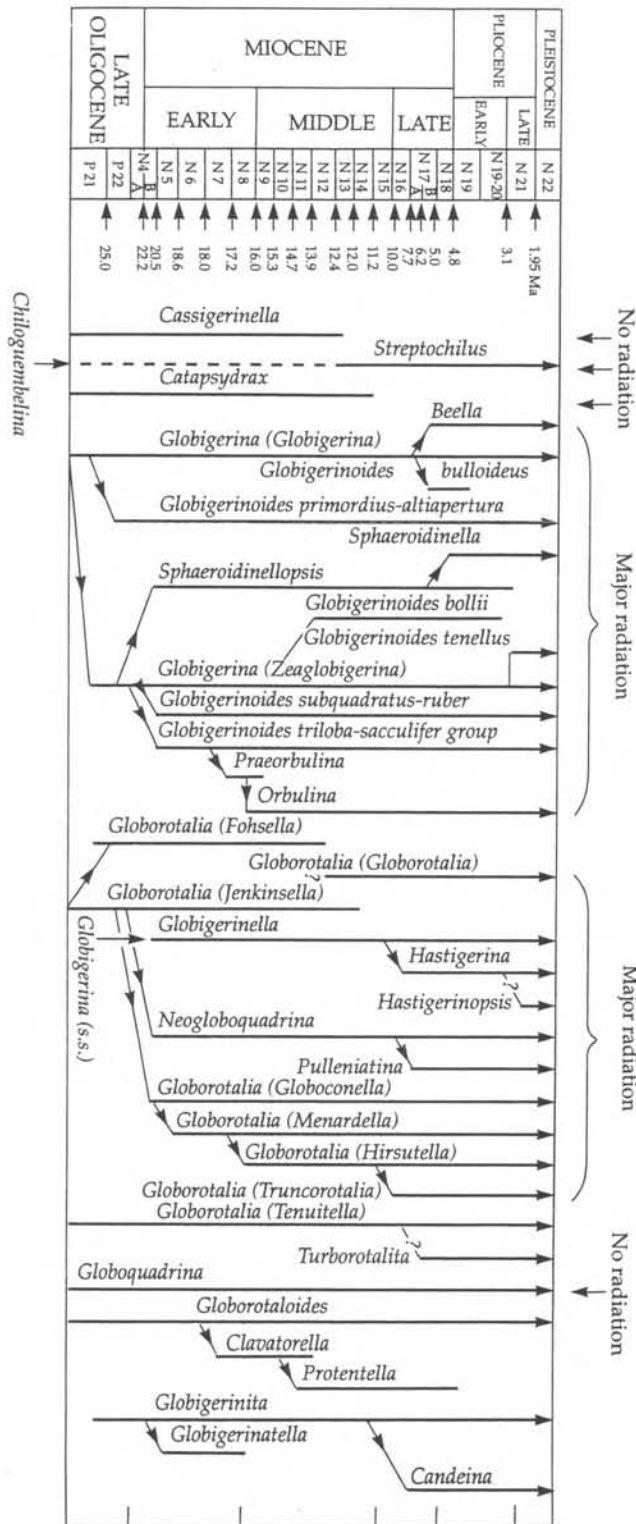
### Predaceous Birds or Mammals?

The third scenario suggests even more convincingly that, at any time of radiation, alternative pathways are equally viable, at least for a few million years. When the large carnivorous dinosaurs died out in the Cretaceous, there was clearly room for a radiation of large carnivores from a lineage that had survived the Cretaceous-Tertiary extinctions. Four different taxa radiated, two in the north and two in the south. In the north, the canids and felids radiated, as well as huge predaceous birds represented by *Diatryma gigantea*, found in Wyoming Eocene deposits (Figure 8-13).

The appearance of this great bird at a time when mammals were, for the most part, of very small size (the contemporary horse was the size of a fox terrier) suggests some interesting possibilities—which never materialized. The great reptiles had died off, and

FIGURE 8-11

Planktonic foraminiferans in groups that radiated and groups that did not radiate in the late Oligocene and early Miocene. Why did some genera radiate while others remained narrow phylogenetic lineages? (From Kennett and Srinivasan 1983)



the surface of the earth was open for conquest. As possible successors there were the mammals and the birds. The former succeeded in the conquest, but the appearance of such a form as *Diatryma* shows that the birds were, at the beginning, rivals of the mammals. (Romer 1945, 270-271)

Gould points out that the "tape" ran again in isolation in South America, and in this case the giant ground birds, or phororhacids, probably did dominate for a while (Figure 8-14). There the potential mammal contenders were marsupials—the borhyaenids. Simpson (1980, 147, 150) explains:

It has sometimes been said that these and other flightless South American birds . . . survived because there were long no placental carnivores on that continent. That speculation is far from convincing. Rheas still survive although there have been placental carnivores in their communities for at least 2 million years. Most of the phororhacids became extinct before, only a straggler or two after, placental carnivores reached South America. Many of the borhyaenids that lived among these birds for many millions of years were highly predaceous. . . . The phororhacids . . . were more likely to kill than to be killed by mammals.

Conway Morris, Simpson, and Gould make a convincing case that the radiation of groups is largely unpredictable. Perhaps the best we can do is to predict that, when a large adaptive zone becomes available, some taxon or other will radiate into it.

### 8.5 TYPES OF ADAPTIVE RADIATION

Despite the case for unpredictability, some general patterns have emerged in the mechanisms involved with adaptive radiation. If we define an **adaptive zone** as "a set of ecological niches that may be occupied by a guild of organisms" and a **guild** as "a group of species that exploits the same resources in a similar manner" (Root 1967), we can identify the following types of adaptive radiation.

#### Type 1: General Adaptation

A new general adaptation opens up new adaptive zones. One example is the evolution of flight in birds, which opened up possibilities for utilization of prey in the air; colonization of islands, cliff faces, and tall trees; and extensive migration. The result has been about 8,600 extant species. Bats have radiated to about 900 extant species.

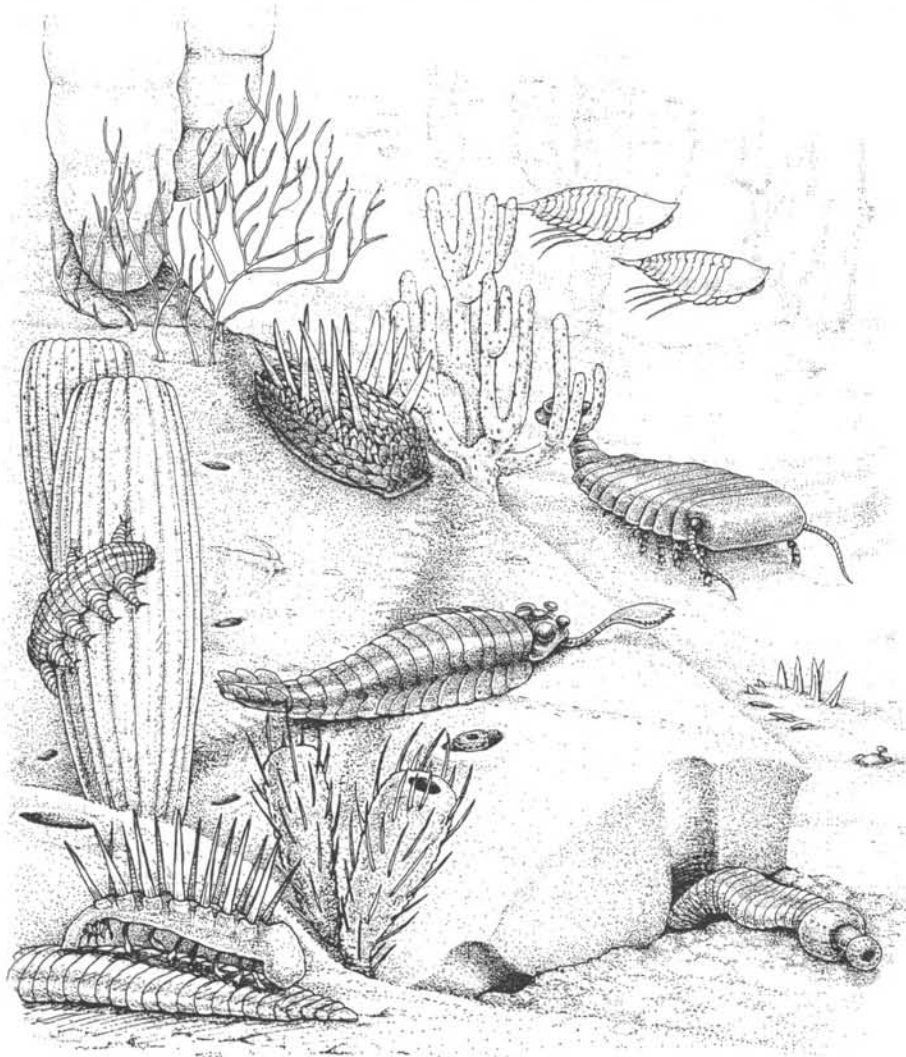
Another possible example is the bark lice (Psocoptera), which colonized birds, became parasitic (Mallophaga), and radiated across bird species and into different microhabitats on the bird's body, with some 1,500 species of bird lice (Phloopteridae) now described (Price 1980). In a similar way, agromyzid

TABLE 8-1 Change in relative abundance of little penis worms (priapulids) and polychaete worms

	Priapulids	Polychaetes
Burgess fauna	6 genera	6 genera
Abundance in Burgess	Very abundant	Much rarer
Present world fauna	9 species	87 families, 1,000 genera, 8,000 species
Habitats	Live in unusually harsh environments	Sea floor, brackish and fresh water, and moist soil in terrestrial habitats

FIGURE 8-12

Some of the strange organisms from 500 to 600 million years ago found in the Burgess Shale. Some animals do not fit any currently recognized phyla: *Hallucigenia sparsa* (bottom left), *Opabinia regalis* (center), and *Wiwaxia corrugata* (top center). *Aysheaia* (left center, on sponge), *Sidneyia* (right middle ground), and *Leanchoilia* (top right) are arthropods of unknown affinity. *Pirania* (bottom center) and *Vauxia* (top center, two species) belong in the phylum Porifera. *Ottoia* (bottom right) is a priapulid worm. (Wiwaxia from Conway Morris 1985; other species from Whittington 1985) (Illustration by Tad Theimer)



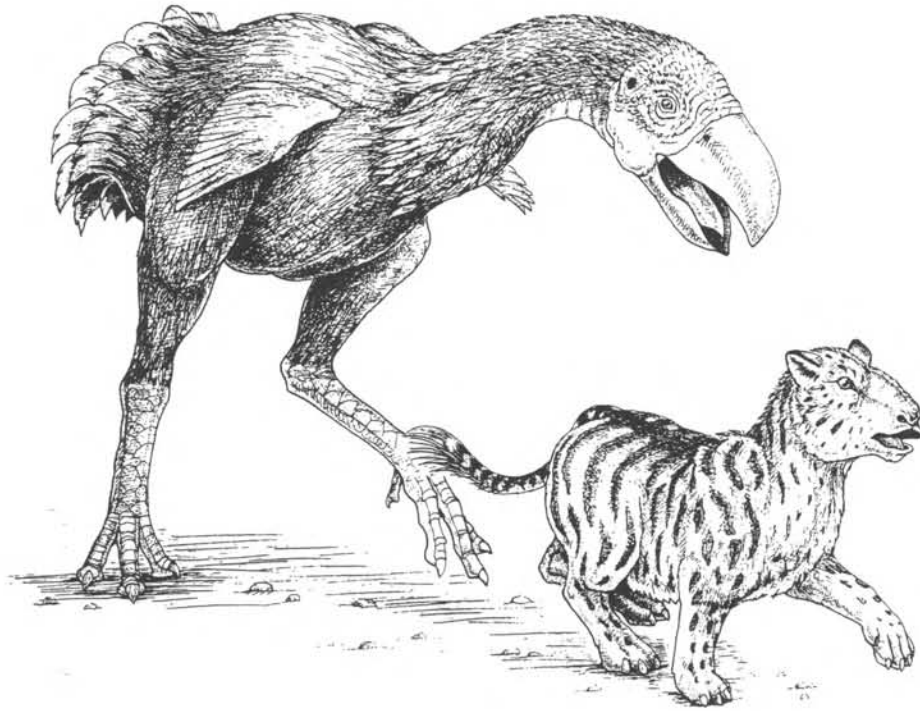


FIGURE 8-13

A reconstruction of *Diatryma* based on skeletons found in North America. This bird reached up to 9 feet in height and lived in Eocene grasslands. It is pictured chasing an oreodont artiodactyl, whose short legs were hardly a match for the great bird's speed. (Based on Špinar 1972) (Illustration by Tad Theimer)



FIGURE 8-14

The large predaceous bird *Phororhacos* as it may have looked during the Tertiary in South America. (Based on Špinar 1972) (Illustration by Stephen Price)

flies acquired the general adaptation of mining and feeding in the leaf tissue of angiosperms. They radiated across plant species and into different plant parts such as leaves, seeds, and stems—the adaptive zones that guilds of flies may occupy.

These examples represent major radiations on continents.

### Type 2: Environmental Change

Environmental change opens new adaptive zones. The ammonites should fulfill this principle, for they radiate as newly flooded continental shelves opened up new habitats. Likewise, as the savannas opened and developed with climatic drying, the ruminants radiated. As the climate in South America became wetter, tropical forests spread from small refugia, or expanded extensively from centers of distribution, and many plant and animal species radiated.

### Type 3: Archipelagoes

We may regard remote, geographically isolated locales with heterogeneity as archipelagoes, whether they are oceanic island groups or habitat islands, such as mountaintops in a sea of desert or rock patches in a large freshwater lake. On an archipelago, adaptive zones remain open in places remote from potential colonists, and the first colonists radiate. This type of adaptive radiation encompasses the classic cases that have received the most attention: the honeycreepers on the Hawaiian Islands (Amadon 1947, 1950) (Figure 8-15); Darwin's finches on the Galapagos Islands (Lack 1947); and the genus *Drosophila* (Carson et al. 1970, Ringo 1977, Templeton 1979), the beetles (Zimmerman 1948), and the silverswords (Carlquist 1974, Carr and Kyhos 1986, Carr et al. 1989) on the Hawaiian Islands.

#### Hawaiian Honeycreepers

Amadon (1950) emphasized the following processes in the radiation of the honeycreepers.

1. Quantum evolution or rapid divergent evolution
2. Isolated biotas with many families absent
3. Plentiful empty ecological niches
4. Absence of competing species outside the radiating taxa
5. Importance of environmental heterogeneity: "The Drepaniidae could not have evolved on the bleak Aleutian Islands" (241)
6. Depauperate predators and parasites that do not "inhibit adaptive radiation by eliminating variant individuals" (241)
7. Importance of competition between radiating species and the resultant character displacement: "On

the islands where but one species of this group (*Loxops virens*) occurs, it has generalized feeding habits. On Kauai where two species are present as a result of a double invasion, they have, so to speak, divided the ecological niche of the parental species between them (and extended it)" (246). *Loxops virens stejnegeri* feeds on insects beneath bark while *Loxops parva* forages on leaves and shallow flowers. "Thus divergence and incipient specialization have resulted from competition between two similar species" (246).

Lack's (1947) scenario for Darwin's finches was essentially the same.

Many habitat archipelagoes occur on continents; these include mountaintops (Brown 1971, Vuilleumier 1970), caves (Vuilleumier 1973, Culver 1982), refuges of vegetation such as tropical forest in Amazonia during the Pleistocene (Prance 1981), and patchy distributions of hosts for parasitic species (Price 1980). Continental archipelagoes have received less attention than oceanic archipelagoes in considerations of adaptive radiation even though they are the sites of much more diversification of species.

#### Hawaiian Silverswords

Relatively recent study of the plant group known as the Hawaiian silverswords suggests a complex array of interacting factors in the process of adaptive radiation. The original tarweed progenitor from North America colonized Kauai less than 6 million years ago, and adaptive radiation has resulted in 28 species in three genera: *Argyroxiphium*, *Dubautia*, and *Wilkesia*. Radiation has occurred particularly in growth form and habitat exploitation. The group includes cushion plants, rosette shrubs, mat-forming woody plants, erect shrubs, trees, and lianas. Species occur in almost all habitats on the Hawaiian Islands, from sea level to 3,750 meters, and occupy places with less than 400 millimeters (about 16 inches) of rainfall per year as well as some of the wettest places in terrestrial environments on earth, with 12,300 millimeters (about 500 inches) of rainfall (Carr et al. 1989). Figure 8-16 illustrates the diversity of leaf forms among the 28 species and one of the most spectacular species.

The mechanisms involved with adaptive radiation in the silverswords probably include interactions among the following factors (Carr et al. 1989).

1. Great diversity of habitats existed within the islands, with close local heterogeneity, as Amadon emphasized.
2. Allopatry and ecological isolation occurred between and within islands.

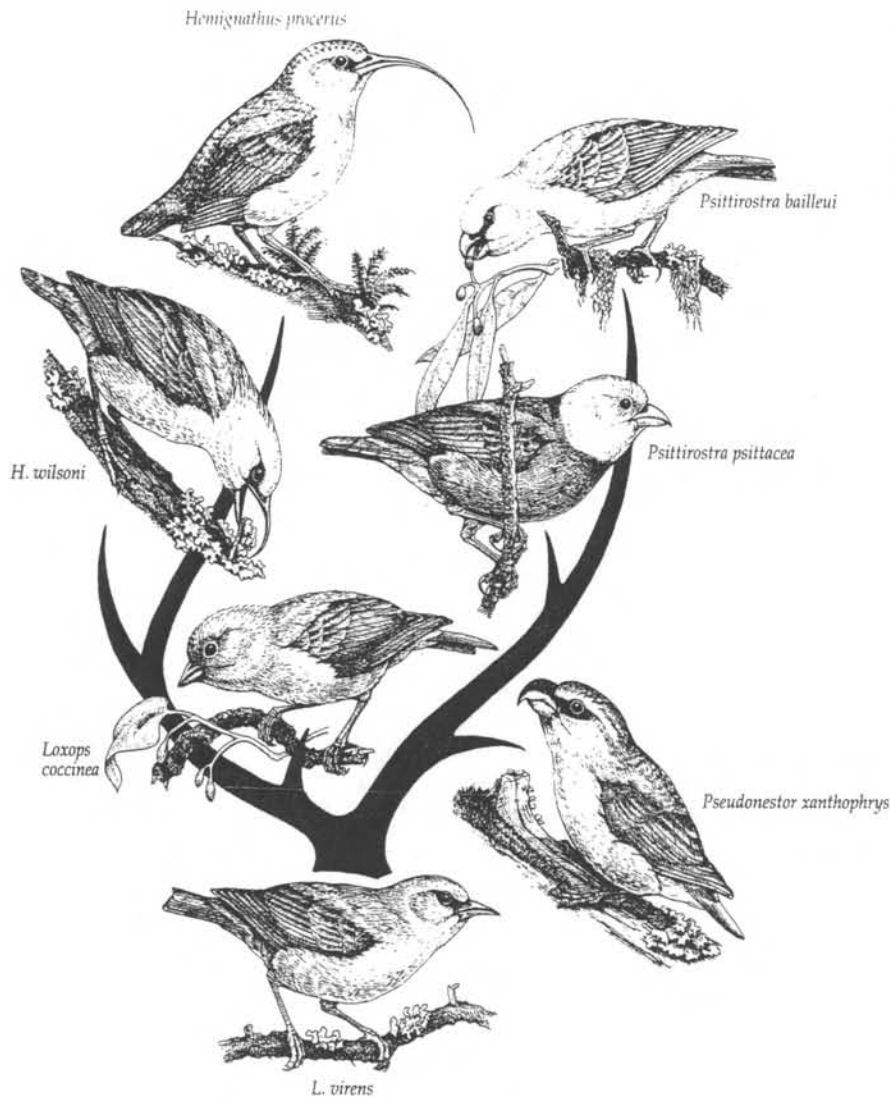


FIGURE 8-15

Adaptive radiation of the Hawaiian honeycreepers in the family Drepanididae, exhibiting great diversification in beak morphology and feeding habits. (From Lewin 1982) (Illustration by Tad Theimer)

3. Reciprocal chromosomal translocations produced reproductive isolation.
4. Major adaptive shifts occurred when long-distance dispersal between islands resulted in founder effects.
5. Novel physiological traits enabled radiation into new habitats; for example, an aneuploid with 13 pairs of chromosomes instead of the ancestral 14 extended the silversword lineage into much drier sites, although the detailed mechanisms are not understood.
6. Self-incompatibility, outcrossing, and hybridization between genotypes adapted to different conditions may have accelerated the radiation process.
7. Volcanic activity repeatedly opened new areas for colonization by novel hybrids.

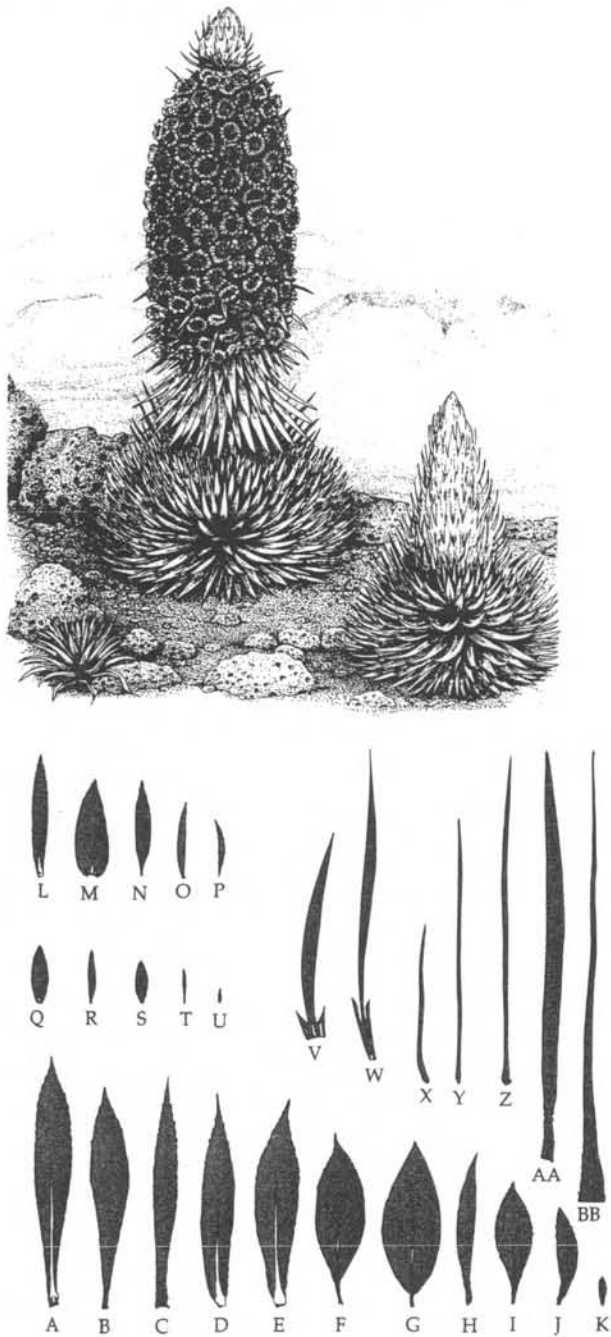
Using Carson's (1983, 1984) overviews on *Drosophila*, Carr et al. (1989) noted the similarities between the adaptive radiation of the silverswords and that of the picture-winged *Drosophila*. The founding events on new islands in the two lineages were similar; great diversity of form has ensued during radiation in both cases; many habitats have been colonized; both groups are obligate outcrossers; and chromosomal evolution has been extensive.

The silverswords "appear to be the most spectacular example of adaptive radiation in the plant kingdom" (Carr et al. 1989, 95). The exciting prospect is



FIGURE 8-16

**Above:** An example of Haleakala, (*Argyroxiphium sandwicense*), one of the most striking silverswords, growing on volcanic ash, with an immature plant on the right and a plant in flower on the left (Illustration by Tad Theimer). **Below:** Leaf silhouettes of the 28 species of Hawaiian silverswords all at a scale of  $\times .25$ , showing the diversity of leaf shape in this radiation. (From Carr et al. 1989)



that, with the help of broadly ranging studies focused on variation (in form, morphology, and anatomy), floral morphology and breeding systems, cytogenetics and hybridization, enzyme polymorphism, and adaptive physiology, we will probably come to understand in much greater detail the complexity of interacting factors in adaptive radiation. A detailed mechanistic view will shed new light on the whole diversification of life on earth.

#### Type 4: Combination of Environmental Change on Archipelagoes

A combination of Types 2 and 3 is necessary to accommodate the fish species flocks in African lakes (McKaye and Gray 1984) (Figures 8-17, 8-18). The lakes change dramatically in water level. When they rise, they flood new areas and open up new habitat. Then, as water levels decline, populations become isolated on a rather local geographic scale and speciate. For example, Lake Nabugabo became cut off from Lake Victoria 4,000 years ago and now harbors five endemic cichlid species (Greenwood 1965).

In addition, for the rock-dwelling cichlids, any lake houses an archipelago of rocky islands, separated by wide expanses of sandy and weedy bottoms, that are available for colonization (McKaye and Gray 1984). Islands are so far apart, and fish so tied to rocky outcrops, that geographic isolation becomes important.

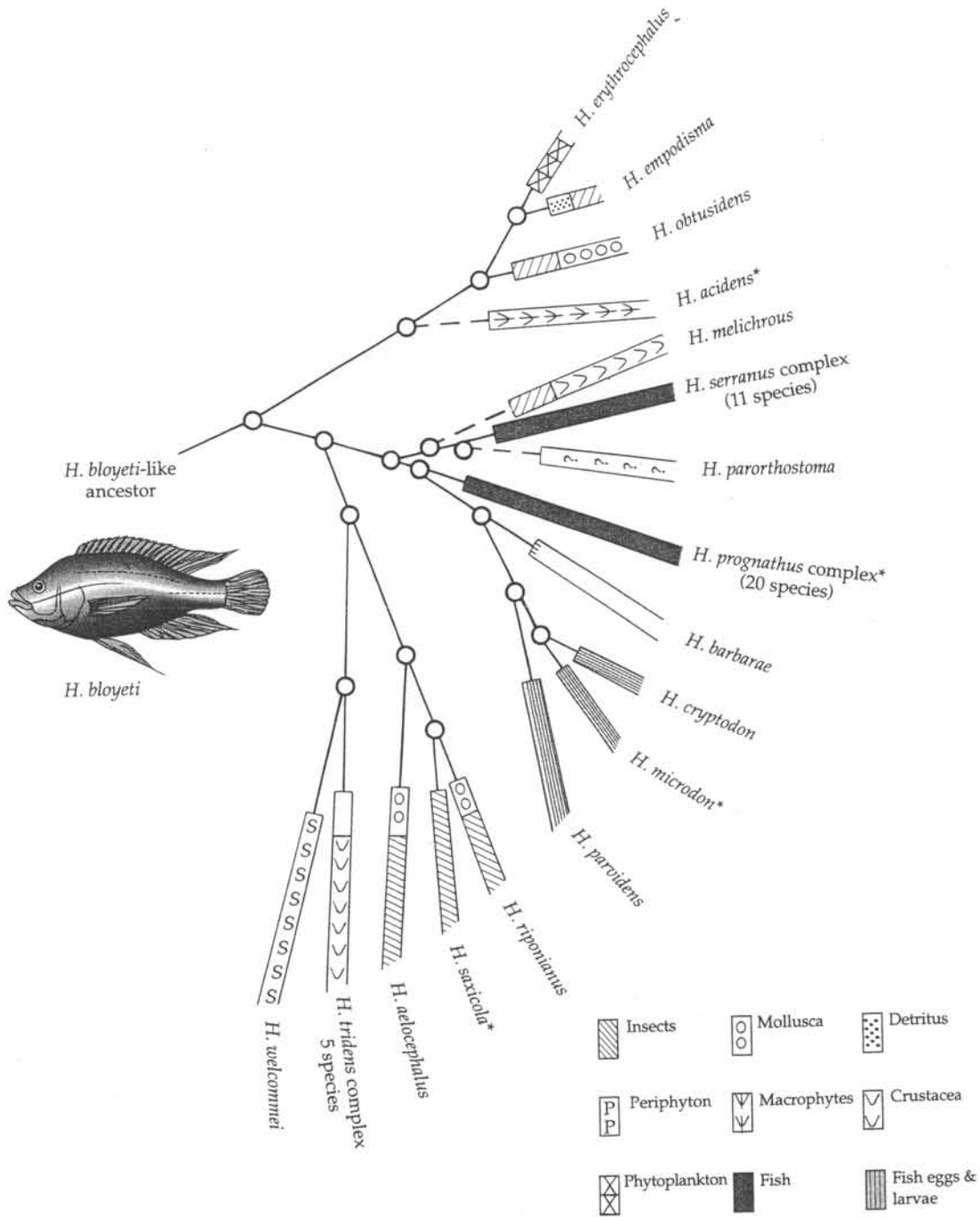
Finally, changes in water level create new rock islands, make some deeper or shallower, or unite formerly isolated populations, alternating habitats for species with shallow-water and deep-water preferences (Figure 8-19). The effect is to change archipelago arrangements and structures quite rapidly, even in a decade. This kind of change opens and closes new sites for colonization and brings new species together, which may then evolve together, resulting in character displacement and finely and narrowly defined ecological niches (Liem 1978, 1980, Liem and Osse 1975).

Very impressive adaptive radiations have resulted from this combination of dynamics. Greenwood (1984) estimated that in the Nile, the source of the colonists of Lake Victoria, 8 percent of fish were cichlids (10 species). In Lake Victoria, however, the cichlids radiated to represent 84 percent of fish species, with about 200 species (Table 8-2). The "cichlid lakes" in Africa contain an amazing diversity of species—some 580 in total.

It is not clear why Lakes Turkana and Albert have remained relatively depauperate in cichlids. Albert may have been part of another drainage system dissociated from the Nile (Greenwood 1974b). Low

FIGURE 8-17

Part of the adaptive radiation in the Lake Victoria genus *Haplochromis*, showing the diversification of feeding ecologies from an *H. bloyeti*-like ancestor. Species with asterisks are illustrated in Figure 8-18. (From Greenwood 1974a)



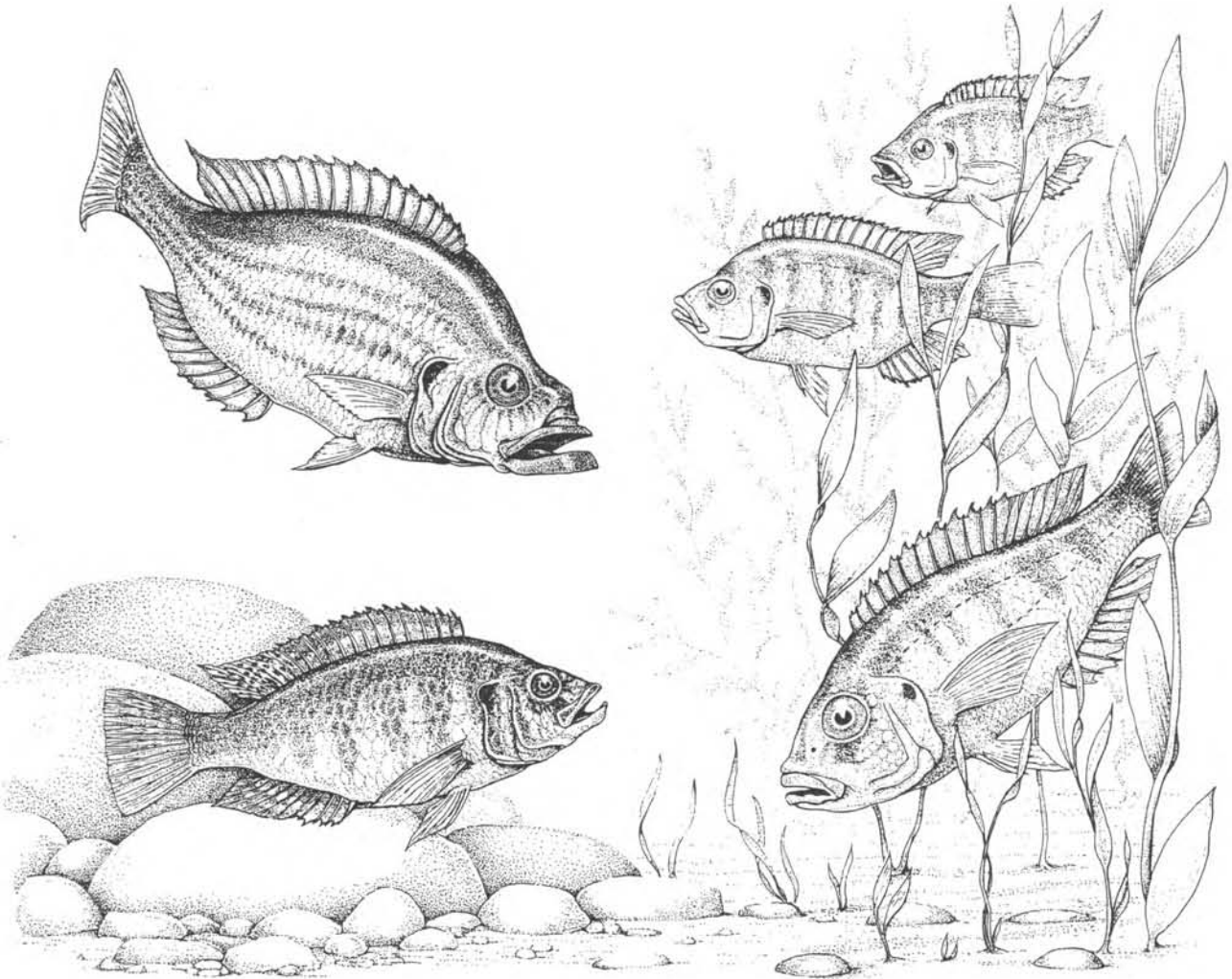
diversity in other lakes, such as Lake Turkana, implicates drying periods in the middle Pleistocene. The whole Great Rift Valley system of East Africa has been so dynamic that geologists are still working out the connections and drainages.

### 8.6 BEYOND THE ADAPTIVE MODEL OF RADIATION

Amadon (1950) and Mayr (1963) both emphasized the importance of natural selection in adaptive radiation.

FIGURE 8-18

Four species of *Haplochromis* from Lake Victoria, in the lineage depicted in Figure 8-17, showing major diversification in ecology without very dramatic changes in morphology. *H. acidens* (upper right), about 6 inches long, is a macrophyte feeder usually found in dense stands of plants; it occupies an almost vacant niche in Lake Victoria. *H. prognathus* (upper left) is a fish predator, about 10 inches long, that occupies areas above hard substrates in exposed and sheltered localities. *H. microdon* (lower left) is about 5½ inches long; it may feed on fish eggs and larvae and tends to occupy littoral zones over firm or soft substrates. *H. saxicola* (lower right) is about 5½ inches long and feeds on insect larvae on the lake bottom. This species may be found on exposed sand or shingle or in dense stands of plants. (From Greenwood 1959, 1967, 1974a) (Illustration by Tad Theimer)



This emphasis may be called the adaptive model of radiation; the term itself implies that selection plays a central role. Other hypotheses have been proposed as well, especially in relation to the impressive radiation of more than 300 species in the genus *Drosophila* on the Hawaiian Islands. That is 25 percent of the genus worldwide, occurring on six small islands. Ringo (1977) and Templeton (1979) summarized four hypotheses.

### The Adaptive Model

The adaptive model of radiation refers to the general pattern discussed in Section 8.2, in which mutation and natural selection play the central role in shifts to new niches and adaptive zones (Dobzhansky 1972, 1976). This model does not explain why Hawaiian species of *Drosophila* are so distinct from each other morphologically and behaviorally. For any level of

FIGURE 8-19

The effects of fluctuating lake levels on the division of habitats for cichlid fishes associated with rocks. In each case (a, b, c), lake water levels rise, with the following consequences. (a) Two populations become united. (b) One population is divided into two. (c) A rock providing habitat for shallow-water species becomes deeply submerged, and new rocky shore habitat becomes available for colonization. (Based on McKaye and Gray 1984)

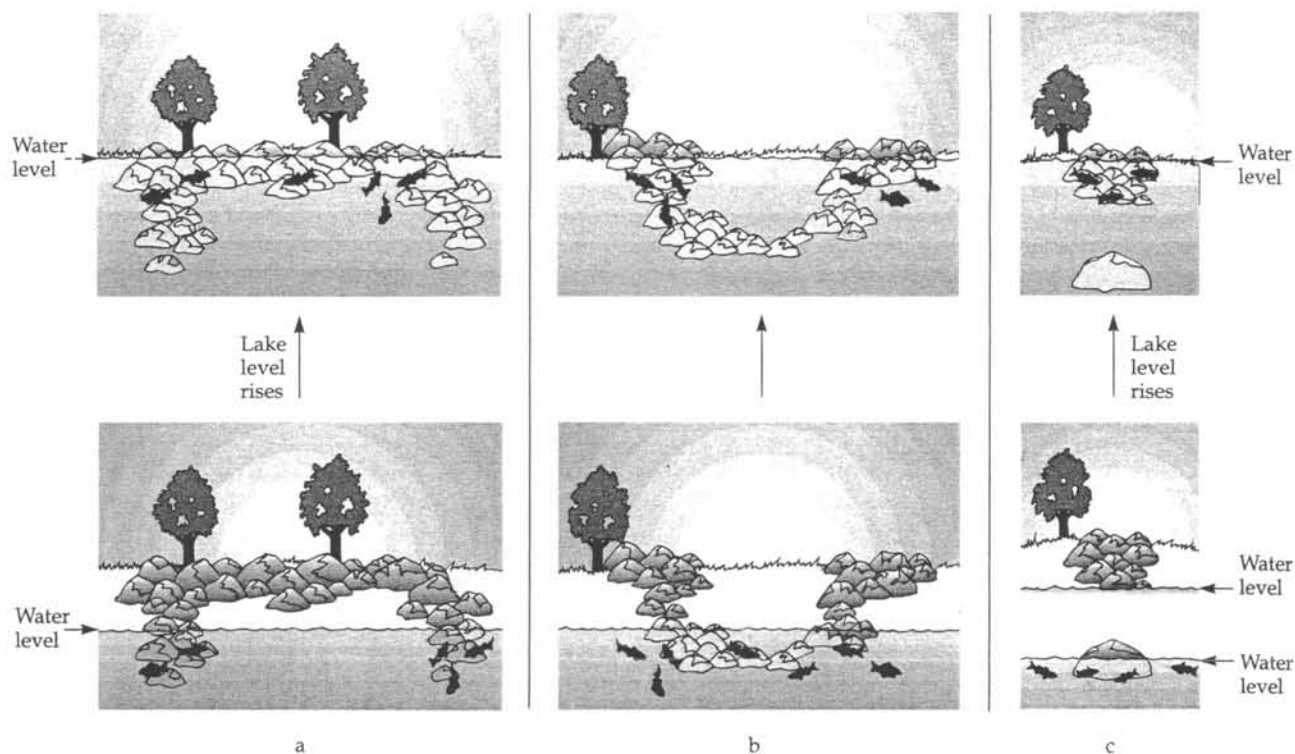


TABLE 8-2 Fish species in African lakes and rivers

Geographic Location <sup>1</sup>	Total Fish Species	Total Cichlid Species	Percent Cichlid Species
Rivers: Zambezi	110	20	18%
Zaire	690	40	6%
Niger	134	10	7%
Nile	115	10	8%
Lakes: Turkana	39	7	18%
Victoria <sup>2</sup>	238	200	84%
Edward <sup>2</sup>	57	40	70%
Albert	46	9	20%
Tanganyika <sup>2</sup>	247	136	55%
Malawi <sup>2</sup>	242	200	83%

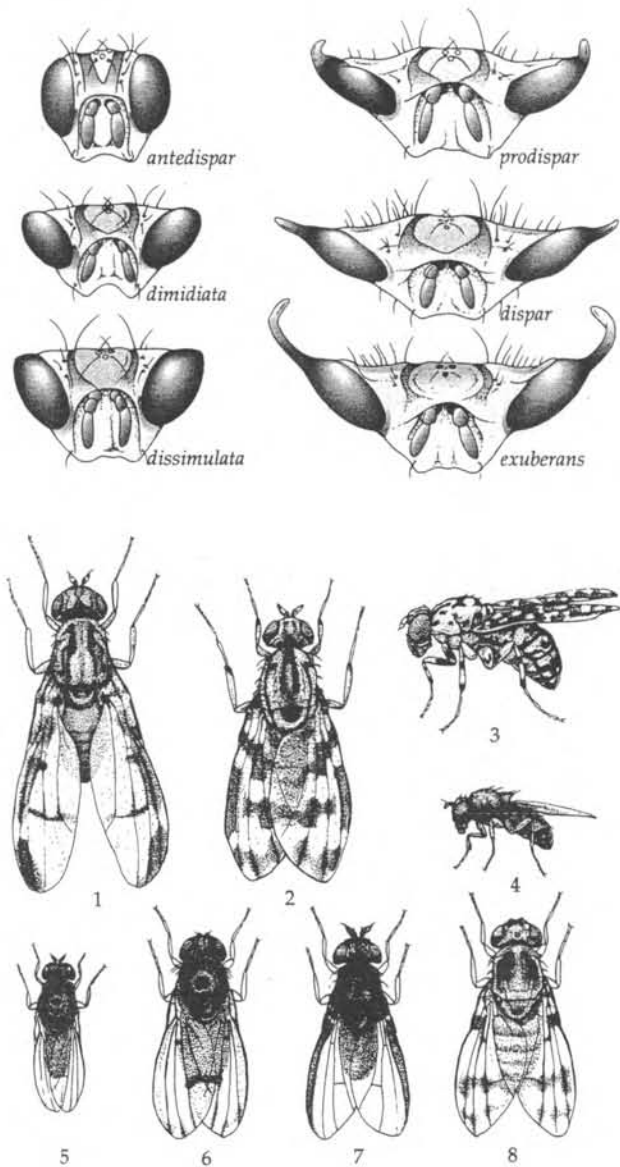
Data from Greenwood 1984.

<sup>1</sup> Brackets (not inclusive) connecting rivers and lakes show faunal relationships.

<sup>2</sup> Cichlid lakes.

FIGURE 8-20

Some species of Hawaiian *Drosophila*, showing the diversification of head structure and picturesque wings so different from those of the small mainland species. Species 4 and 5 below are about the size of the common mainland species, *D. melanogaster*. (Based on Lawrence 1992, and Yoon 1989)



genetic similarity, they are more different phenetically than continental species. In morphology, they have distinct wing patterning, prominent bristles, stalked eyes, and strange tarsi, and the sexes are distinct (Figure 8-20). Behaviorally, in many species males are territorial. They frequently aggregate in leks away from oviposition sites. There they attract females, and copulation occurs. Males also engage in intricate displays and complex courtship patterns, all

more extreme than those of continental species. Simple adaptation cannot account for these differences between Hawaiian and continental *Drosophila* species.

### The Genetic Drift Model

Carson (1970, 1975) proposed that island hopping by founding individuals, followed by genetic drift, could account for the extensive speciation of *Drosophila* on the Hawaiian Islands. However, this process is unlikely to result uniformly in significant phenotypic differences between closely related species. It seems as if character displacement really must play a role beyond the effects of drift.

### The Sexual Selection Model

Spith (1974a, 1974b) argued that predation at oviposition sites (which were conspicuous to the predators) was strong enough to select for lekking behavior away from those sites, and lekking fostered sexual selection between males. Ringo (1977) envisaged a two-step scenario.

- A. Speciation starts with colonization of new islands, which produces geographic isolation.
- B. "Strong directional intrasexual selection acts as the heritable variation in male reproductive structures and behavior and in female preference, causing rapid changes in the frequencies of alleles responsible both for the preferred behavior and for the preference" (695).

Templeton (1979) criticized Ringo's model, arguing that sexual selection is strongly stabilizing. In place of selection for deviant males, female choice forces male morphology and behavior into a narrowly defined range of acceptable males and thus drives sexual selection.

### The Drift Plus Sexual Selection Model

Templeton (1979) argued that both drift and sexual selection are essential in a speciation model, to account for the patterns in genetic variation and behavioral and morphological differences. The actual speciation event occurs as in Carson's genetic drift model. Sexual selection reinforces this speciation event in two ways.

1. "With a founder event, the release of genetic variability in the mate recognition system coincides with a new external selective environment that frees the species from its old constraints and may even actively select for a new mate recognition system—i.e., the sexual selection may become temporarily directional, rather than stabilizing in the founding population. These conditions are optimal

next page for 179  
for causing a rapid reorganization of the mate recognition system that could serve as the basis of speciation" (516).

2. The development of strong pre-mating reproductive isolating mechanisms, and the potential in their rapid shifts through directional selection, reduce the chances of hybridization with sympatric populations and preserve the speciation event.

The important point differentiating Templeton's model from the sexual selection model just discussed is that, during the founding effect, genetic drift causes a shift from the parental adaptive peak, and sexual selection then establishes a new stabilized mating system that may be substantially different from the parental core adaptations (Carson and Templeton 1984).

### 8.7 SOURCES OF RADIATION IN DOMINANT GROUPS

Scenarios for adaptive radiation in the archipelago-like arenas are fairly well developed. Radiations on large continental landmasses or in the ocean, while contributing in a major way to biotic diversity, have undergone less conceptual scrutiny. Eisenberg's (1981) book *The Mammalian Radiations* provides little that is generalizable, despite its name. Much earlier, Darlington (1959) asked where dominant groups of animals evolved and what factors permitted some groups to expand geographically and radiate. Dominant groups must possess adaptations that are of general utility, i.e., that are adaptive in every environment. Brown (1958) contrasted the general adaptations of dominant species with adaptations specific to a particular set of environmental conditions. General adaptations may increase an animal's efficiency in food utilization, rate of development, or efficiency of locomotion. To occupy a large area, a group must have qualities such as superior competitive ability, effective colonizing ability, and traits enabling exploitation of many different environments. The group must possess numerous general adaptations.

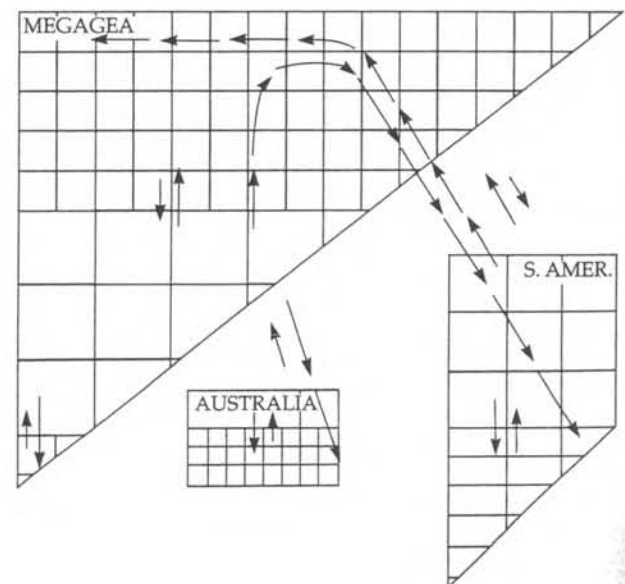
Darlington examined the evidence for the origins of several dominant groups of animals. The family Bovidae is the most recent family of artiodactyls to evolve and has radiated extensively into the cattle, antelopes, sheep, and goats. The Bovidae are most numerous and diverse in Africa, where they probably originated. The earliest fossils of the elephant-mastodont group were found in Egypt, and Simpson (1940) argued that these animals radiated from North Africa. The murid rodents, or Old World rats and mice, are most diverse in the Old World tropics and are dominant almost everywhere they have dispersed. Humans probably also evolved in the Old World tropics.

In fact, evidence suggests that many groups evolved in the Old World tropics, radiated there, and then dispersed to other parts of the globe. Much less movement has occurred in the other direction (Figure 8-21). The mechanisms associated with this pattern, identified by Darlington, are as follows:

1. Dominant groups originate in the largest areas.
2. The largest areas also have the most favorable climates.
3. Because many other species are present, species evolve strong competitive ability, an important general adaptation. They do not evolve to tolerate stressful abiotic environmental conditions such as exist at higher latitudes.
4. In warmer climates, generation time is reduced, and so evolutionary rates are higher than in colder climates.
5. Large areas contain many populations. The larger the area, the more numerous the populations, the greater the maintained genetic diversity, and the greater the evolutionary potential of the species and of the group as a whole (see also Brown 1957 on centrifugal speciation).

FIGURE 8-21

Darlington's view of the major movement patterns of radiating groups of organisms. Large land area in a favorable climate results in many populations per unit area (indicated by large squares) and evolution of new generally adapted species. Such species then disperse, principally in the directions indicated by long arrows, with little dispersal in the opposite direction, indicated by short arrows. Megagea is the landmass composed of Africa in the south, Eurasia, and North America. (From Darlington 1959)



6. Because larger areas contain more species, the probability of species moving from species-rich areas is greater than the probability of the reverse. Recent studies on the faunal relationships across Beringia and across the Isthmus of Panama (Hopkins et al. 1984, Kontrimavichus 1985 on Beringia; Marshall et al. 1982, Stehli and Webb 1985 on the Isthmus of Panama) still support this grand, global pattern, which contrasts with findings of more narrowly focused studies.

The processes of adaptive radiation have been central issues in the development of evolutionary the-

ory, but much remains to be discovered. What were the driving forces for the fish species flocks in Africa's cichlid lakes? Do we have any power to predict the approximate extent to which adaptive radiation can proceed? Is the process of radiation over large areas, such as mainlands and continental shelves, essentially the same as that on isolated archipelagoes? What really makes Hawaiian *Drosophila* species so different from mainland species? This fascinating subject has captured many an evolutionist's imagination, from Darwin to the present, and continues to be a stimulus for research and debate.

## S U M M A R Y

**Adaptive radiation** is the relatively rapid evolutionary divergence of members of a single phyletic line, more or less simultaneously, into a series of rather different ecological niches or different sets of similar niches. Generally, such radiation occurs in a new ecological setting, free from competition and natural enemies and often involving impoverished archipelagoes. The fossil record illustrates many such radiations, with small lineages erupting into diverse clades. Ammonites, echinoids, brachiopods, and foraminiferans exemplify the probably unpredictable nature of cladogenesis, with one lineage radiating extensively while others diverge narrowly and slowly, showing a pattern of **progressive occupation**.

Direct examination of the predictability and repeatability of radiations indicates that alternative pathways are generally viable and outcomes are not foreseeable. Wiwaxiids and clams, and priapulids and polychaete worms, all from the Burgess Shales, illustrate the unpredictability of success in the long-term fossil record. Had humans been able to evaluate the situation after the demise of the predaceous dinosaurs, they would not have anticipated the ultimate predominance of predaceous mammals over large avian predators.

Adaptive radiation may be classified into four main types.

1. General adaptive breakthroughs may open up new adaptive zones, as occurred in the evolution of wings in lineages leading to birds and bats. Development of the parasitic habitat resulted in greatly enriched chances of radiation across animals and plant host species.
2. Environmental change opened up new adaptive opportunities—for instance, newly flooded continental shelves for ammonite radiation and extensive savannas in which the ruminants radiated.
3. On isolated and therefore depauperate archipela-

goes, early colonists may diversify into adaptive zones well beyond the extents of their mainland progenitors. Honeycreepers, *Drosophila* species, and silverswords have all radiated on the Hawaiian Islands, and Darwin's finches on the Galapagos Islands are another classic case. The silversword alliance provides evidence for the complex interplay of factors in adaptive radiation: habitat heterogeneity, allopatric isolation on different islands and ecological isolation within islands, chromosomal translocations, founder effects, aneuploidy, and volcanic activity.

4. A combination of environmental changes and archipelagoes may best explain the impressive radiations of some fishes in the cichlid lakes in the Great Rift Valley system of East Africa. Islands of rock in these large lakes form archipelagoes, and shifts in water level change the configurations of these habitats for many cichlid species, creating an ever-changing set of geographically isolated "islands."

The special case of radiation in Hawaiian *Drosophila* species raises questions about the adequacy of the adaptive model of radiation. Divergence of morphology and behavior appears to be more extreme than that predicted by the adaptive model, stimulating debate on alternative hypotheses of the process of radiation. The genetic drift model recognizes the potential importance of frequent founding events on new islands and subsequent rapid drift in small populations. The sexual selection model invokes strong selection among males and rapid divergence from the parental type on a new island. A third model combines the elements of drift and sexual selection.

The dominant taxa that radiate on continents have commonly originated in the Old World tropics, where landmass area is large, climate is favorable, and population sizes and species richness are high.

## QUESTIONS FOR DISCUSSION

1. Diversification of species has been much more extensive on large landmasses and in the sea than on oceanic archipelagoes. Do you think that archipelago-like topography on the continents and in the oceans was important or essential in this diversification?
2. The ammonites were an extremely diverse group of organisms, showing several major radiations in the fossil record, but are now extinct. Does this suggest, in your opinion, that groups with explosive evolutionary potential have habitats or biological traits that predispose them to catastrophic declines in diversity and even extinction?
3. Does the evidence for adaptive radiation suggest that, given the right physical conditions, any lineage is likely to radiate, or must the potential for radiation include special biological traits, such as common reciprocal chromosomal translocations in the silverswords?
4. What research would you undertake to convincingly establish the argument that a group has actually undergone adaptive radiation rather than progressive occupation?
5. Do you agree that a special case needs to be made for the adaptive radiation of the genus *Drosophila* on the Hawaiian Islands?
6. Given that the specific examples of adaptive radiation discussed in this chapter come from tropical archipelagoes and lakes, can we infer that most adaptive breakthroughs have occurred in tropical latitudes, and northern latitudes have been populated by novel forms that subsequently dispersed from the tropics?
7. Do you think that the panglossian paradigm is too prominent in arguments for the processes involved with adaptive radiation?
8. If it is true that the silverswords represent a most spectacular case of adaptive radiation in the plant kingdom but number only 28 species, must we conclude that most diversification of plants has involved progressive occupation?
9. Generally speaking, after episodes of adaptive radiation in a lineage on an archipelago, recolonization of the mainland source of the lineage has not occurred. What factors would you argue are important for an understanding of this phenomenon, and how would you partition factors among characteristics of the archipelagoes themselves, traits of the organisms involved, and conditions on the mainland?
10. If you received relevant information on a given set of habitats, such as the Galapagos Islands, and the characteristics of a named invading species, do you think you could predict the course of adaptive radiation in the resulting lineage? Would several independently developed scenarios be similar, in your opinion?

## REFERENCES

- Amadon, D. 1947. Ecology and the evolution of some Hawaiian birds. *Evolution* 1:63-68.
- . 1950. The Hawaiian honeycreepers (Aves, Drepanidae). *Bull. Amer. Mus. Nat. Hist.* 95:151-262.
- Ben-Tuvia, A. 1971. Revised list of the Mediterranean fishes of Israel. *Israel J. Zool.* 20:1-39.
- Boucot, A. J. 1975. *Evolution and Extinction Rate Controls*. Elsevier Sci. Pub., Amsterdam.
- Briggs, D. E. G., and H. B. Whittington. 1985. Terror of the trilobites. *Natur. Hist.* 94(12):34-39.
- Brown, J. H. 1971. Mammals on mountaintops: Nonequilibrium insular biogeography. *Amer. Natur.* 105:467-478.
- Brown, W. L. 1957. Centrifugal speciation. *Quart. Rev. Biol.* 32:247-277.
- . 1958. General adaptation and evolution. *Syst. Zool.* 7:157-168.
- Carlquist, S. 1974. *Island Biology*. Columbia Univ. Press, New York.
- Carr, G. D., and D. W. Kyhos. 1986. Adaptive radiation in the Hawaiian silversword alliance (Compositae-Madiinae), [Part] II: Cytogenetics of artificial and natural hybrids. *Evolution* 40:959-976.
- Carr, G. D., R. H. Robichaux, M. S. Witter, and D. W. Kyhos. 1989. Adaptive radiation of the Hawaiian silversword alliance (Compositae-Madiinae): A comparison with Hawaiian picture-winged *Drosophila*, pp. 79-97. In L. V. Giddings, K. Y. Kaneshiro, and W. W. Anderson (eds.). *Genetics, Speciation and the Founder Principle*. Oxford Univ. Press, New York.
- Carson, H. L. 1970. Chromosome tracers of the origin of species. *Science* 168:1414-1418.
- . 1975. The genetics of speciation at the diploid level. *Amer. Natur.* 109:83-92.
- . 1983. Chromosomal sequences and interisland colonizations in Hawaiian *Drosophila*. *Genetics* 103:465-482.
- . 1984. Speciation and the founder effect on a new oceanic island, pp. 45-54. In F. J. Radovsky, P. H. Raven, and S. H. Sohmer (eds.). *Biogeography of the Tropical Pacific*. B. P. Bishop Museum Special Publication 72.
- Carson, H. L., and A. R. Templeton. 1984. Genetic revolutions in relation to speciation phenomena: The founding of new populations. *Ann. Rev. Ecol. Syst.* 15:97-131.
- Carson, H. L., D. E. Hardy, H. T. Spieth, and W. S. Stone. 1970. The evolutionary biology of the Hawaiian *Drosophilidae*, pp. 437-543. In M. K. Hecht and W. C.



- Steere (eds.). *Essays in Evolution and Genetics in Honor of Theodosius Dobzhansky*. Appleton-Century-Crofts, New York.
- Conway Morris, S. 1977. Fossil priapulid worms. *Special Papers in Paleontology* No. 20. Paleontological Assoc., London.
- . 1985. The middle Cambrian metazoan *Wiwaxia corrugata* (Matthew) from the Burgess Shale and Ogygopsis Shale, British Columbia, Canada, pp. 507–582. *Phil. Trans. Royal Soc., London B* 307.
- Culver, D. C. 1982. *Cave Life: Evolution and Ecology*. Harvard Univ. Press, Cambridge, Mass.
- Darlington, P. J. 1959. Area, climate, and evolution. *Evolution* 13:488–510.
- Dial, K. P., and J. M. Marzluff. 1989. Nonrandom diversification within taxonomic assemblages. *Syst. Zool.* 38:26–37.
- Dobzhansky, T. 1972. Species of *Drosophila*. *Science* 177:664–669.
- . 1976. Organismic and molecular aspects of species formation, pp. 95–105. In A. J. Ayala (ed.). *Molecular Evolution*. Sinauer, Sunderland, Mass.
- Drake, J. A., H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson (eds.). 1989. *Biological Invasions: A Global Perspective*. Wiley, New York.
- Eisenberg, J. F. 1981. *The Mammalian Radiations*. Univ. of Chicago Press.
- Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. Methuen, London.
- Futuyma, D. J. 1986. *Evolutionary Biology*. 2d ed. Sinauer, Sunderland, Mass.
- Gould, S. J. 1985. Treasures in a taxonomic wastebasket. *Natur. Hist.* 94(12):22–33.
- . 1986. Play it again, Life. *Natur. Hist.* 95(2):18–26.
- . 1989. *Wonderful Life: The Burgess Shale and the Nature of History*. Norton, New York.
- Greenwood, P. H. 1959. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae), Part III. *Bull. Brit. Mus. Natur. Hist. (Zool.)* 5:179–218.
- . 1965. The cichlid fishes of Lake Nabugabo, Uganda. *Bull. Brit. Mus. Natur. Hist. (Zool.)* 12:315–357.
- . 1967. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae), Part VI. *Bull. Brit. Mus. Natur. Hist. (Zool.)* 15:29–119.
- . 1974a. The cichlid fishes of Lake Victoria, East Africa: The biology and evolution of a species flock. *Bull. Brit. Mus. Natur. Hist. (Zool.)* Suppl. 6:1–134.
- . 1974b. The *Haplochromis* species (Pisces: Cichlidae) of Lake Rudolf, East Africa. *Bull. Brit. Mus. Natur. Hist. (Zool.)* 27:139–165.
- . 1984. African cichlids and evolutionary theories. pp. 141–154. In A. A. Echelle and I. Kornfield (eds.). *Evolution of Fish Species Flocks*. Univ. of Maine Press, Orono.
- Hopkins, et al. (eds.). 1984. *Paleoecology of Beringia*. Academic, New York.
- Kennett, J. P., and M. S. Srinivasan. 1983. Neogene Planktonic Foraminifera. Hutchinson Ross, Stroudsburg, Penn.
- Kontrimavichus, V. L. (ed.). 1985. *Beringia in the Cenozoic Era*. Int. Publ. Serv. Accord, Mass.
- Kosswig, C. 1950. Erythraische Fische in Mittelmeer und an der Grenze der Agäis, pp. 203–212. *Syllegomena Biol. Festschr. Kleinschmidt, Wittenberg*.
- Lack, D. 1947. *Darwin's Finches*. Cambridge Univ. Press, Cambridge, England.
- Lawrence, P. A. 1992. *The Making of a Fly: The Genetics of Animal Design*. Blackwell Scientific Publications, Cambridge, England.
- Lehmann, U. 1981. *The Ammonites*. Cambridge Univ. Press, Cambridge, England.
- Lewin, R. 1982. *Thread of Life*. Smithsonian Books, Washington, D.C.
- Liem, K. F. 1978. Mandibulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes, Part 1: Piscivores. *J. Morph.* 158:323–360.
- . 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Amer. Zool.* 20:295–314.
- Liem, K. F., and J. W. M. Osse. 1975. Biological versatility, evolution and food resource exploitation in African cichlid fishes. *Amer. Zool.* 15:427–454.
- Margulis, L. 1981. *Symbiosis in Cell Evolution*. W. H. Freeman, San Francisco.
- Marshall, L. G., S. D. Webb, J. J. Sepkoski, and D. M. Raup. 1982. Mammalian evolution and the great American interchange. *Science* 215:1351–1357.
- Mayr, E. 1963. *Animal Species and Evolution*. Belknap Press of Harvard Univ. Press, Cambridge, Mass.
- McKaye, K. R., and W. N. Gray. 1984. Extrinsic barriers to gene flow in rock-dwelling cichlids of Lake Malawi: Microhabitat heterogeneity and reef colonization, pp. 169–183. In A. A. Echelle and I. Kornfield (eds.). *Evolution of Fish Species Flocks*. Univ. of Maine Press, Orono.
- Moore, R. C. (ed.) 1957. *Treatise on Invertebrate Paleontology*, Part L. Univ. of Kansas Press, Lawrence.
- Prance, G. T. 1981. Discussion, pp. 395–405. In G. Nelson and D. E. Rosen (eds.). *Vicariance Biogeography: A Critique*. Columbia Univ. Press, New York.
- Price, P. W. 1980. *Evolutionary Biology of Parasites*. Princeton Univ. Press, Princeton, N.J.
- Ramsköld, L. 1992. The second leg row of *Hallucigenia* discovered. *Lethaia* 25:221–224.
- Ramsköld, L., and H. Xianguang. 1991. New early Cambrian animal and onychophoran affinities of enigmatic metazoans. *Nature* 351:225–228.
- Ringo, J. M. 1977. Why 300 species of Hawaiian *Drosophila*? The sexual selection hypothesis. *Evolution* 31:694–696.
- Romer, A. S. 1945. *Vertebrate Paleontology*. 2d ed. Univ. of Chicago Press.
- Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol. Monogr.* 37:317–350.
- Simpson, G. G. 1940. Mammals and land bridges. *J. Wash. Acad. Sci.* 30:137–163.
- . 1953. *The Major Features of Evolution*. Columbia Univ. Press, New York.
- . 1980. *Splendid Isolation: The Curious History of South American Mammals*. Yale Univ. Press, New Haven, Conn.
- Smith, A. 1984. *Echinoid Palaeobiology*. George Allen and Unwin, London.

- Spieth, H. T. 1974a. Courtship behavior in *Drosophila*. *Ann. Rev. Entomol.* 19:385-405.
- . 1974b. Mating behavior and evolution of the Hawaiian *Drosophila*. pp. 94-101. *In* M. J. D. White (ed.). *Genetic Mechanisms of Speciation in Insects*. D. Reidel, Dordrecht, Holland.
- Špínar, Z. V. 1972. *Life Before Man*. Thames and Hudson, London.
- Stehli, F. G., and S. D. Webb (eds.). 1985. *The Great American Biotic Interchange*. Plenum, New York.
- Templeton, A. R. 1979. Once again, why 300 species of Hawaiian *Drosophila*? *Evolution* 33:513-517.
- Vuilleumier, F. 1970. Insular biogeography in continental regions, [Part] I: The northern Andes of South America. *Amer. Natur.* 104:373-388.
- . 1973. Insular biogeography in continental regions, [Part] II: Cave faunas from Tessin, southern Switzerland. *Syst. Zool.* 22:64-76.
- Weidmann, J. 1969. The heteromorphs and ammonoid extinction. *Biol. Rev.* 44:563-602.
- . 1973. Evolution or revolution of ammonoids at Mesozoic system boundaries? *Biol. Rev.* 48:159-194.
- Westoll, T. S. 1949. On the evolution of the Dipnoi, pp. 121-184. *In* G. L. Jepsen, E. Mayr, and G. G. Simpson (eds.). *Genetics, Paleontology, and Evolution*. Princeton Univ. Press, Princeton, N.J.
- Whittington, H. B. 1985. *The Burgess Shale*. Yale Univ. Press, New Haven, Conn.
- Yoon, J. S. 1989. Chromosomal evolution and speciation in Hawaiian *Drosophila*, pp. 129-147. *In* L. V. Giddings, K. Y. Kaneshiro, and W. W. Anderson (eds.). *Genetics, Speciation, and the Founder Principle*. Oxford Univ. Press, New York.
- Zimmerman, E. C. 1948. *Insects of Hawaii*. Univ. of Hawaii Press, Honolulu.