

Mesozoic and Early Cenozoic Terrestrial Ecosystems

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1 INTRODUCTION

As discussed in chapter 5, the basic trophic structure of modern terrestrial ecosystems was established no later than the Late Permian, when vertebrate herbivores joined the terrestrial food pyramid for the first time. Although the fundamental template for subsequent terrestrial communities was created during the first 150-to-200 My of life on land, the 200-My interval encompassed by the Mesozoic and early Cenozoic records major shifts in vegetational structure, in the functional attributes of herbivorous animals, and in the degree and nature of inferred interactions between plants and herbivores, as well as the two greatest mass-extinction episodes in the history of terrestrial ecosystems. We have included the Paleocene and Eocene with the Mesozoic because this facilitates comparison of terrestrial ecosystems before and after the Cretaceous/Tertiary (K/T) extinctions.

Mesozoic and early Cenozoic terrestrial ecosystems are temporally intermediate between the first integrated ecosystems of the Late Permian and middle to late Tertiary ecosystems that have close living analogues. Taxonomic modernization during this interval was "progressive" (though hardly uniformly so), but our paleoecological inferences suggest this was not true for the structure of terrestrial vegetation or the dynamics of plant-animal interactions. For example, the dynamics of some late Eocene ecosystems may be more analogous to those of the later Mesozoic than of the Paleocene and early Eocene ecosystems that immediately preceded them. Similarly, in some aspects of trophic relationships and vertebrate-plant interactions, the Paleocene may more closely resemble the late Paleozoic than the Late Cretaceous. These major fluctuations in the nature of Mesozoic and early Cenozoic ecosystems contrast with the more directional progression of the Paleozoic and may give us greater insight into the response of terrestrial ecosystems to major perturbations.

Increasing complexity and interdependence of ecological systems during

the Paleozoic seems to have been related to evolutionary innovations among terrestrial animals and plants (e.g., development of tree habit in plants, herbivory in animals). During the Mesozoic and early Cenozoic, there were periods of stability and change in type of herbivory and architecture of vegetation that appear to be related to climatic shifts, major extinctions, and perhaps cybernetic properties of ecosystems, though evolutionary innovations continued to play an important role in expanding the array of ecological interactions between terrestrial organisms. The contrast between the Paleozoic and Mesozoic-Paleogene can be seen as the difference between observing the behavior of a system during its assembly and observing its response to perturbation once it is established.

Data on the paleoecology and spatiotemporal distribution of fossil plants and herbivorous animals can be culled from various reference works (vertebrates in general: Carroll 1988; dinosaurs: Weishampel et al. 1990; insects: Hennig 1981; plants: Taylor 1981; Stewart 1983; Meyen 1987), but they are rarely integrated with one another. We think this review of the combined animal and plant data from an evolutionary perspective has generated new questions. It will be clear from the temporal, geographic, and environmental distribution of the fossil localities discussed here that many inferences about past ecological interactions would benefit from more evidence. Perhaps the single most important defect of the fossil record is that insects and other terrestrial invertebrates are poorly known, or are described only in systematic terms, making it difficult to evaluate their possible ecological interactions with other land organisms. In present-day ecosystems, herbivory by insects and other invertebrates (including acarids, tardigrades, myriapods, nematodes and gastropods) is approximately of the same order of magnitude as that by vertebrates, although the latter generally have a far greater impact on the structure of vegetation (Crawley 1983). Because modern types of arthropod herbivory probably were established by the mid-Pennsylvanian (Labandeira 1990; Scott 1991), the selective impact of arthropod herbivory on plants may have changed relatively little since the early Mesozoic. Thus, our scant knowledge of the fossil record of terrestrial invertebrates may not distort too seriously our understanding of changes in herbivory during the Mesozoic and early Cenozoic. In the modern world, terrestrial arthropods also play a major role in plant reproduction, and though there have been recent advances in interpreting past pollination interactions (e.g., Crepet and Friis 1987), these are based more on plant fossils than on arthropod fossils, leaving open the possibility that interpretations will change substantially when better information is available on the pollinators themselves.

This report is divided into three main parts. Sections 2–5 summarize the geographic, temporal, and environmental distribution of important fossil assemblages of terrestrial plants and herbivorous tetrapods and insects, and provide a chronological summary of first-order inferences about changing

vegetation and faunas during the Mesozoic and early Cenozoic. In syntheses following the reviews of the fossil record for each of the Mesozoic periods and for the Paleocene-Eocene, we highlight the outstanding paleoecological characteristics of the respective floras and faunas of the Triassic, Jurassic, Cretaceous, and Paleogene, and we make some inferences concerning the ecological interactions between contemporaneous animals and plants. We also relate ecological inferences to prominent evolutionary events among animals and plants, to extinctions and diversifications, and to paleoclimatic changes. We place special emphasis on times and places where ecological and evolutionary changes are strongly concordant or discordant and on offering explanations for these patterns. We also make predictions about what will be found in the fossil record if our explanations are correct.

In §6 we discuss how various kinds of ecological interactions appear to have changed through time. In §7 we use examples to take up the connection between environmental conditions and inferred community structure, the implications of change in community structure and dynamics for the evolution of individual lineages (and vice versa), and the way in which large-scale perturbations might have affected ecological structure and evolutionary opportunity.

2 TRIASSIC BIOTAS

The history of Mesozoic terrestrial ecosystems is marked by a series of large-scale perturbations. The basis for the boundary between the Paleozoic and Mesozoic is the largest marine extinction of the Phanerozoic. However, in contrast to the estimates of a 91% to 97% loss of species in shallow-water marine faunas (Raup 1986), estimates of the diversity decline in terrestrial organisms range from about 20% for species of plants (Niklas et al. 1980) to a questionable 50% for genera of tetrapods (Benton 1985, 1987; Padian and Clemens 1985). Disappearance of most Permian pollen types exactly at the Permian-Triassic boundary in Israel and reduced diversity in Early Triassic assemblages are thought to reflect a preservational or depositional hiatus rather than a catastrophic extinction (Eshet 1990). The relatively smaller decrease in diversity among terrestrial organisms, particularly plants, should not detract attention from the very high rates of turnover at the generic and familial level; for example, similarities between Permian and Triassic floras are mostly restricted to family and higher taxonomic levels. Also, unlike some of the extinctions in the shallow-water marine fauna, floristic turnover during the Permian-Triassic interval appears to have been a prolonged process. Worldwide it took place over a period of at least 25 my, although in any one place it could have been more rapid (Frederiksen 1972; Knoll 1984; Eshet 1990). On the basis of our present understanding of the tempo and paleoecological characteristics (at least among plants) of the Permian/Triassic extinctions, it seems most probable that they reflect large-scale climatic and paleogeographic

alterations rather than a sudden catastrophic mortality (Knoll 1984; Traverse 1988). This is consistent with recent understanding of the Permian/Triassic extinctions in the marine realm (Erwin 1990).

Correlation of early Mesozoic continental deposits generally is difficult (see Olsen and Sues 1986), and chronostratigraphic resolution is poor. This is a consequence of several factors, including the occurrence of important fossil assemblages in relatively condensed stratigraphic sections and especially poor correlation with the marine standard sequences (Olsen and Sues 1986). Consequently it is difficult to determine whether some differences in Triassic terrestrial biotas represent change through time or geographic variation controlled by climate or other regional factors.

The maximum development of Pangaea occurred at approximately the Middle/Late Triassic boundary (Veevers 1989; comparable to Early Jurassic paleogeography shown in fig. 6.1), and throughout the period this landmass moved slowly northward. In spite of the contiguity of the continental masses forming Pangaea, Triassic faunas and floras were markedly provincial, probably reflecting monsoonal climatic zonation and extreme seasonality caused by continentality and the symmetrical placement of Pangaea about the equator (Parrish et al. 1982; Crowley et al. 1989; Kutzbach and Gallimore 1989). Triassic Pangaeian biotas are commonly divided into northern (Laurasian) and southern (Gondwanan) realms, with several cases of documented overlap, especially in India where a Gondwanan flora (Dobruskina 1987) occurs together with characteristically Laurasian tetrapods (Olsen and Sues 1986). During the Middle to Late Triassic, Laurasian floras were divided into Siberian and Eurasian provinces. However, endemism in both floras (Meyen 1987) and vertebrate faunas (Olsen and Sues 1986) significantly decreased during the Triassic. High-latitude climates were relatively warm, an inference based in part on the common occurrence of large amphibians in Early Triassic assemblages from Australia, Antarctica, eastern Greenland, and Spitzbergen. Coal-rich sequences have been recorded from both high northern and high southern paleolatitudes; these reflect climates that were wetter than those of lower paleolatitudes.

The biotic character of the Triassic is probably linked to dry or highly seasonal climates associated with the coalescence of Pangaea. Such features include: (1) the continued increase in diversity of gymnospermous seed plants, particularly of xeromorphic groups of scale-leaved conifers and thick-cuticled seed ferns and cycadophytes; (2) the increase in diversity and abundance of diapsid (presumed uric-acid-excreting, more water-efficient), rather than synapsid (presumed urea-excreting, less water-efficient), amniotes (Robinson 1971); and (3) decrease in diversity of many groups of plants and herbivorous tetrapods, especially during the time interval from the late Carnian to Hettangian (Olsen and Sues 1986). The existence, timing, and causes of plant and vertebrate extinctions at the Carnian/Norian boundary have been debated, but

the most recent work links these events to a late Carnian wet period followed by a return to dry climates in the early Norian (Simms and Ruffell 1989).

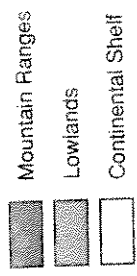
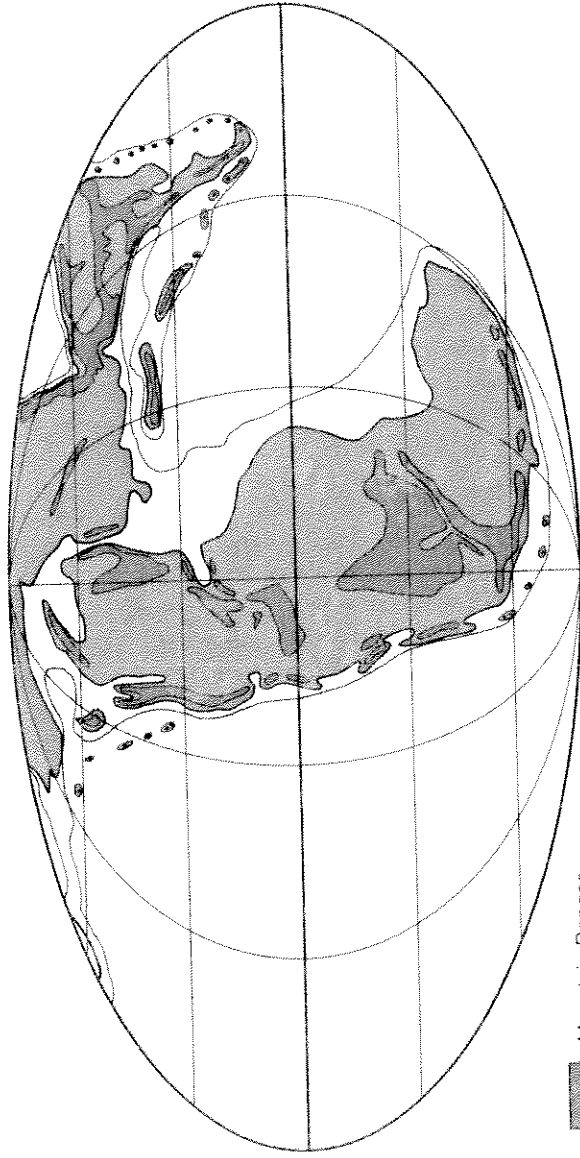
Like its beginning, the end of the Triassic was marked by a substantial extinction among terrestrial vertebrates. Unlike the Permian/Triassic extinctions, however, the Triassic/Jurassic extinctions occurred over a relatively short period of time, and during the initial breakup of Pangaea. Typical Early Jurassic assemblages have been estimated to occur as little as 100 ky to 200 ky after the Triassic/Jurassic boundary (Olsen et al. 1987), although the extinctions may have occurred over a period of up to 2 my. Olsen et al. (1987) suggest that the terminal Triassic extinctions were associated with the bolide impact that created the large Manicouagan crater (> 70 km in diameter) in Quebec (Olsen et al. 1987). More recent observations of impact ejecta associated with bivalve extinctions near the Triassic/Jurassic boundary in marine deposits in Europe (Newton and McRoberts 1990) and of an increase in fern spore abundance in earliest Jurassic palynofloras of North America (Fowell 1990) offer some support for the theory that the extinctions were impact related.

2.1 Triassic Vegetation of Laurasia

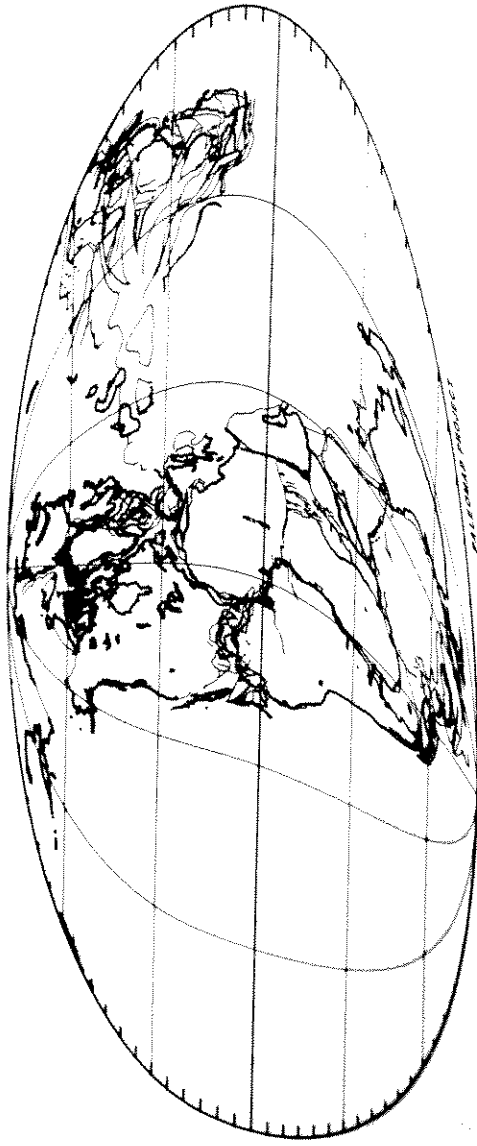
Laurasian Triassic floras can be characterized generally as a mixture of primitive conifers (Voltziaceae and Lebachiaceae) along with various cycadaleans, bennettitaleans, "pteridosperms," ferns (including some of tree habit), and sphenopsids (Dobruskina 1987). Ginkgoaleans (e.g., *Sphenobaiera*) were more abundant and diverse at northerly paleolatitudes. Most of the conifers and ginkgoaleans are thought to have been medium-sized to large trees that perhaps formed a diffuse canopy. Mesozoic conifer seeds were generally small and winged, suggesting that they were not animal dispersed and that they required well-lit environments for germination and early growth (Tiffney 1986a). Conifers were probably the "big trees" in many Triassic landscapes. This idea is based on the observation that almost all of the large silicified trunks of this age are attributable to conifers. (Note, however, that *Araucarioxylon* is a form genus for rather generalized and primitive dense wood that may belong to a wide variety of gymnosperms.) Although the diversity of plant habits among Triassic conifers may have been considerably greater than it is in the present-day angiosperm-dominated world, there is little fossil evidence for dramatically different forms (e.g., herbs, lianas, floating aquatics). Ash (1987a) has reported a possible cordaitalean of small stature from the Late Triassic of the southwestern United States, but it is unclear whether the fossils represent a mature shrubby or herbaceous plant or the sapling of a tree in which the wood has not been preserved.

Many living Araucariaceae form diffuse canopies. Some extant species of *Araucaria* and *Agathis* have leaves with sharp apices that persist on the trunk

EARLY JURASSIC (195 Ma)



Paleotopography



Hand-drawn map of the world showing continents and a grid of latitude and longitude lines.

and main branches, gradually becoming surrounded by secondary tissue. These "armored" trunks and branches may be (or may have been) a defense against vertebrate herbivores, but it is not known if this is a retained primitive trait that also would have characterized Mesozoic araucarians.

Primitive ginkgoaleans (e.g., *Sphenobaiera* and *Glossophyllum*) were probably small-seeded, short, underbrush trees in conifer forests (Krassilov 1975a). During the Mesozoic the lineage increased in size, a trend accompanied by the appearance of larger seeds, longer petioles, less dissected leaves, and deciduousness (Krassilov 1975b). The sole extant species, *Ginkgo biloba*, is notable for having seeds consisting of a fleshy, odoriferous outer layer surrounding an inner stony layer. At maturity, the seeds are shed en masse from the tree. It has been suggested that these features are relict adaptations for dispersal by terrestrial reptiles (saurochory *sensu* Van der Pijl 1982), although the persistence of *Ginkgo* throughout the Tertiary argues against complete dependence on dinosaurian dispersers.

Most living cycads are relatively short, stout, and unbranched. Exceptions include species of *Macrozamia* that reach 20 m in height and branch several times. Living cycads characteristically have very slow growth rates but display a wide range of habits spanning epiphytes, mangroves, and fire-tolerant shrubs (Norstog 1987). The structure of cycad seeds and the manner of their presentation both match the suite of traits postulated to be associated with reptile dispersal (van der Pijl 1982). Cycad foliage is toxic to mammals (Chamberlain 1935).

The range of habits and growth forms among Mesozoic cycads is likely to have been greater than what is seen even in living species (Spicer 1987). Some Mesozoic cycads had short trunks, but others were more slender and branched; the existence of a relatively slender form in the Late Triassic (*Leptocycas*) raises the possibility that this is the primitive condition for the whole group (Delevoryas and Hope 1976). The lax cones of *Beania* and *Androstrobus* indicate that wind pollination was much better developed in some Mesozoic cycads than in any extant species.

The widespread continental climates of the Late Permian and early Mesozoic may have selected against pteridophytes with water-dependent sexual reproduction. The Paleozoic-Mesozoic transition was an interval of turnover among pteridophyte groups. The Marattiaceae and Osmundaceae carried over from the Paleozoic, but the early Mesozoic was a time of diversification of many modern "lower" fern groups, such as Schizaeaceae, Osmundaceae, Dipteridaceae, and Gleicheniaceae.

Mesozoic marattiacean ferns appear to have been more similar to the extant genera in the family than to Paleozoic forms such as *Psaronius*. Living species are tropical, understory trees with short, unbranched stems up to 60 cm in diameter and thick, pinnately compound leaves up to 4 m long. All extant species are specialized for growth on wet, shaded forest floors. The extant

families Osmundaceae, Dipteridaceae, and perhaps Polypodiaceae are also known from Mesozoic deposits. Although many of the living species in these families occupy wet, shaded spots under forest canopies, there is no direct evidence for the habits or habitats of the Mesozoic species.

Ferns in the families Matoniaceae and Gleicheniaceae may have been major colonists of open, dry, or even nutrient-poor substrates during much of the Mesozoic, perhaps forming vegetation analogous to savannas or grasslands now dominated by herbaceous angiosperms (Coe et al. 1987). Matoniaceae were rhizomatously spreading, relatively thick-cuticled ferns less than 2 m high. Living Gleicheniaceae generally have similar growth habits and are colonists of disturbed tropical habitats. Although the Gleicheniaceae are virtually absent in the Triassic, the family has been recognized in the late Paleozoic, and *Gleichenia*-like plants became common in the Jurassic and Cretaceous (Taylor 1981).

Both sphenopsids and lycopsids decreased in diversity, and both became increasingly restricted to herbaceous forms during the Triassic. Sphenopsid fossils are particularly abundant and are often preserved in situ, probably because they tended to grow on freshly deposited substrates that are common in active depositional settings. All Mesozoic sphenopsids were based on the same basic body plan as present-day *Equisetum*, having unbranched central axes bearing whorls of leaves. They reproduced by spores, although rhizomatous growth also characterizes the group. Extant species of *Equisetum* contain numerous large, siliceous phytoliths in their tissues, which may serve as an herbivore deterrent, but there is no direct evidence for these structures in the fossils. During the early Mesozoic, axes of genera such as *Neocalamites* were 10–30 cm thick and may have attained heights of 10 m. The genus *Schizoneura* (Triassic–Early Jurassic) had an axis 2 cm wide and up to 2 m tall. Smaller equisetaleans are also abundant in Mesozoic floras. The anatomy and distribution of Mesozoic sphenopsids is consistent with primary colonization of open or disturbed damp habitats, but their rhizomatous growth and moderate size may have allowed them to form dense thickets that could have inhibited colonization by later successional forms.

Early Triassic coastal vegetation in the northern part of Laurasia and Australia was dominated by stands of the lycopsid *Pleuromeia*. *Pleuromeia* was a genus of unbranched, herbaceous plants 1–2 m tall and about 10 cm in diameter. *Pleuromeia* stems were covered with narrow leaves about 10 cm long and were terminated by an apical cone. These plants were heterosporous and dioecious. They occur in extensive monospecific assemblages together with freshwater-to-marine invertebrates, suggesting they formed dense growths along coasts of lakes, estuaries, and oceans (Retallack 1975). The *Pleuromeia* associations represent the last vegetation type in which lycopsids were the major structural element, although species of *Pleuromeia*-like plants survived later into the Triassic.

During the latter half of the Triassic, east-west provinciality decreased in the equatorial region of Laurasia, and cycadales, bennettitaleans, and more advanced conifers (including Pinaceae and early Cheirolepidiaceae) became more abundant in many areas. Palynofloras from eastern North America show major reductions in diversity in the Carnian and again at the Triassic/Jurassic boundary (Cornet and Olsen 1985; Olsen and Sues 1986; Boulter et al. 1988). Late Triassic floras of Eurasia typically contain a diverse mixture of peltaspermeaceous seed ferns, bennettitaleans, cycadales, conifers, ginkgoaleans, and a number of ferns, including species in the Marattiaceae, Osmundales, Diplazidaceae, and Matoniaceae (Vakhrameev et al. 1978). Peltaspermeaceae were probably small-to-moderate-sized plants with small seeds and bipinnate fronds about 0.5 m long. Foliage of the peltasperm *Lepidopteris ottonis* had a thick cuticle with stomata on both sides; this seed fern occurs in near-shore marine sediments, suggesting that it was a mangrove.

Specific Laurasian Plant Assemblages

The Late Triassic flora of the Chinle Formation in the area of the Petrified Forest National Park in Arizona is late Carnian to early Norian in age (Olsen and Sues 1986; Ash et al. 1986; Litwin 1986) and has been reconstructed as representing three vegetation types (Gottesfeld 1972). Proximal floodplains were occupied by low-statured vegetation dominated by the bennettitalean *Otozamites* and the ferns *Phlebopteris*, *Clathropteris*, and *Todites*. *Schilderia*, a buttressed tree possibly related to the living Gnetales, also occupied proximal floodplain areas. Large *Neocalamites* (30 cm stem diameter and at least 6 m tall) grew along the channels in disturbed sites. Slightly more distal floodplains supported forests of *Araucarioxylon* trees 40–60 m high. Close spacing of in situ stumps and the rarity of branching (even on long sections of trunks) led Gottesfeld (1972) to suggest that the *Araucarioxylon* forests were dense. Palynomorphs provide evidence of an understory of ferns and at least one bennettitalean. The relatively unbranched nature of *Araucarioxylon* might imply self-pruning in a low-light subcanopy habitat (Gottesfeld 1972). However, sparse canopies are common in some living swamp conifers, apparently as a consequence of stressed conditions associated with waterlogged soils (Brown 1981). The existence of an “upland” flora (i.e., vegetation existing on surfaces slightly higher than the floodplain) consisting of cordaites (*Dadoxylon*), ginkgoaleans, and caytonialean seed ferns is inferred from palynofloras and rare specimens of fossil wood (Gottesfeld 1972). Elements of the Petrified Forest National Park flora not discussed by Gottesfeld include another probable araucarian, *Woodworthia* (generally smaller than *Araucarioxylon* and with persistent short shoots on the trunk), a cycad (*Lyssoxylon*), a variety of ferns (including two tree ferns), and several herbaceous lycopsids (Ash 1972c).

Late Triassic plant assemblages approximately coeval with those of the Petrified Forest are known from two other depositional settings in the southwestern United States, lake shore and oxidized floodplain deposits (Ash 1978, 1987b). The Ciniza lake-bed assemblages probably were deposited in a shallow body of water of limited areal coverage and represent vegetation growing in the immediate vicinity of the lake margin (Ash 1978). The flora is of low diversity (8–14 species) but includes four types of possibly araucarian conifer foliage (*Pagiophyllum*), a bennettitalean (*Nilssoniopteris*), and the enigmatic gymnosperm *Dinophyton* (Ash 1978). The vegetation on the lake margin is thought to have been dominated by *Equisetites*, *Phlebopteris*, and *Nilssoniopteris* (the tallest plant in this community). Somewhat dryer sites farther away from the lake margin apparently supported conifer forest with an understory of the ferns *Todites* and *Clathropteris* and a subcanopy level including bennettitaleans and caytoniaceae seed ferns (Ash 1978). The relative rarity of ferns in these assemblages may reflect the tendency of ferns not to abscise leaves, thus releasing fewer leaves for transport into lacustrine sediments.

The “red bed” flora described by Ash (1987b) is possibly Norian in age and thus somewhat younger than that of the Ciniza Lake Beds or the Petrified Forest, but compositional differences appear to be related more to depositional environment than to time. The red-bed flora is extremely depauperate; only seven genera are known from six localities: *Neocalamites*, *Pagiophyllum*, *Araucarioxylon*, *Pelourdea*, *Woodworthia*, *Schilderia*, and *Sanmiguelia*. Another curiosity of this flora is the in situ burial of nearly whole plants at several sites (Ash 1987b). Ash interpreted some of these assemblages as representing low-diversity, low-statured vegetation growing on river levees. Alternatively, in a location with frequent depositional events, small in situ plants could represent saplings of species that attained larger size in more stable settings.

The Late Triassic floras of the American Southwest provide some of the best available examples of early Mesozoic vegetation. Generally these floras are of moderate to low diversity and contain relatively few species that are likely to have been large trees, though some conifers clearly formed tall forests. Matoniaceae, osmundaceae, and other ferns were evidently the most abundant and diverse element of the understory, particularly in wet soils. Bennettitales were probably important, both as low-statured plants of open settings and as understory elements in conifer forest. Most calamites were probably colonizers of disturbed sites.

Another Late Triassic flora, probably of late Norian age, was described from the Scoresby Sound area of eastern Greenland (Harris 1937 and references therein). The fossiliferous deposits were formed in abandoned fluvial channels. Although this specific environment has not been identified as producing megafossil assemblages in the Chinle Formation, the Scoresby Sound assemblages and most of the Chinle floral occurrences presumably are derived from wet floodplain vegetation, and thus differences in composition are not

likely to reflect purely taphonomic effects. The most striking difference between the Scoresby Sound and American assemblages is in simple numbers of species (200 vs. 60), but unfortunately it is hard to determine the degree to which this reflects differences in sampling and taxonomic treatment. The Scoresby Sound flora was collected from over 70 "major" plant beds (Harris 1937) and presumably even more individual localities distributed through a significant stratigraphic interval, while the Chinle flora appears to have been collected from between 10 and 20 major sites (Ash 1972). Thus, the much greater species richness of the Scoresby Sound flora may result in part from better sampling of heterogeneous floodplain vegetation, and from combining floras across a longer time interval. However, the presence of coal beds in the Scoresby Sound sequence and of many species with mesomorphic cuticles (even in groups, such as the conifers, that commonly display some degree of xeromorphy) suggests that the Late Triassic floras from eastern Greenland grew under a wetter climate than that characteristic of the southwestern United States during the Late Triassic. This climatic difference has been predicted on the basis of the proximity of East Greenland to the Arctic Basin and its paleo-latitudinal position at about 45 to 50 degrees north (Parrish et al. 1982). Therefore the greater number of species in the Scoresby Sound flora could reflect a genuinely more diverse, mesic vegetation.

Regardless of the relative diversity of the Chinle and Scoresby Sound floras, it is clear that the Greenland assemblages reflect a rich and diverse forest vegetation. Harris (1937) mentions large pieces of poorly preserved fossil wood that demonstrate the presence of trees, but this also is documented by the compression flora. Tiffney (1986a) measured and tabulated the seeds described by Harris and reported a mean seed size of 188 mm^3 , with a maximum of $1,600 \text{ mm}^3$ and a minimum of 0.64 mm^3 (based on 30 form species). The larger seeds in this flora generally were borne by the cycads and ginkgoaleans, with bennettitaleans and seed ferns producing medium-to-small-sized seeds. As a whole, the Scoresby Sound flora has somewhat smaller seed sizes than the summed Triassic floras (Tiffney 1986a).

All of the major Triassic plant groups occur in the Scoresby Sound flora, including lycopoids, sphenopsids, ferns, ginkgoaleans, bennettitaleans, cycadaleans, pteridosperms, and conifers. Diversity is also very high in groups likely to have had an arborescent habit. Based on foliar material alone, Harris (1937) reported 28 conifer species, 20 cycads, 19 bennettitaleans, 10 ginkgoaleans, 8 pteridosperms, and 4 czekanowskialean. Thus, even assuming that all of the ferns and sphenopsids can be classified accurately as herbaceous, about 90 species of woody plants with shrub-to-tree habit grew on the Scoresby Sound floodplains. The Scoresby stratigraphic sequence represents a considerable interval of time, and therefore not all of these species necessarily coexisted. Nevertheless the number of species identified in the Scoresby flora is more similar to the number found in the angiosperm-dominated floras of the

Late Cretaceous and Tertiary than in most other Mesozoic floras. This implies that during the Late Triassic complex and diverse forest vegetation may have flourished under warm, wet climates, even at latitudes that dictated substantial seasonal variation in day length and a moderately low angle of solar radiation.

2.2 Triassic Vegetation of Gondwana

Toward the end of the Permian in the Southern Hemisphere, the *Glossopteris* flora declined. Early Triassic vegetation in the same areas came to be dominated by the corystospermaceous seed fern *Dicroidium*, although a transitional flora characterized by a high abundance of the seed fern *Thinnfeldia* is known from a few places (Retallack 1977; Anderson and Anderson 1983a, b). *Dicroidium* played a leading role in a variety of vegetation types, from heath to broad-leaved forest to dry woodland, and is sometimes found in virtually monospecific stands (Retallack and Dilcher 1988). Voltziacean and primitive podocarpaceous conifers also were part of Gondwanan Triassic floras, and they became more important during the Middle to Late Triassic, along with other peltaspermeaceous seed ferns and some Laurasian groups of cycadaleans and ginkgos. At or near the end of the Triassic, the *Dicroidium* flora declined and was replaced by a more cosmopolitan conifer-bennettitalean flora.

Specific Gondwanan Plant Assemblages

Retallack (1977) reported on several Late Permian through Triassic assemblages from eastern Australia and identified a series of vegetational types based on floral composition, depositional environment, and paleosol characteristics. In much of Gondwana, Early Triassic coastal vegetation consisted of monodominant stands of small, arborescent lycopsids such as *Pleuromeia* and *Gregicaulis*, but, by the Middle to Late Triassic, these same environments were dominated by the seed fern *Pachypteris* (Retallack 1975, 1977; Anderson and Anderson 1983b). In the Early Triassic (Scythian and early Anisian) of eastern Australia, delta-top and lagoon-margin woody vegetation comprised sphenopsids (*Neocalamites*), ferns (*Cladophlebis*), seed ferns such as *Dicroidium*, *Lepidopteris*, and *Pachypteris*, and the cycadophyte *Taeniopteris*. *Neocalamites* was probably most important in early succession. *Taeniopteris lentriculiformis* is inferred to have been a slender-branched coastal scrub and was an important part of coastal vegetation through the early and middle Anisian. Assemblages dominated by the primitive conifer *Voltziopsis* also are known from the Early Triassic of this area and may represent a different kind of lowland forest vegetation than those assemblages characterized by *Dicroidium*. Vegetation of drier areas is reconstructed as a woodland dominated by *Dicroidium* and *Xylopteris* associated with *Sphenobaiera* and *Czekanowskia*. The most taxonomically diverse and structurally complex vegetation reported by Retallack (1977) from eastern Gondwana was late Ani-

sian to early Ladinian broadleaf forest composed of sphenopsids, ferns, seed ferns, cycadales, ginkgoaleans, and conifers. This forest included *Neocalamites*, *Phyllothea*, *Asterothea*, *Cladophlebis*, *Coniopteris*, *Dictyophyllum*, *Dicroidium*, *Lepidopteris*, *Pachypteris*, *Johnstonia*, *Tetraptilon*, *Sphenobaiera*, *Ginkgoites*, *Phoenicopsis*, *Rissikia*, *Taeniopteris*, *Pterophyllum*, and *Pseudoctenis*. *Phoenicopsis* sometimes occurred as a monodominant in levee settings. The assemblages described by Retallack (1977) suggest a high degree of vegetational and landscape heterogeneity in east Gondwana during the first part of the Triassic.

Early to Middle Triassic assemblages are also known from South Africa (Anderson and Anderson 1983a, b). The seed ferns *Dicroidium* and *Lepidopteris*, along with sphenopsids and lycopsids, are reported as dominant in a wet or seasonally wet inland basin environment. Interpreted vegetational associations include forest or woodland dominated by *Dicroidium* and *Lepidopteris* that grew on levees or other elevated areas, monospecific sphenopsid stands in wet areas, and monospecific lycopsid stands fringing bodies of water (Anderson and Anderson 1983b). Middle Triassic (Anisian-Ladinian?) floras from the Molteno Formation are known from more than 70 sites and include some 115 species; individual sites produce from 1 to more than 60 species, with a mean of about 10 (Anderson and Anderson 1983b). The Molteno sequence was deposited in an inland basin at a paleolatitude of about 55–60 degrees S under a seasonal but moist climate. In distance from the paleoequator, overall climate, and in some of the depositional settings preserved, the Molteno floral assemblages show similarities to the late Norian Scoresby Sound flora of Greenland. Overall the Molteno flora is dominated by *Dicroidium*, the conifer *Heidiphyllum*, the ginkgophyte *Sphenobaiera*, and *Neocalamites*. Anderson and Anderson (1983b) recognized 25 associations of fossil plants that they interpreted to represent four types of vegetation: (1) monospecific *Neocalamites* thickets in wet areas; (2) monodominant or low-diversity assemblages of *Heidiphyllum* in slightly less wet areas, sometimes found directly above *Neocalamites* assemblages; (3) low-diversity shrubby vegetation of *Sphenobaiera*; and (4) moderately diverse (>20 species) forest or woodland on more elevated ground, dominated by *Dicroidium*. The most diverse assemblages are dominated by species of *Dicroidium* (50%–60% of specimens) but also typically include *Neocalamites*, various ferns such as *Todites*, *Cladophlebis*, and *Dictyophyllum*, the ginkgophyte *Sphenobaiera*, the seed ferns *Lepidopteris*, *Glossopteris*, and *Yabeiella*, the bennettitalean *Pseudoctenis*, the cycadophyte *Taeniopteris*, and the conifers *Rissikia* and *Heidiphyllum*. The predominance of 1 or 2 species of *Dicroidium* at diverse localities, with many rare forms, may imply that the relative abundance of the common species was enhanced by deciduousness and/or large size, both of which have been suggested for *Dicroidium* on morphological grounds (discussed under the name *Umkomasia granulata* by Retallack and Dilcher [1988]). Although the diversity of the

Molteno floras is not spread across all major taxonomic groups to the degree that it is in the Scoresby Sound flora, the South African assemblages are nevertheless quite diverse for local floodplain floras. The relatively high diversity again seems to suggest that under moist, though seasonal, climates, Triassic floras may have attained greater diversity and structural complexity than they did under monsoonal dry or arid climates of the low-latitude regions.

2.3 Triassic Faunas

At least five orders of Paleozoic insects with probable plant-sucking habits did not survive into the Triassic. Continuing from the Permian were the Orthoptera (at least some of which were herbivorous), Hemiptera, Thysanoptera (including possible pollen feeders), and Coleoptera (which did not yet include definitely herbivorous forms). Chewing stick insects (Phasmida) and xyeloid hymenopterans (which have herbivorous larvae) made their first appearance in the fossil record.

Triassic terrestrial vertebrate faunas were a mixture of groups that persisted from the late Paleozoic and the stem groups or earliest known representatives of most extant major taxa. The establishment of herbivory in several lineages of amniote tetrapods during the late Paleozoic was followed by a great radiation of herbivorous synapsids in the Permian. Although this group suffered a major decrease in diversity toward the end of the Permian, the two major groups of Late Permian herbivores, Dicynodontia and Procolophonoidea, were still represented in Early Triassic faunas.

Early Triassic herbivorous tetrapods in general seem to have been smaller than those of the Late Permian, at least in Gondwana, where the fossil record is most complete (Benton 1983). These forms (e.g., those from the *Lystrosaurus*-Zone fauna) show a limited range of body sizes (0.5 to < 2.0 m body length). The dominance and diversity of large herbivores increased during the Middle and Late Triassic, especially with the appearance of prosauropod dinosaurs in the Carnian. Early Triassic faunas retained the dicynodonts, the dominant Late Permian group of small-to-large quadrupedal herbivores. The dicynodont *Lystrosaurus* was the characteristic herbivore of many Early Triassic tetrapod assemblages, especially in the Gondwanan realm. Dicynodonts had robustly built, presumably akinetic skulls. The typically edentulous upper and lower jaws were covered by horny beaks (rhamphothecae), between which plant fodder was cut by retraction of the mandible (Crompton and Hotton 1967; King 1981). Some Middle and Late Triassic dicynodonts, such as *Dinodontosaurus*, probably reached body weights in excess of 1,000 kg ("megaherbivores" *sensu* Owen-Smith 1987) and were very common in Gondwanan faunas (Cox 1965). Foraging heights ranged between 1 and 2 meters above the ground.

The Middle Triassic also witnessed a radiation of gomphodont cynodonts

(Diademodontidae, Trirachodontidae, and the probably paraphyletic Traversodontidae). They formed a fairly diverse group with a considerable range in body size and were especially diverse in the Gondwanan realm. A few Carnian traversodont cynodonts, such as *Exaeretodon* from Argentina and Brazil and *Scalenodontoides* from southern Africa, reached a length of 3 m. They had large, massive skulls and large molariform teeth that met in complex occlusion and show extensive wear. They employed bilateral mastication and a palinal power stroke (Crompton 1972; Crompton and Attridge 1986). These features, combined with evidence for muscular cheeks, imply that these cynodonts were capable of oral processing of very tough vegetation.

Rhynchosaurs were another important group of late Middle to Late Triassic medium-sized (1–2 m body length) herbivores that employed a high degree of oral food processing. These archosauromorph diapsids are characterized by large tooth plates and powerful development of the jaw adductor muscles (Sill 1971; Benton 1983). The lower teeth cut into a groove in the maxillary dentition. Plant material was probably positioned across the maxillary groove and cut when the lower teeth were brought diagonally into occlusal contact from a posterior to anterior position (precision-shear style of mastication; Benton 1983, 1984). Rhynchosaurs were particularly diverse in the Gondwanan realm, where they were the most abundant herbivorous forms in many tetrapod assemblages (Bonaparte 1982; Benton 1983). Their quadrupedal posture suggests foraging ranges of up to a meter above the ground; Benton (1983) noted that the structure of the limb skeleton suggests rhynchosaurs might have dug up food items such as rhizomes. (Some Mesozoic and Cenozoic equisetaleans had thick rhizomes [Brown 1962], and these may have been one food source for rhynchosaurs and other Mesozoic “rooting” herbivores.)

Another important group in Late Triassic faunas were the Stagonolepididae, which were heavily armored, possibly herbivorous archosaurian reptiles up to 3 or 4 meters long. They had simple, leaf-shaped teeth and blunt snouts that may have been covered in part by a horny beak, or rhamphotheca (Walker 1961). Jaw motion was orthal, with teeth passing adjacent to one another to slice food items.

The Procolophonidae were a group of small primitive amniotes that persisted as a common element from the Late Permian to the Late Triassic. Their robust, presumably akinetic skulls typically had heterodont dentitions with transversely expanded posterior teeth that show evidence for some tooth-to-tooth occlusion. The jaw adductor musculature was prominently developed, and the mandibular symphysis was robust. Mastication consisted of an orthal puncture-crushing chewing stroke (Weishampel and Norman 1989).

The Trilophosauridae are only known with certainty from the Late Triassic of North America (Gregory 1945). The relatively broad snout probably supported a horny beak. The posterior teeth were transversely expanded and

rather high-crowned, and the pattern of tooth wear suggests orthal jaw motion. The volume of the adductor musculature was large relative to the occlusal surface (Weishampel and Norman 1989). Foraging ranges were restricted to within 1 meter above the ground.

The appearance of prosauropod dinosaurs in the Carnian marked the first radiation of high-browsing terrestrial herbivores (Bakker 1978; Galton 1986). Prosauropods were facultatively bipedal forms up to 10 m long and >1000 kg in weight that could have fed at heights of up to 4 m above the ground. They had large but lightly constructed skulls and little tooth wear, suggesting that their teeth were used merely for gathering food items (Galton 1985, 1986). Mechanical breakdown of the fodder was accomplished in a gastric mill through the action of gastroliths (Raath 1974). The genus *Plateosaurus* is especially abundant in late Norian assemblages from Germany (Galton 1986), and melanorosaurid prosauropods form a major element in Norian faunas from Argentina (Bonaparte 1982) and southern Africa (Galton 1986).

The Late Triassic radiation of ornithischian dinosaurs produced a number of low-browsing (within 1 meter above the ground) herbivorous forms. The Fabrosauridae, the most primitive known ornithischians, were small (1–3 m) bipedal dinosaurs. Best documented by the Early Jurassic *Lesothosaurus* from southern Africa, these animals had lightly built skulls with beaks (Thulborn 1970a). The development of nearly vertical wear facets on the maxillary and dentary teeth (Thulborn 1970b; Weishampel 1984b; Weishampel and Norman 1989) indicates some degree of oral food processing (orthal slicing). As was the case in all ornithischians, the gut capacity of fabrosaurs presumably was substantially increased relative to overall body size by the retroversion of the pubes. Large gut capacity may have been important in allowing fermentation of plant material. Foraging probably took place within a meter above the ground.

The late Carnian and Norian produced a major turnover, not only in the groups of herbivorous tetrapods present but also in the nature of vertebrate herbivory. Early and Middle Triassic herbivorous tetrapod faunas were composed largely of forms that foraged within a meter above the ground. Some of these animals had dental and jaw forms consistent with sophisticated oral processing of plant material, such as highly organized puncture crushing (rhynchosaurs and trilophosaurs) and incorporation of a palinal power stroke into the masticatory cycle (dicynodonts and gomphodont cynodonts) (see Weishampel and Norman 1989). Although the timing, tempo, and cause of a possible Late Triassic faunal turnover and the Triassic/Jurassic mass extinction among tetrapods are still controversial (Benton 1985, 1986; Olsen and Sues 1986; Olsen et al. 1987), by the end of the Triassic the functional attributes of the dominant herbivores were markedly different from those of earlier forms (Crompton and Attridge 1986; Galton 1986). Norian herbivore faunas were characterized by species with much larger body size and higher

browsing range, and by the predominance of prosauropod dinosaurs that used a gastric mill to break down plant material.

2.4 Triassic Ecological and Evolutionary Trends

The Permian/Triassic extinctions severely reduced the diversity of terrestrial vertebrates, and floral turnover appears to have been rapid during this interval. However, the extinctions do not seem to have affected particular habitat or trophic groups differentially, as has been documented for the K/T vertebrate extinctions, in which small and aquatic vertebrates suffered much lower rates of extinction (e.g., Hutchison and Archibald 1986). Similar herbivorous adaptations and some of the same clades were present among Late Permian and Early Triassic tetrapods, and there was no dramatic change in body size distribution. At least among Gondwanan plants, a major taxonomic change occurred from the *Glossopteris* flora to the *Dicroidium* flora, but the vegetational consequences of this are not fully understood. No short-term increase in early successional plants of the type observed in the earliest Jurassic and earliest Paleocene has been noted in the earliest Triassic. The absence of a strong ecological pattern in the Permian/Triassic extinctions of plants and continental vertebrates suggests that the extinction episode did not result in a major restructuring of terrestrial ecosystems. The similar biotic patterns at the end of the Paleozoic and the beginning of the Mesozoic may reflect the existence of a similar range of terrestrial environments, which in turn reflect a continuity of climatic conditions induced by the continued presence of Pangaea. The similarity of Late Permian and Early Triassic terrestrial ecosystems also may be related to a gradual or stepwise, rather than catastrophic, pattern of extinction that would have allowed guild structure to remain intact during taxonomic turnover. This would have conserved the existing structure and dynamics of communities, thereby restricting the opportunities for the establishment of new ways of making a living. Regardless of the importance of Permian/Triassic extinctions for shallow-water marine faunas, they do not appear to have been a major landmark in the history of terrestrial ecosystems. This is implicit in the recognition of a Paleophytic/Mesophytic boundary within the Permian period (Frederiksen 1972; Traverse 1988).

Both faunas and floras underwent considerable high-level taxonomic turnover during the Triassic, particularly beginning in the Carnian. Floristic changes include the initial rise of the *Dicroidium* flora in the Early Triassic of Gondwana, an increase in conifer dominance and decrease in floral diversity in equatorial regions during the Middle to Late Triassic, and the demise of the *Dicroidium* flora in Gondwana during the Late Triassic. Among vertebrate herbivores, there was the diversification of low-statured, herbivorous, urea-excreting, nonmammalian synapsids with complex masticatory adaptations during the Early and Middle Triassic, and their almost complete replacement

by high-browsing, uric-acid-excreting dinosaurian herbivores with gastric mills in the Late Triassic. Some of these faunal and floral trends were probably related to the development of monsoonal or seasonally dry climates in the low-latitude regions of the world (Parrish et al. 1982; Parrish and Peterson 1988; Crowley et al. 1989), although it has been argued that a "pluvial" phase in the mid-to-late Carnian, followed by a return to dry conditions in the early Norian, was responsible for faunal and floral turnover, as well as extinctions in marine faunas (Simms and Ruffell 1989).

The faunal and floral changes that occurred during the Triassic apparently involved major modifications of trophic relationships or ecological roles in some cases, but replacement on an ecological theme in others. Throughout the Triassic, many of the herbivore species were quadrupedal forms that foraged within a meter of ground level and had body weights of between 10 and 1,000 kg, although smaller herbivores such as procolophonids and possibly sphenodontids (< 10 kg) were also numerous (Fraser and Sues, unpublished data). Today large terrestrial herbivores tend to be most diverse and abundant in relatively open vegetation (e.g., Eisenberg 1981, chap. 20), which is typical of regions that do not receive heavy, year-round rainfall. Smaller, generally arboreal, frugivore/herbivores are more important in dense forest vegetation typical of wet climates (Eisenberg 1981, chap. 20; Emmons et al. 1983). Body-size distribution among herbivores in many Triassic faunas is more consistent with open, low-statured vegetation than with closed forests, as are many paleoclimatic indicators. In some areas (e.g., parts of the Chinle Formation of Arizona), there is reasonably good paleobotanical evidence for denser forest vegetation. However, these forests are believed to have coexisted with nearby more open vegetation (Gottesfeld 1972), which may have formed the habitat of larger herbivores (J. M. Parrish 1989).

The weight of the evidence from functional morphology and body size favors the idea that Early and Middle Triassic herbivore faunas were dominated by generalist browsers that would have relied on plant productivity within about 1 meter of the ground. This implies that herbaceous pteridophytes, low-statured cycadales or seed ferns, and seedlings of all types received the brunt of browsing activity. Plants that dropped fleshy, perhaps strong-smelling, seeds on the ground in large quantities could also have provided an important food source for larger herbivores. This combination of features has been termed the saurochorous dispersal syndrome in extant plants (Van der Pijl 1982). There is little direct evidence for saurochory in Triassic plants, but animal dispersal is known in modern conifers and, to a lesser extent, in ginkgoaleans and cycads.

The increase in browsing height from 1 to 4 meters that occurred with the advent of prosauropod dinosaurs in the Late Triassic may well have been a trophic change of great ecological and evolutionary significance. Increased browsing height would have exposed plants to vertebrate herbivory over a

longer period of their life cycle, thus directly affecting competitive interactions between plants and the amount of energy invested in defense mechanisms, as well as aspects of life history, such as the optimal age for reproduction and seed size. The ability to tap plant resources at higher levels also may have been a factor in the radiation of herbivorous dinosaurs.

During the Triassic, six major methods of food processing occurred in vertebrate herbivores: orthal pulping, orthal slicing, orthal puncture crushing, propalinal grinding, transverse grinding, and gut processing (Weishampel and Norman 1989). The Late Triassic records reduction in diversity of clades using propalinal grinding, orthal pulping, and orthal puncture crushing, with an increase in the number of gut-processing species (fig. 6.2; Weishampel and Norman 1989). Much has been made of this general shift from oral to gastric-mill processing of food in early Mesozoic herbivores (Galton 1986; Crompton and Attridge 1986), but though the change in method of processing plant fodder was structurally striking, its effect on vegetation is difficult to assess. All large herbivores would be expected to have a substantial impact on vegetation regardless of how the plant matter was processed and digested, and both synapsid dentitions and prosauropod gastric mills should have been capable of dealing with tough plant material. However, if the shift from oral to gastric processing was also related to changes in body size and metabolic rate, then

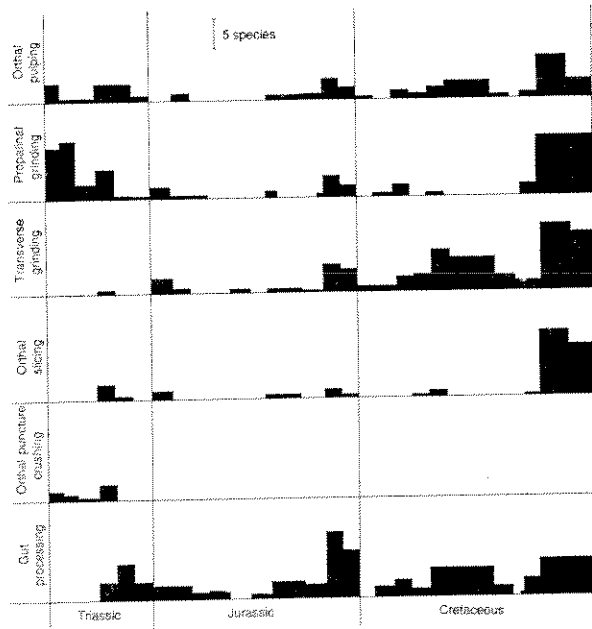


Fig. 6.2. Changing species diversity in 6 categories of herbivores. Based on data from Weishampel and Norman 1989.

the processing method may have indirectly affected the rate, amount, and type of vegetation consumed. Oral and gastric processing methods might also be expected to affect seed viability differently, although there is no direct evidence that large herbivores were involved in seed dispersal at this time.

Although the dominant interaction between herbivorous tetrapods and plants in the Triassic probably was generalized browsing, the existence of smaller herbivores raises the possibility of specialized vertebrate seed dispersal as well. There exists as yet no solid evidence for arboreal herbivores at any time during the Triassic. The only possible herbivores small enough to have been facultatively arboreal were the haramiyid synapsids, which first appear in the Norian (Lillegraven et al. 1979), and some sphenodontian lepidosaurs. Thus, during the entire Early and Middle Triassic, woody plants more than a few meters in height and with enough structural strength to resist felling would have been essentially free from vertebrate herbivory, although, of course, phytophagous insects would have been undeterred by height. Herbivorous arthropods were well established as arboreal primary consumers during this same interval. Although gliding, and therefore presumably arboreal, insectivorous tetrapods are known from the Late Triassic, the evolution of canopy-living vertebrate herbivores may not have occurred until the Late Cretaceous or Early Tertiary. Arthropods, insectivorous tetrapods, and herbivorous tetrapods apparently came to live in the canopy in the same sequence in which they assumed importance in terrestrial ecosystems; arthropods and carnivorous vertebrates exploited resources in previously unoccupied portions of ecosystems in advance of vertebrate herbivores.

The causes for the turnover in faunal composition during the Triassic (Bonaparte 1982) have been a subject of considerable debate, although there is little evidence for the various scenarios proposed to date. Replacement traditionally has been attributed to competition between synapsids and later-appearing archosaurian reptiles such as dinosaurs, with the newcomers succeeding as a result of superior locomotory abilities or physiological characteristics that were favored under the drier climates and more open vegetation of the later Triassic (see Charig 1984). Benton (e.g., 1986) has suggested that competition did not play a major role in faunal change. Instead, he implicated climatic and vegetational shifts in the extinction of nonmammalian synapsids and rhynchosaurs, which left empty adaptive space into which archosaurs could diversify. These explanations may not be mutually incompatible, because they both invoke an underlying cause of climatic and vegetational change (Zawiskie 1986). The success of prosauropods may have resulted from successful competition for low-level browse coupled with their unique access to high-level plant resources, which were unavailable to lower-statured animals. Very large body size and high mobility might also have been advantageous in permitting seasonal migration and greater ability to withstand short-term environmental fluctuations.

As mentioned above, the Triassic ended with a major extinction among terrestrial vertebrates. The relative suddenness of this event (200 k.y.?) makes it difficult to explain in terms of the long-term paleoclimatic changes that are associated with other Triassic biotic turnovers. The impact hypothesis presented by Olsen et al. (1987) is consistent with the tempo of the extinctions, and the size of the Manicouagan crater in Quebec is approximately as large as that predicted for a bolide with a diameter of 10 km (Silver and Schultz 1982)—the same size as is estimated for the end-Cretaceous bolide. The Triassic/Jurassic extinction was fairly severe in terms of percentage of tetrapod families lost (Olsen and Sues 1986). Shocked quartz crystals at the Triassic/Jurassic boundary (Newton and McRoberts 1990) and greatly increased fern spore abundance in the earliest Jurassic (Fowell 1990) also suggest parallels with the K/T event, but the ecological pattern of the two vertebrate extinctions is not similar.

One of the most significant differences between the two extinctions is in the survival of herbivorous vertebrates. Two clades of megaherbivores (Anchisauridae and Melanorosauridae) and a number of small-to-medium-sized herbivores, such as some sphenodontians, primitive ornithischians, and haramiyid synapsids, survived the Triassic/Jurassic boundary (Olsen and Sues 1986). This is in sharp contrast to the K/T extinctions, which wiped out all medium-to-large vertebrate herbivores. The immediate dependence of large herbivorous tetrapods on plant productivity would be expected to make them particularly vulnerable to even short interruptions in primary productivity, compared with smaller omnivores or carnivore/scavengers. Therefore the different survival rates of large herbivores across the Triassic/Jurassic and K/T boundaries suggest two possibilities: either our understanding of prosauropod diets is faulty (i.e., they were not obligate herbivores; Cooper 1981), or the nature and magnitude of ecological disruption at the Triassic/Jurassic boundary differed substantially from that at the K/T boundary. Ecological differences between the two extinctions, both of which are linked to bolide impacts of similar size, suggest that other environmental factors must play an important role in mediating the biological effects of such bolide impacts.

3 JURASSIC BIOTAS

Although the rifting of Pangaea commenced in the Late Triassic and continued slowly throughout the Early Jurassic, dispersal of the major continental areas and separation by ocean basins probably did not occur until the Middle or early Late Jurassic (Veevers 1989; fig. 6.3). In the absence of impassable barriers to dispersal, Jurassic faunas and floras included numerous cosmopolitan elements. Generally speaking, Gondwanan and Laurasian biotas were less distinctive during the Jurassic than they had been in the Triassic.

Global climates continued to be warm during the Jurassic, as indicated

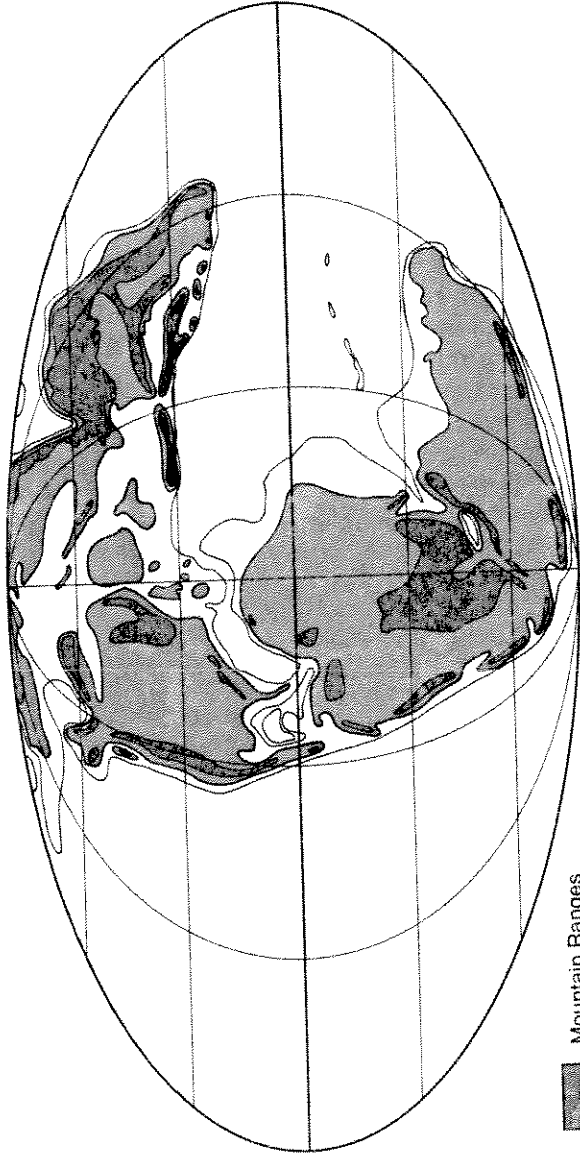
by high-latitude floras from Siberia (Vakhrameev 1970; Vakhrameev et al. 1978; Hallam 1984), evidence from the marine realm, and absence of glacial deposits at high latitudes (e.g., Frakes 1986). Frakes (1986) suggested that subtropical climates may have extended as far northward as 60 degrees latitude. The distribution of climatically sensitive sediments such as coals and evaporites indicates that aridity and seasonal aridity were widespread during the Early and Middle Jurassic in low-to-middle latitudes, particularly in western Pangaea. Major Lower to Middle Jurassic coal beds in higher paleolatitudes of both the Southern and Northern Hemisphere (e.g., Ordos Basin of northern China: E. A. Johnson et al. 1989) suggests these areas had wet climates (Parrish et al. 1982; Hallam 1984). Increasing aridity in southern Laurasia during the Middle and Late Jurassic has been attributed to a breakdown of the monsoonal circulation that typified the Late Triassic and part of the Early Jurassic (Parrish and Doyle 1984). Strong latitudinal variation in climate, particularly rainfall, continued throughout most of the Jurassic and was probably responsible for minor north-south floral provincialism (Doyle and Parrish 1984), although it does not seem to have barred continuing interchange between the Northern and Southern Hemispheres, especially among vertebrates.

3.1 Jurassic Vegetation

Jurassic vegetation was composed of a mixture of various woody gymnospermous groups and largely herbaceous pteridophytes, a pattern similar to that of the Triassic. Conifers continued to be the most diverse large trees; species of the extant families Araucariaceae, Cephalotaxaceae, Pinaceae, Podocarpaceae, Taxaceae, and Taxodiaceae, together with members of the extinct family Cheirolepidiaceae, numerically dominated many Jurassic assemblages. *Ginkgo*-like plants also continued to be important in many floras, particularly in northern mid-to-high latitudes. During the Jurassic, the bennettitaleans became the most important group of small trees and shrubs, while seed ferns and marattiacean ferns apparently declined in abundance and diversity. Dicksoniaceae ferns and caytoniaceae seed ferns also may have been relatively successful groups of small tree stature (Wesley 1973). Among herbaceous groups, lycopsids continued to be of relatively minor importance, and *Neocalamites* was largely replaced by the smaller *Equisetum*. Osmundaceous, matoniaceae, and dipteridaceous ferns were probably the dominant herbs in many floras (Wesley 1973).

During the Early Jurassic on the southern continents, Gondwanan floras came to resemble more closely those of the northern continents. Typically equatorial groups like Bennettitales and Cheirolepidiaceae, along with dipteridaceous and matoniaceae ferns, became more important components of the Gondwanan flora. Major differences between Jurassic floras of Gondwana

LATE JURASSIC (152 Ma)



- Mountain Ranges
- Lowlands
- Continental Shelf

Paleotopography

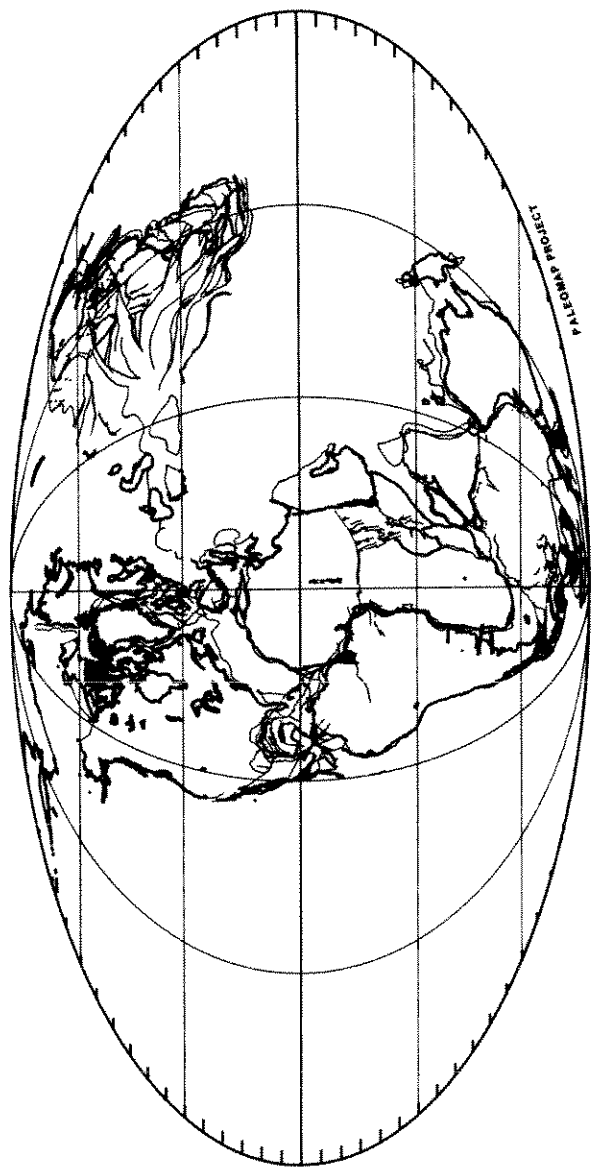


Plate Positions

Fig. 6.3. Generalized continental positions and orography in the Late Jurassic. (Courtesy of C. R. Scotese and the Paleomap Project, University of Texas, Arlington)

and Laurasia included the relative paucity of Ginkgoales and Czekanowskiales and the greater importance of podocarpaceous conifers in the southern regions, although podocarps are known from Laurasia as well.

Two groups of plants appear to have dominated low-latitude vegetation during the Jurassic: the conifer family Cheirolepidiaceae and the cycadophytic Bennettitales. The Cheirolepidiaceae first appeared in the Late Triassic but became a major element in palynofloras (*Classopollis* [*Corollina*]) and megaflores (e.g., some species of *Brachyphyllum* and *Cupressinocladus*) in the Jurassic and Early Cretaceous (Barnard 1973). These conifers apparently ranged in stature from tall forest trees (Alvin 1982, 1983) to small bushes (Vakhrameev 1970). Direct evidence on the stature of *Cupressinocladus* from the Purbeck Beds (Late Jurassic) of southern England shows that this particular genus was moderately tall, sparsely branched (Francis 1983), and in some cases had multiple, thick trunks arising from a single rootstock (Spicer, unpublished data). Most cheirolepidiaceous conifers had small, short, pointed leaves similar to those of many living conifers, but in some genera, such as *Frenelopsis* and *Pseudofrenelopsis*, the main photosynthetic organs were unbranched, cylindrical, succulent-looking shoots covered with thick cuticles showing sunken or otherwise protected stomata (Alvin 1983). Large accumulations of this "foliage" on some bedding planes, coupled with shoot morphology, wood anatomy, and other ecological considerations (Alvin et al. 1981), raise the possibility that some species were deciduous. The strongly xeromorphic attributes of many cheirolepidiaceous conifers and their worldwide abundance at low paleolatitude (<40 degrees) sites with sedimentary indicators of aridity suggest they were dominants in dry-climate vegetation (Vakhrameev 1970; Upchurch and Doyle 1981; Alvin et al. 1978; Francis 1983). Indeed the relative abundance of *Classopollis* in palynofloras has been used as an index of aridity (e.g., Vakhrameev 1970). The abundance of Cheirolepidiaceae in certain marginal marine rocks probably indicates that some species were halophytic (Watson 1977; Daghljan and Person 1977). However, the group was diverse both in number of species and in morphology and no doubt occupied a wide array of situations in many kinds of vegetation (Batten 1974; Alvin et al. 1978; Upchurch and Doyle 1981).

Although many bennettitaleans were pachycaulous (thick-stemmed) relative to most extant angiosperms, they exhibited a range of growth forms. Short, stout forms, typified by the Cretaceous *Cycadeoidea*, had globose, 0.5-to-3-m-tall trunks that contained large amounts of soft tissue but were covered with tough, persistent leaf bases and bore large, pinnately compound, leathery leaves near the apex. Intermediate types such as *Zamites gigas* and some *Williamsonia* species were several meters tall with sparsely branched trunks about 30 cm in diameter that bore pinnately compound foliage near the top. Species of *Wielandiella* and *Williamsoniella* were small, more highly branched plants with stems a few centimeters in diameter, bearing a small

number of thick-textured, simple or pinnately-lobed (pinnatifid) leaves (clustered at the nodes in *Wielandiella*). This range of growth habits implies that the group played a variety of vegetational roles. However, no large tree-sized bennettitaleans are known, and other aspects of their morphology and inferred biology are less variable.

Most bennettitalean foliage shows xeromorphic features such as small, reflexed pinnae, sunken stomata, and papillae or hairs on the leaf surfaces. A number of bennettitalean reproductive structures are known, and though the Late Triassic *Vardekloeftia* did not have specializations for insect pollination (Pedersen et al. 1989), many later species are thought to have been either self-pollinated or insect-pollinated (Crepet 1974; Crepet and Friis 1987). Bennettitales are thus another gymnospermous group that, along with various seed ferns and cycads, was insect-pollinated. Most bennettitaleans had small seeds with thin, hairlike projections; pollination, fertilization, and embryo development probably followed one another in rapid succession (Doyle 1978). Bennettitalean receptacles were fleshy, bore closely packed seeds, and disintegrated at maturity (Harris 1969). Bennettitalean receptacle cuticle has been recovered from Jurassic coprolites (Hill 1976), suggesting predation and possible dispersal by vertebrates (endozoochory), a mode of dispersal consistent with the fleshy receptacle of bennettitaleans (Harris 1973). Abiotic dispersal of bennettitaleans also has been suggested, partly on the basis of the small size of the seeds (Tiffney 1986a).

Retallack and Dilcher (1981) postulated that bennettitaleans were early successional plants. Crane (1987) summarized the probable biology of bennettitaleans and concurred that they were shrubby plants that occupied open habitats. The "armored" appearance of the stem in the short and medium forms of Bennettitales may have protected them from fire damage, and their seeds may have been released by fire (Harris 1973). At least some members of the group probably were deciduous (Delavoryas 1968; Krassilov 1975b). Krassilov (1981) maintained that many of these plants were ecologically analogous to extant shrubs; certainly the small size of their seeds means there would have been little food stored for the embryo, and thus the requirement of high light conditions for successful seedling establishment. Some taxa have been suggested as bog shrubs (*Nilssoniopteris*; Krassilov 1975b) or even mangroves (some species of *Ptilophyllum*; Krassilov 1975b).

Other groups of plants that achieved importance in Jurassic vegetation include the caytoniaceous seed ferns and the dicksoniaceous and cyatheaceous ferns. Like most of the other Mesozoic seed fern groups, Caytoniaceae have been reconstructed as shrub-to-small-tree-sized plants. *Caytonia* had palmately compound leaves ("*Sagenopteris*"). Its seeds were carried in an in-rolled, fleshy receptacle, and both seeds and receptacles have been found in coprolites (Harris 1964). However, the structure and abundance of dispersed seeds in some deposits suggest dispersal through abiotic means rather than as

a result of consumption by animals. This is another group for which the importance of animal dispersal is unresolved.

Living Dicksoniaceae and Cyatheaceae are tall tree ferns that bear very large, dissected, pinnately compound leaves and usually occupy moist-to-wet tropical forests. Most species are part of the upper understory or lower canopy vegetation, although some Cyatheaceae may reach heights of 20 m and become part of the canopy in forests of moderate stature (LaPasha and Miller 1984; Tryon and Tryon 1982). Fossil members of these two taxa are known from stem petrifications and leaf compression/impressions that generally resemble the extant forms. Fossil dicksoniaceous tree ferns have been described as important understory elements in conifer forest, but also as participants in coastal marsh vegetation (Krassilov 1975b; LaPasha and Miller 1984).

Specific Plant Assemblages

Probably the best-known lower-latitude Jurassic flora is that from the Middle Jurassic of Yorkshire, England (e.g., Harris 1961, 1964, 1969, 1979, 1983; Harris, Millington, and Miller 1974; Spicer and Hill 1979). Over 80 genera of plants have been described from this flora, but because the flora comprises many separate assemblages from a variety of depositional environments and distributed through a considerable thickness of section, it is difficult to interpret this number in terms of the true species richness of the vegetation at any particular moment in time. A Yorkshire locality reported by Hill et al. (1985) has yielded 31 organ-species that probably represent 23 biological species. The common elements of the local floral assemblage are two species of equisetaleans, the bennettitalean *Williamsonia*, *Czekanowskia*, and the conifer *Elatides*. These are associated with rarer specimens of ferns, lycopsids, cycads, ginkgoaleans, and conifers. The Hasty Bank locality exhibits several lithologies, each with somewhat different floras; but it generally is dominated by *Equisetum*, *Nilssonina* (Cycadales), *Pachypteris* (Corystospermaceae), *Ptilophyllum* (Bennettitales), *Sphenobaiera* (Ginkgoales), and *Brachyphyllum* (Cheirolepidiaceae) (Spicer and Hill 1979). Because of the xeromorphic features of its leaves and its tendency to occur in monodominant assemblages along with brackish-to-marine fauna, the species of *Pachypteris* is thought to have been a mangrove (Harris 1983).

The seeds of the Yorkshire flora were measured and tabulated by Tiffney (1986a), who reported a mean size of 304 mm³, maximum of 3050 mm³, and minimum of 1.0 mm³ (based on a sample of 19). Compared to the summed Jurassic data, the Yorkshire flora has relatively small seeds. The larger seeds in the flora were produced by cycads and ginkgoaleans.

The impression of Middle Jurassic equatorial vegetation derived from Yorkshire is that the major trees were cheirolepidiaceous conifers (producers of *Classopollis*) and rarer ginkgoaleans (such as *Baiera*), and that bennetti-

taleans, seed ferns, czezanowskialean, and cycads formed the undergrowth in conifer forests or grew in open, low-stature vegetation with ferns and sphenopsids.

Several Late Jurassic assemblages from France have been reviewed by Barale (1981). The total diversity of these floras is about 60 species, with the most diverse localities producing 30–40 forms (approximately 25–35 species). As in Yorkshire, most of these Kimmeridgian French assemblages are dominated by cheirolepidiaceous conifers and bennettitaleans. However, at two localities these groups account for less than 40% of the specimens, and here both ferns (*Stachypteris*, *Sphenopteris*) and pteridosperms (*Pachypteris*, *Raphidopteris*) are more abundant. It is difficult to assess whether the association of ferns and seed ferns records an original vegetation type, but the carbonate mud sediment from which the plant material was derived is consistent with deposition in a lagoonal setting (Barale 1981). If the depositional environment has been inferred correctly, the fossil plant assemblages probably experienced relatively little transport and may represent a low-statured coastal vegetation.

On the basis of the “fossil forests” of the Purbeck Formation, where in situ bennettitalean stems occur scattered among the dominant cheirolepidiaceous conifers (Francis 1983), it appears that the typical low-latitude Middle Jurassic vegetation continued unabated into the latest part of the period. A Late Jurassic assemblage from northwestern China also contains silicified trees in growth position, in this case showing the presence of a mature forest (trees up to 2.5 m in diameter) composed exclusively of conifers (*Araucarioxylon*) with seasonal growth rings in their wood (McKnight et al. 1990).

Although the Morrison Formation of the western United States is more noted for its fossil vertebrates, there are scattered reports of plant compression fossils and pollen and spores from the northern portion of the outcrop area in Montana (R. W. Brown 1956; J. T. Brown 1975; Miller 1987; Pocock 1962; Dodson et al. 1980), and of silicified wood from Utah (Arnold 1962; Tidwell and Rushforth 1970; Medlyn and Tidwell 1975). The compression floras are dominated by probable bennettitaleans such as *Zamites* and *Nilssonina* but also contain seed ferns (*Sagenopteris*), ferns (e.g., *Cladophlebis* and *Coniopteris*), conifers (e.g., *Podozamites*, *Pityophyllum*, *Pagiophyllum*), and ginkgos. Cycadophyte remains are more abundant than those of conifers at all localities, and Miller (1987) interpreted Morrison vegetation as relatively open with scattered conifers and an understory of cycadophytes, tree ferns, and ferns. Similar vegetation is thought to have extended northward from Montana into southern Canada (Miller 1987).

Krassilov (1975b) divided the Jurassic flora from Kamenka in the Donets Basin, Russia, into a series of environmental-vegetational units. Mangrove and coastal marshes were dominated by monospecific thickets of large *Equisetites*, along with small *Coniopteris* (Dicksoniaceae) and the bennettitalean

Ptilophyllum, the last being a putative mangrove. Pioneer arborescent vegetation consisted of *Podozamites* and *Czekanowskia*, with the scrambling fern *Klukia* (Schizaeaceae). Wet "bog" forests were largely composed of *Nilssoniopteris* (Bennettitales) and *Pityophyllum*, with *Elatides* (conifer) being more important near channel margins; the lower story here consisted of *Todites* (Osmundaceae), *Caytonia*, *Ptilophyllum*, and *Dictyophyllum* (fern). Finally the higher-ground forest was dominated by *Ginkgoites* and *Phoenicopsis*. Whether these separate assemblages represent distinct vegetation types or seral stages of vegetation in the same area is not yet determined (Krassilov 1987). Krassilov (1975b) reconstructed the Jurassic genus *Phoenicopsis* as a large tree. Ginkgoaleans having *Ginkgo*-like leaves were almost certainly deciduous, and many had moderate-to-large, fleshy seeds that could well have been animal dispersed (Tiffney 1986a).

More northerly floras typically had a higher component of conifers other than Cheirolepidiaceae. As in the Donets Basin flora, ginkgoaleans and *Czekanowskia*les were also important groups in high-latitude Northern Hemisphere vegetation (Smiley 1969; Spicer 1987). Generally, ferns, sphenophytes and cycadaleans formed the understory in these forests, although there was a poleward decrease in cycad diversity. Podocarpaceous conifers apparently were an important component of higher-latitude Southern Hemisphere floras, as perhaps were the Pentoxylales, a gymnosperm group of uncertain taxonomic affinity.

A latest Jurassic or earliest Cretaceous flora from Hope Bay on the Antarctic peninsula provides one of the best examples of high southern latitude floras (65-to-70 degrees S) during the middle of the Mesozoic (Gee 1989). The assemblage includes a total of 43 species that probably grew under a warm-temperate climate. Ferns are the most diverse element of the flora (15 spp. in the genera *Coniopteris*, *Dictyophyllum*, and *Todites*, among others), with bennettitaleans (9 spp.), conifers (8 spp.), and seed ferns (7 spp.) making up most of the remaining species. Cycads were a minor element of the flora.

3.2 Jurassic Faunas

Numerous groups of herbivorous insects were present in the Jurassic, including sawflies, leafhoppers (Cicadelloidea and Fulgoroidea), plant hoppers (Psylloidea), shield bugs (Pentatomoidea), plant bugs (Cimicoidea), and herbivorous representatives of the Orthoptera. In addition, most of the extant groups of Coleoptera appeared in the Jurassic, as did the earliest undoubted thrips (Thysanoptera).

Early Jurassic herbivorous tetrapod assemblages were dominated by prosauropods, cynodont synapsids, and a variety of mostly small ornithischian dinosaurs. The latter included, in addition to the Fabrosauridae, the Hetero-

dontosauridae and the armored Scelidosauridae. The Heterodontosauridae were bipedal forms that foraged 1 meter above the ground. The skull was sturdily built and had a well-developed dentition with robust, closely spaced cheek teeth with distinct wear facets along the length of the tooth row (Weishampel 1984a). These dinosaurs would have been capable of processing relatively tough plant material (Weishampel 1984a; Galton 1986). The Scelidosauridae were quadrupedal forms characterized by robust, leaf-shaped teeth with high-angle double wear facets (Weishampel and Norman 1989). Their foraging range was probably within 1 meter above the ground.

The Tritylodontidae were small to medium-sized, extremely mammal-like cynodont synapsids, which persisted well into the Middle Jurassic. They had multicuspid cheek teeth that met in complex occlusion and an extensive palinal power stroke, well suited for shredding fibrous plant material (Crompton 1972; Sues 1986). These quadrupedal forms foraged within a meter above ground level. The structure of the shoulder girdle and forelimb suggests capability for digging, and wear on the enlarged incisors is consistent with digging for underground plant parts (Sues 1984).

By the Middle Jurassic, dinosaur-dominated herbivore faunas were well developed. Such assemblages are most thoroughly documented from the Middle to Late Jurassic of China (Dong et al. 1983) and from the Late Jurassic of western North America (Coombs 1975) and Tanzania (Dodson et al. 1980). The largest species in these faunas were the sauropods, which presumably could have browsed at heights up to 10 m in a quadrupedal posture (and possibly even higher if they could have assumed a tripod stance; Bakker 1978; Alexander 1985). Some sauropods weighed more than 50 tons and were the largest terrestrial herbivores of all time (Coombs 1975). Sauropods are first known from the Early Jurassic, by which time they already had attained large body size (Jain et al. 1975). Sauropod dentitions consist of peglike or spatulate teeth that show few signs of tooth wear, implying that oral processing of plant material was not extensive and that, as in prosauropods, the teeth were used in cropping. Food was broken down mechanically in a gastric mill, and the capacious abdominal cavity suggests the presence of a voluminous gut (Farlow 1987).

The second most abundant element in these herbivore assemblages were the armored Stegosauria. These heavily built quadrupeds were up to 7 m long, weighed up to 5 t, and had relatively narrow, elongate snouts with simple spatulate teeth. The teeth occasionally show obliquely inclined wear facets that suggest some form of orthal puncture crushing (Weishampel and Norman 1989). Stegosauria would have fed mostly within a meter of the ground, but Bakker (1978) has argued that they were capable of a tripod stance to forage at heights of 2–3 meters above ground level.

An important radiation of mostly smaller, facultatively (if not obligately) bipedal herbivores was represented by ornithomimid dinosaurs, including *Camp-*

tosaurus (length up to 7 m and weight up to 500 kg), Dryosauridae (3–4 m long), and Hypsilophodontidae (1–3 m long). These forms show well-developed capabilities for oral food processing involving a transverse power stroke (Weishampel 1984a; Norman and Weishampel 1985; Weishampel and Norman 1989). Advanced ornithopods, much like the Heterodontosauridae, had closely spaced cheek teeth that, with continuing wear, formed long and relatively wide occlusal surfaces. Furthermore, movement along skull sutures permitted inclusion of a transverse power stroke (Weishampel 1984a; Norman and Weishampel 1985). These ornithopods foraged mainly within 1–2 m (perhaps up to 4 m) above the ground and were very abundant in many communities.

Even smaller Jurassic herbivores and/or omnivores included sphenodontids, which were relatively ubiquitous, and by Mid to Late Jurassic times, lizards and docodont and multituberculate mammals (Lillegraven et al. 1979). Multituberculates developed distinctive dentitions with capabilities for orthal slicing and palinal grinding (Krause 1982). All these forms would have foraged close to the ground, but at least some of them may have been facultatively arboreal, thus dramatically increasing their foraging ranges.

3.3 *Jurassic Ecological and Evolutionary Trends*

The ecological dominants of Jurassic terrestrial herbivore faunas were the very large, high-browsing sauropods. Simply by virtue of size, these dinosaurs must have had considerable caloric requirements even if they had lower metabolic rates than large herbivorous mammals (Coe et al. 1987). Analogy to extant ecosystems with “megaherbivores” suggests that contemporary vegetation should have produced large amounts of leafy material and should have had a high capacity for regrowth. A further prediction is that evolution in a variety of plant lineages (particularly those with slower growth, delayed maturation, and/or large seeds) would have led to the development of mechanical or chemical mechanisms to deter herbivory (Bakker 1978; Janzen and Martin 1982; Janzen 1986; Coe et al. 1987; Owen-Smith 1987; Wing and Tiffney 1987).

Judging from the structure of fossil leaves and, for some taxa, the habits of living relatives, the major groups of Jurassic trees (araucariacean and cheirolepidiacean conifers, cycads, bennettitaleans, ginkgoaleans) probably did not produce large quantities of foliage, nor is there evidence that they had high growth rates that would have allowed regrowth following feeding events. The ubiquity of mechanical and chemical defenses cannot be judged from known fossil data, but the common occurrence of spiny foliage among living araucarians and cycads and their tendency to retain dead foliage around the trunk raise the possibility that these were important defenses for their Jurassic relatives. Many living cycads also have toxic foliage (Chamberlain 1935).

Furthermore, the thick texture of many Jurassic leaves may have been an herbivore deterrent as well as an adaptation to dry climates. On the whole, it seems more probable that Jurassic trees had mechanical or chemical defences against herbivores than that they were capable of rapid growth and high productivity. Paradoxically, in light of the supposed high-browsing adaptations of sauropods, the Jurassic plant groups most likely to have produced abundant vertebrate fodder were low-statured (e.g., gleicheniaceae, schizaeaceae, and matoniaceae ferns, sphenopsids, possibly certain seed ferns, and many cycadophytes).

The contrast between high diversity of large herbivores and probable low productivity of terrestrial vegetation is illustrated well by the Morrison Formation biota. In Montana, the presence of coals suggests a fairly wet climate during Morrison time, and open, fern- and seed-fern-dominated vegetation (Miller 1987) may have been productive enough to support dinosaur herbivore faunas. However, most vertebrate remains come from more southerly strata of the Morrison Formation, where paleosols and lithological features have been interpreted as indicating a seasonally dry climate in southern Wyoming (Dodson et al. 1980). Recent work on the sedimentological characteristics of the upper part of the formation has raised the possibility that the climate during Morrison time may have been extremely arid at times, especially in Utah and Colorado (Turner and Fishman 1991). Although high diversity and biomass of large herbivores is seen today in seasonally dry regions like the Serengeti (Sinclair and Norton-Griffiths 1979), it is based largely on the productivity of herbaceous angiosperms (especially grasses). It is not clear what groups of Mesozoic plants would have been able to maintain high levels of productivity in a seasonally arid or arid climate.

The conflict between animal and plant evidence suggests two (not necessarily mutually exclusive) possibilities. First, the degree of productivity of Mesozoic plants has been underestimated because of inadequate knowledge of their biologies. This is not unlikely, given the difficulty of estimating the amount of edible material produced by extinct plants, especially for lineages that are entirely extinct, such as Cheirolepidiaceae. Second, the browsing pressure on Mesozoic vegetation has been overestimated, because either per individual consumption or total herbivore density has been overestimated. Estimates of per capita consumption depend strongly on the contentious matter of dinosaurian metabolic rates (see Olson and Thomas 1980), and furthermore, physiological parameters may have varied among the various taxa of herbivorous dinosaurs. There is no accepted method for estimating standing biomass of herbivores directly from fossil assemblages, and some authors have assumed that fossil communities had the same total rates of plant consumption as do present-day systems. This assumption, coupled with a questionably low figure for dinosaur metabolic rate, led Coe et al. (1987) to suggest that the standing herbivore biomass in the ecosystem represented by

the Upper Jurassic Morrison Formation was 20 times the equivalent figure for Amboseli Park, Kenya. It seems equally plausible that this Jurassic ecosystem had low primary productivity and low population density of large herbivores.

4 CRETACEOUS BIOTAS

4.1 Early Cretaceous Vegetation

Earliest Cretaceous (Neocomian) floras generally lack angiosperms and bear many similarities to the preceding Late Jurassic assemblages. By Barremian to Aptian times, floras showed a substantial difference between equatorial regions and higher latitudes to the north and south. Brenner (1976) recognized four main floral provinces based on pollen assemblages: northern Laurasia, southern Laurasia, northern Gondwana, and southern Gondwana. (Figure 6.4 shows reconstructed paleogeography for the early Late Cretaceous, which is broadly similar to that for the Early Cretaceous.) Lower-latitude palynofloral assemblages from the Barremian-Aptian show that angiosperms had appeared and were undergoing significant diversification, although pollen similar to that of the extant xerophytic gymnosperm *Ephedra* was also abundant in the northern Gondwana area (Brenner 1976; Doyle et al. 1982; Crane and Lidgard 1989). Climate in the southern Laurasian and northern Gondwanan provinces is inferred to have been seasonally dry on the basis of palynological and sedimentary indicators (Brenner 1976; Ziegler et al. 1987). Fern and conifer palynomorphs were of greater importance in the northern Laurasian and southern Gondwanan regions, which are thought to have had cooler and wetter climates (Brenner 1976; Ziegler et al. 1987).

Although angiosperms were a significant component in low-latitude palynofloras of the Early Cretaceous, they were slow to dominate in middle-to-high latitudes (Brenner 1976; Crabtree 1987; Drinnan and Crane 1990). At mid latitudes, angiosperms became a significant part of disturbed riparian plant communities during Aptian and Albian times but did not develop understory tree/shrub habits until the Cenomanian (Doyle and Hickey 1976; Hickey and Doyle 1977). Angiosperms were even less important in high-latitude regions. For instance, an Early Cretaceous (Aptian) flora from Koonwarra, Australia, containing one of the oldest angiosperm megafossils (Taylor and Hickey 1990), is thought to represent a forest dominated by ginkgoaleans and podocarpalean conifers with an understory of ferns, pentoxylaleans, and sphenophytes (Drinnan and Chambers 1986). The presence of only a single type of angiosperm pollen in the Koonwarra palynoflora of 62 taxa (Dettmann 1986) and the herbaceous character of the single known angiosperm megafossil imply that flowering plants formed a minor component of this particular vegetation. The low diversity of angiosperms is typical of Early Cretaceous Australian floras; there were only 6 species of angiosperms known from Neocomian-through-Albian collections from southern Victoria at 70-to-80 de-

grees S paleolatitude (Douglas and Williams 1982). The Australian pattern is also seen in small Neocomian-Albian floras from South Africa, which lack angiosperm megafossils and have only a few types of angiosperm pollen (Anderson and Anderson 1983a, 1985; Drinnan and Crane 1990). Just a few species of angiosperms occur in a conifer-cycadophyte assemblage from volcaniclastic Aptian rocks in southern Argentina (Romero and Archangelsky 1986), although angiosperm pollen is known from Barremian assemblages in Argentina (Archangelsky 1980). Angiosperms were also rare or absent in middle northern latitudes during the Aptian (e.g., LaPasha and Miller 1984) and were essentially absent from Arctic floras until near the end of the Albian (Spicer 1990). The 20–30 my lag between the first appearance of flowering plants in equatorial regions and their rise to importance in mid- to high-latitude vegetation has been attributed to slow evolution of cold tolerance in angiosperms (e.g., Brenner 1976).

During the Early Cretaceous, wetland areas still supported abundant equisetaleans and small lycopsids such as *Isoetes* (Batten 1974; Kovach and Dilcher 1985). Osmundaceous ferns also were common in wet areas, as are the living species, although at least one Cretaceous species in this family is thought to have been an epiphyte (Harris 1961).

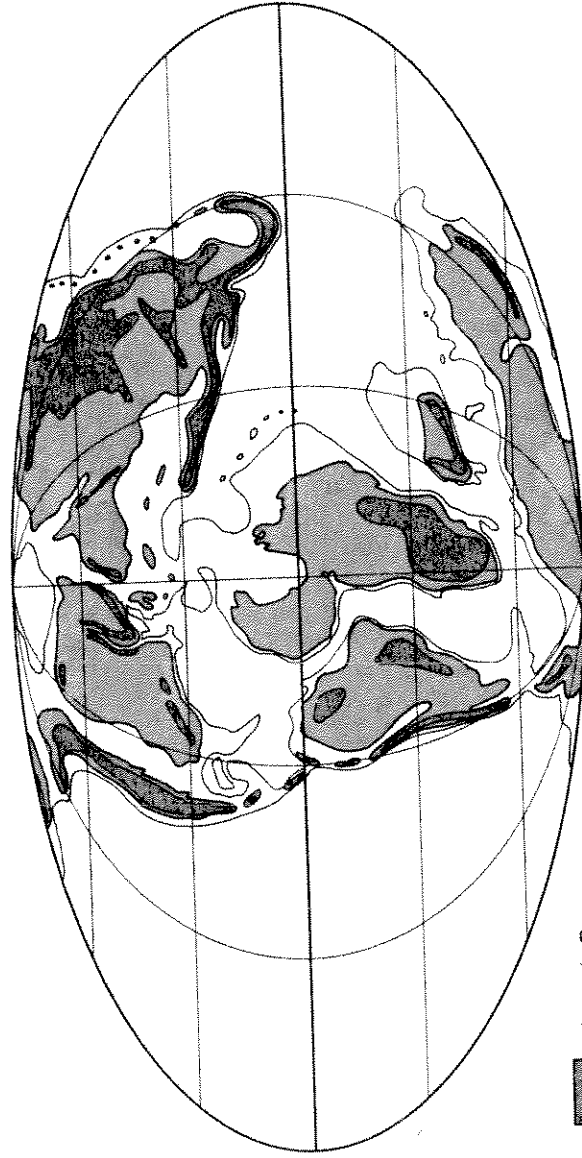
Ferns of the families Schizaeaceae and Gleicheniaceae were rhizomatously spreading plants less than 2 m high that were probably major colonizers of open, perhaps even dry and/or low-nutrient, substrates during much of the Mesozoic. Ferns of these families may have formed vegetation analogous to savannas or grasslands now dominated by herbaceous angiosperms (Coe et al. 1987). Fusinized leaves of these families are abundant at some Lower Cretaceous localities (Alvin 1974; Harris 1981), and their spores are common elements in palynofloras (e.g., Batten 1974). Furthermore, most living species of Gleicheniaceae and Schizaeaceae are thicket-forming or scrambling types that occupy open, sometimes fire-disturbed, habitats in tropical-to-subtropical areas (Tryon and Tryon 1982). One particularly enigmatic element of Early Cretaceous vegetation was *Tempskya*, which had a large pseudo-trunk, composed of many small, intertwining stems, that was up to 40 cm thick but only 4.5 m tall (Read and Brown 1936). The ecological role of *Tempskya* is difficult to infer, because it so little resembles any other living or fossil form.

Conifers, cycads, cycadeoids, and other gymnosperms such as Cheirolepidiaceae and Czekanowskiales continued from the Jurassic into the Cretaceous without major changes.

Specific Plant Assemblages

Good examples of Early Cretaceous vegetation without angiosperms come from western North America (LaPasha and Miller 1984), eastern Siberia (Krassilov 1973, 1975a), and from the Wealden of western Europe (e.g., Daber

EARLY LATE CRETACEOUS (94 Ma)



- Mountain Ranges
- Lowlands
- Continental Shelf

Paleotopography

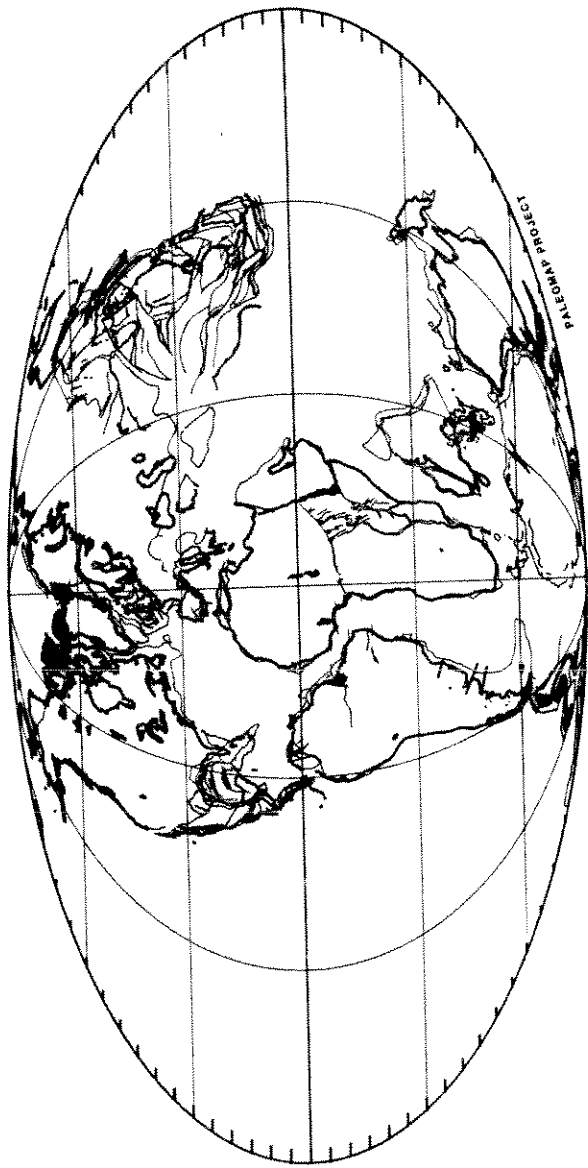


Plate Positions

Fig. 6.4. Generalized continental positions and orography in the Late Cretaceous. (Courtesy of C. R. Scotese and the Paleomap Project, University of Texas, Arlington)

1968; Batten 1974; Oldham 1976; Riegel et al. 1986; Pelzer 1987). The Kootenai flora from the upper Aptian of Montana contains 25 species of vascular plants, the most common of which are ferns (*Coniopteris*, *Acrostichopteris*, *Sphenopteris*, and *Cladophlebis*), caytoniaceous pteridosperms (*Sagenopteris*), and conifers (*Athrotaxites*, *Elatides*, and *Elatocladus*). LaPasha and Miller (1984) interpreted the vegetation to have been a conifer- (*Athrotaxites*) dominated swamp forest with a high understory of *Coniopteris*. *Sagenopteris williamsii* also is thought to have been a swamp plant. Several species of ferns, two species of *Sagenopteris*, *Ginkgo*, and the conifers *Elatides* and *Elatocladus* are thought to have occupied slightly better drained areas. Remains of the bennettitalean *Zamites* are rare and appear strongly allochthonous.

Early Cretaceous floras from the Vladivostok region of the far east of Russia described by Krassilov (1973) are floristically somewhat similar to those from the Kootenai Formation. The coal-swamp assemblage consists of conifers (*Athrotaxites* and *Cephalotaxus*), ferns (*Cladophlebis*), and bennettitaleans (*Nilssoniopteris*). Stream borders were occupied by *Zamiophyllum*, *Subzamites*, *Nilssonia*, and *Podocarpus*. The floodplain supported a diverse vegetation including many species of ferns, conifers, and cycadales, but the dominant forms were the cycads *Ctenis* and *Cycadites*. Krassilov also noted that the majority of conifers occurring in the cycadophyte-dominated assemblages were probably relatively small trees, suggesting that interfluves may have held a low-stature, chaparral type vegetation.

Wealden pollen assemblages from southern England show a reduced importance of cheirolepidiaceous pollen compared to Jurassic floras, but these conifers probably still formed an important part of coastal vegetation (Batten 1974; Watson 1977). Batten (1974) envisioned the vegetation as a savannalike open forest with coniferous trees and a fern/lycopsid herb layer. Alvin (1983) reconstructed one of the dominant conifers of the Wealden, *Pseudofrenelopsis parceramosa*, as a moderate-to-large tree with whorled branching and xeromorphic shoots that might have been shed during times of water stress. However, he found no evidence that *P. parceramosa* was halophytic (salt-tolerant). In a study of dispersed cuticles from Wealden deltaic deposits in southern England, Oldham (1976) found that conifer remains were most abundant, followed by bennettitaleans, cycads, ginkgoaleans, and seed ferns. Among the conifers, Cheirolepidiaceae were the most ubiquitous and abundant, Cupressaceae were sporadically abundant, Taxodiaceae were rare, and only pollen of Araucariaceae and Pinaceae was found. Oldham suggested that the vegetation of the Wealden might have been loosely comparable to that of southern Florida today, with extensive low-lying flooded marshes interspersed with slightly higher ground occupied by more diverse forest. In some floodplain areas with oxidized soils, *Weichselia*, *Phlebopteris*, and *Gleichenites* appear to have formed fern heaths or savannas that were basically devoid of arborescent

vegetation, probably as a result of frequent burning (Harris 1981). Similar *Weichselia*-dominated assemblages are also known from the Wealden of northern Germany (Daber 1968), and the Early Cretaceous of Venezuela (P. Crane, pers. comm., 1990).

Wealden sediments in Germany preserve a number of nearly autochthonous vegetational associations (Pelzer 1987; Pelzer and Wilde 1987). Pollen floras indicate that peat substrates were dominated by gymnosperms, and megaflores from these environments consist mainly of leaves of the conifer *Abietites*. Natural levees in the lower delta plain supported plant communities including *Ruffordia*, *Zamites*, and *Sphenolepis*. Wet back-swamp settings, indicated by carbonaceous shale deposition, preserve a flora containing *Matonidium*, *Nilssonia*, *Sagenopteris*, *Zamites*, *Ginkgoites*, and *Dictyophyllum* (Riegel et al. 1986; Pelzer and Wilde 1987). On the basis of sedimentological and paleobotanical evidence, Pelzer and Wilde (1987) inferred a shift from semiarid conditions in the Late Jurassic of northwest Europe to wetter, although still seasonally dry, climate in the Early Cretaceous.

4.2 Late Cretaceous Vegetation

During the early Late Cretaceous, angiosperm diversity increased explosively, especially in middle-to-high paleolatitudes, and by the end of the Late Cretaceous 50% to 80% of the species in typical local fossil assemblages were flowering plants (Crabtree 1987; Lidgard and Crane 1990). This proportional gain in diversity for flowering plants was largely at the expense of cycadophytes and ferns (broadly speaking), while the proportion of conifer species in local assemblages was relatively unchanged (Lidgard and Crane 1988, 1990). The increase in within-assemblage angiosperm diversity during the Late Cretaceous is less noticeable in palynofloras than in megaflores (Lidgard and Crane 1990).

Although angiosperms became much more diverse, abundant, and widespread in the Late Cretaceous, there is little evidence that, prior to the Campanian and Maastrichtian, they achieved the range of habits and ecological roles they occupy today. Occurrences of Cretaceous angiosperm wood are rare in comparison to those of flowers, leaves, and pollen from the same time, and in comparison with coniferous wood (Wing and Tiffney 1987). Cretaceous angiosperm wood is generalized and shows little anatomical variation (E. Wheeler, pers. comm., 1991). These observations are consistent with the idea that mid-Cretaceous angiosperms tended to be small trees. Angiosperm seeds in the Late Cretaceous were very small, which also is consistent with derivation from relatively "weedy" plants that dominated mostly disturbed, early successional settings (Tiffney 1984). Angiosperms dominated early successional forests and were locally abundant in brackish habitats (Retallack and

Dilcher 1981, 1985; Upchurch and Dilcher 1990); they also may have occupied the understory of relatively open forests. (See Crabtree 1987 and Crane 1987 for opposing views on the importance of angiosperms in late successional vegetation.) Conifers, including podocarpaceous, araucariaceous, and taxodiaceous forms, apparently were the dominant large trees. Wolfe and Upchurch (1987a) reviewed a large suite of floras from the Late Cretaceous of North America and concluded that the small leaf size of most angiosperms, coupled with the rarity of drip tips and of liana leaf types, implied that multi-stratal rain forest of the modern type was not present. Rather, leaf physiognomy suggests an open woodland vegetation, reflecting a relatively dry climate (Wolfe and Upchurch 1987a, b).

The pollination biology of Late Cretaceous angiosperms was distinctly less modern than in the early Tertiary, with most flowers being actinomorphic (radially symmetrical) and probably pollinated by either wind or a broad range of insects (Friis and Crepet 1987; Crepet and Friis 1987). However, advanced eusocial bees are known from the Campanian (Michener and Grimaldi 1988), and the morphology of Cenomanian lauraceous flowers is consistent with bee pollination (Drinnan et al. 1990).

The Cheirolepidiaceae underwent a drastic decline in diversity at about the Cenomanian/Turonian boundary, especially at low latitudes (P. Crane, pers. comm., 1990), and went extinct later in the Cretaceous. During the same interval, Pinaceae became more important (Krassilov 1978b, 1981). Cycadophytes were still present, though rare in most assemblages, and ferns and sphenophytes continued to be common herbaceous elements. Based on the abundance of their megaspores, *Isoetes*-like lycopsids were important elements in wetland or floodplain floras (Kovach and Dilcher 1985; Kovach 1988).

High-latitude Late Cretaceous floras from Alaska indicate a somewhat different kind of vegetation. In these assemblages, angiosperms were less abundant than at midlatitudes, and the forests mostly consisted of taxodiaceous and podozamitean conifers, along with a number of ginkgoaleans and cycadaleans and the usual fern-sphenophyte ground cover. Most or all of the species are thought to have been deciduous. Conifer diversity was initially fairly low in higher latitudes of the Northern Hemisphere but increased sharply during the mid-Cretaceous. The wood structure of some species indicates very rapid growth in the season of light, and coals reflect a high rate of productivity (Spicer and Parrish 1986; Parrish and Spicer 1988b). Similar observations apply to conifer-dominated assemblages from the Antarctic peninsula (Francis 1986).

By Maastrichtian times, climatic deterioration had caused a dramatic drop in diversity in these high-latitude assemblages and also in the stature and productivity of the vegetation (Spicer and Parrish 1986). Fossil wood and oxygen isotope data derived from marine mollusk shells of the Antarctic peninsula

also record declining temperatures from the Santonian-Campanian interval to the Maastrichtian (Francis 1989; Pirrie and Marshall 1990). Similar climatic trends for both northern and southern high latitudes imply the Late Cretaceous cooling was a global event.

Specific Plant Assemblages

Although Late Cretaceous floras are numerous (e.g., Crabtree 1987; McClammer and Crabtree 1989), few have been studied from a vegetational or paleoecological perspective. One exception is the flora of the Blackhawk Formation (probably Campanian) in central Utah (Parker 1976). Autochthonous plant fossils from the Blackhawk Formation occur in two major sedimentary environments: swamps and "bottomlands." The swamp vegetation was dominated by a taxodiaceous conifer, *Sequoia cuneata*, and a deciduous dicot, *Rhamnites eminens*, but 8 other conifers (including species of *Brachyphyllum*, *Moriconia*, and *Protophyllocladus*) and 8 other species of dicots were also moderately abundant in the swamp assemblages and were probably canopy or subcanopy trees. The palm *Geonomites*, the cycadophyte *Nageiopsis*, and several ferns were abundant locally and probably were understory or forest floor plants. In contrast to the swamps, the assemblages from slightly drier "bottomland" areas are dominated in numbers and species by dicots. The bottomland vegetation was probably dominated by species of *Cercidiphyllum*, *Platanus*, and *Dryophyllum*, although 10 other dicot species occur in moderate abundance. The 2 conifers found in the bottomland assemblages are rare elements. It is interesting to note that even as late as the Campanian, conifers were still vegetational dominants in swamp settings, and that 7 or 8 species co-occurred in the same local area; this is a far-higher local species richness than is seen in Paleogene or contemporary conifer swamps.

The Santonian-age Mgachi locality on Sakhalin island, Russia, has produced an assemblage typical of the Late Cretaceous "North Pacific refugium" (Vakhrameev 1987), in which archaic forms were especially common, particularly *Sequoia* (Taxodiaceae), followed by *Araucarites* (Araucariaceae), *Protophyllocladus* (Podocarpaceae?), *Araliaephyllum* (platanoid angiosperm), and *Cupressinocladus* (conifer), along with 3 taxa of angiosperms, 3 ferns, and 1 taxon each of cycad, ginkgoalean, and caytonialean that together make up about 22% of the specimens studied (Krassilov 1975a). These relative abundances probably indicate a conifer forest with ferns, cycads, and seed ferns either in the understory or in nearby riparian habitats.

A sequence of floras from the North Slope of Alaska span the Late Cretaceous and provide evidence for cooling climate and less-diverse vegetation during this interval of time (Parrish and Spicer 1988a, b; Spicer and Parrish 1990a, b; Frederiksen et al. 1988). Latest Albian or Cenomanian assemblages

from the Nanushuk Group have produced 67 species of angiosperms, 18 ferns, perhaps as many as 12 species of conifers, 4 ginkgoaleans, and 2 cycadophytes. Angiosperm fossils are most abundant in fluvial channel and lake margin settings, although they also occur in ponded-water environments (Spicer and Parrish 1990b). By the Coniacian, the ginkgoaleans were reduced to 1 species and the cycadophytes were absent. The physiognomy of these Coniacian assemblages has been compared to extant low montane mixed coniferous forest growing under mean annual temperatures of less than 13 degrees C. By the Campanian and Maastrichtian, the diversity and productivity of high Arctic vegetation had both been decreased. Only 2 species of conifers are known as megafossils, fossil trunks are generally smaller in diameter, and a sizable proportion of the angiosperm diversity may have been in herbaceous species (Spicer and Parrish 1990b, Frederiksen et al. 1988). Equisetaleans probably were the dominant component of the herb layer in Campanian-Maastrichtian vegetation of the North Slope (Brouwers et al. 1987).

4.3 *Cretaceous Faunas*

Although some evidence exists for the presence of Lepidoptera (or at least very closely related taxa) in the Jurassic, the oldest unambiguous records (referable to the Micropterigidae) date from the Early Cretaceous (Whalley 1986). Adults of extant micropterigids subsist on pollen, whereas their caterpillars feed on mosses, liverworts, and detrital organic matter. Evidence for angiosperm leaves mined by lepidopterans also is recorded from the Late Cretaceous (Dilcher in Whalley 1986; Gall and Tiffney 1983). Aphids (Homoptera: Aphidoidea), short-horned grasshoppers (Orthoptera: Acridoidea), and gall wasps (Hymenoptera: Cynipidae) all first appear in the Cretaceous. The oldest-known termites (Isoptera) and ants (Formicoidea) are Late Cretaceous in age (Hennig 1981; Wilson 1987). Of great significance to the ecology and evolution of flowering plants is the presence of advanced eusocial bees in the Late Cretaceous (Michener and Grimaldi 1988).

By the Early Cretaceous, tetrapod faunas appear to show pronounced differences between Northern and Southern Hemisphere assemblages (Bonaparte 1987, 1990), although some interchange is still evident. In the Northern Hemisphere, the main change among herbivorous tetrapods was a decrease in diversity and abundance of high-browsing sauropods (Weishampel and Norman 1989). Stegosaurs were also very much reduced in importance in the Early Cretaceous. Another group of large armored quadrupedal ornithischians, the Ankylosauria, slowly increased in diversity and abundance throughout the Early Cretaceous (Maryanska 1977; Coombs 1978). These dinosaurs reached a length of up to 6 m and a weight of up to 2 t. They had massive skulls with fusion of most cranial bones. The teeth are small, spatulate, and

very simple. Although no clear pattern of tooth wear is apparent, many teeth show obliquely inclined wear facets, suggesting some sort of puncture crushing (Russell 1940; Weishampel and Norman 1989). Ankylosaurs had been present as a small part of some Jurassic faunas and did not diversify until the Cretaceous.

The Ornithopoda underwent a rapid radiation during the Cretaceous. Some Early Cretaceous ornithopods such as *Iguanodon* and *Tenontosaurus* reached larger body size (length up to 10 m and weight up to 2 t) and thus presumably foraged at higher levels above the ground than did their Jurassic predecessors. They continued the trend toward elaboration of dental occlusion for oral processing of food (Norman and Weishampel 1985; Weishampel and Norman 1989).

The first Ceratopsia appeared in the Cretaceous. They included the bipedal Psittacosauridae from the Early Cretaceous (Osborn 1923) and the quadrupedal Protoceratopsidae from the Late Cretaceous of East Asia and western North America (Russell 1970; Maryanska and Osmolska 1974). The closely packed, interlocking teeth of psittacosaurids had wear facets oriented approximately 60 degrees to the horizontal, and it would appear that the chewing stroke involved both palinal and orthal movements of the mandible (Weishampel and Norman 1989). In the Protoceratopsidae, the wear facets are virtually vertically oriented, suggesting strictly orthal, slicing jaw motion, much as in the Ceratopsidae (Ostrom 1966; Weishampel and Norman 1989).

Small herbivores and/or omnivores of this time period included multituberculates and broad-toothed sphenodontians, all of which presumably foraged within the first meter above the ground. At least some of the multituberculates were arboreal (Krause and Jenkins 1983) and thus had substantially increased vertical foraging ranges. The Early Cretaceous sphenodontian lepidosaur *Toxolophosaurus* has transversely broadened and closely packed teeth, and wear facets suggest a back-to-front chewing stroke (Throckmorton et al. 1981).

The main difference between Northern and Southern Hemisphere tetrapod faunas is that in the Southern Hemisphere sauropods apparently continued to be the dominant element among the herbivores, with hadrosaurid ornithopods being quite rare (Bonaparte 1987). Recently recovered mammalian assemblages from the Upper Cretaceous of Patagonia are notable for the complete lack of eutherian and metatherian taxa and the presence of many endemic taxa, including the hypsodont *Gondwanatherium* (Bonaparte 1986, 1990).

Late Cretaceous assemblages of large herbivores in the Northern Hemisphere were dominated, in the numbers of both specimens and species, by hadrosaurid ornithopods (length up to 12 m and weight up to 4 t) and ceratopsid ceratopsians (length up to 10 m and weight up to 9 t). The former group had a circumboreal distribution, whereas ceratopsids were apparently restricted to North America. Both hadrosaurids and ceratopsids had elaborate

dentitions with closely packed, interlocking teeth. Unlike the condition in hadrosaurids, the nearly vertical orientation of the wear facets in ceratopsids (and protoceratopsids) suggests that the power stroke was restricted to an orthal slicing movement (Ostrom 1966; Weishampel and Norman 1989). The browsing range for the quadrupedal ceratopsids was probably within one or two meters above the ground. Taphonomic evidence suggests that both ceratopsids (Currie and Dodson 1984) and hadrosaurids (J. R. Horner, pers. comm., 1989) may have foraged as herds.

Pachycephalosaurs were another group of small-to-medium-sized bipedal ornithischians that first appeared in the Early Cretaceous (Maryanska and Osmolska 1974; Sues and Galton 1987). They have relatively simple spatulate teeth with some wear, suggesting some form of puncture crushing, and a rather extensive gut capacity. They probably foraged within one to three meters above ground level, and all had relatively simple teeth that would have sufficed for cropping but must have relied on other means of breaking down plant fodder, such as gut fermentation (Farlow 1987). The major difference between Campanian-Maastrichtian and earlier tetrapod assemblages is the abundance and diversity of small mammalian herbivores, mostly multituberculates. These mouse-to-woodchuck-sized animals had dentitions well suited to processing discrete food items such as fruits and seeds (Krause 1982). By Maastrichtian times, the taxonomic diversity of small mammalian herbivores, including eutherians, equaled or exceeded that of dinosaurian herbivores in some Northern Hemisphere faunas. Gondwanan herbivore faunas were dominated by the large sauropods of the family Titanosauridae, which included a number of armored forms. Only a few hadrosaurs are known from the Late Cretaceous of South America (Bonaparte 1987), and the mammalian faunas are highly endemic (Bonaparte 1986, 1990).

4.4 Cretaceous Ecological and Evolutionary Trends

The Early Cretaceous appearance of flowering plants marks the change from the Mesophytic to the Cenophytic. Although this appearance, and the subsequent radiation of angiosperms during the mid-Cretaceous, are undoubtedly among the most significant evolutionary events in the history of life on land, the ecological consequences are less striking. It has long been held that the initial radiation of flowering plants (Barremian-Albian) took place largely in disturbed or ephemeral habitats (Hickey and Doyle 1977). The impressive taxonomic diversification of angiosperms during the mid-Cretaceous and their tendency to make up the great majority of species in local floras of Cenomanian and later age (Crabtree 1987; Lidgard and Crane 1988, 1990) have led to the tacit belief that angiosperms dominated terrestrial vegetation by the early Late Cretaceous.

However, high diversity within a clade does not necessarily indicate it has

an important role in structuring vegetation (e.g., Orchidaceae or Asteraceae in extant vegetation), and few studies have quantified the abundance of Cretaceous angiosperm remains in addition to their diversity. Because leaf number has a fairly high correlation with stem basal area of a species (Burnham et al. 1992), the relative biomass of angiosperms vs. other plants in the Cretaceous could be assessed roughly by comparison of relative abundances of leaf fossils. Such data have been published for the Late Cretaceous Blackhawk Formation flora, in which 4 of the 9 taxa represented by more than 100 specimens (out of a total 7,400 specimens) are conifers or cycadophytes (Parker 1976). These numbers imply that in this local area, gymnosperms were codominant with flowering plants, even in the last half of the Late Cretaceous.

Other lines of evidence, including angiosperm diaspore size distributions (Tiffney 1984), angiosperm leaf physiognomy (Wolfe and Upchurch 1987a, b), angiosperm trunk size (Wing and Tiffney 1987), and angiosperm palynomorph diversity (Crabtree 1987), are also consistent with the suggestion that flowering plants were not major canopy elements until at least the Campanian or Maastrichtian. In spite of this probable lag in becoming important canopy trees, there is little doubt that, from the Albian onward, angiosperms were extremely abundant in disturbed habitats such as riparian corridors or recently burned areas. The evolutionary radiation of angiosperms might thus have had an important effect on the rate of colonization and productivity of disturbed sites.

The increase in the relative abundance and diversity of angiosperms in disturbed areas more or less coincides with an increase in the relative abundance and diversity of two groups of large herbivores: the hadrosaurid ornithomorphs and ceratopsid ceratopsians (Bakker 1978; Wing and Tiffney 1987; Weishampel and Norman 1989). Both groups of dinosaurs were adapted to extensive oral processing of plant food and may have foraged in herds. The coincidence of the two radiations may reflect diffuse coevolution, in which increased abundance and productivity of disturbed-site vegetation led to the success of these two herbivore groups, and in which herbivore disturbance in turn favored the success of relatively "weedy" plants, such as angiosperms (Bakker 1978). Given this scenario, the pattern of co-occurrence of herbivore communities dominated by hadrosaurids and ceratopsids and floras dominated by weedy angiosperms should persist at finer geographic and temporal scales. A possible test case is represented by the Late Cretaceous biotas of South America, where titanosaurid sauropods, rather than low-browsing hadrosaurs and ceratopsians, were the dominant herbivores. If the coevolutionary scenario is valid, then South American Late Cretaceous vegetation should have been significantly different from coeval North American vegetation. Specifically, areas of disturbed angiosperm-dominated vegetation should have been less common, either because South American angiosperms were less weedy in their habits or because they were a less important element in the vegetation.

Limited evidence from the southern continents does indicate that angiosperms were very slow to invade high southern latitudes, perhaps not becoming diverse there until the Cenomanian or later (e.g., Drinnan and Crane 1990).

5 PALEOGENE BIOTAS

5.1 *The K/T Boundary and Earliest Paleocene Vegetation*

Earliest Paleocene vegetation is known best from palynological assemblages. In North America these assemblages record a low-diversity flora with few angiosperms that contrasts sharply with latest Cretaceous, angiosperm-rich pollen floras. In several parts of western North America, palynofloras from the first few centimeters above the boundary consist of just a few kinds of fern spores, forming the "fern spike" (Orth et al. 1981; Nichols et al. 1986). In sections displaying a clear fern spike, angiosperm pollen does not predominate again until 10–20 cm above the K/T boundary (Tschudy and Tschudy 1986). These palynofloral changes in western North America are thought to indicate the nearly instantaneous destruction of diverse, angiosperm-dominated latest Cretaceous vegetation, its replacement by low-diversity, early successional vegetation dominated by a few species of ferns, then the return to angiosperm-dominated vegetation with a rather different composition (Orth et al. 1981; Tschudy et al. 1984; Tschudy and Tschudy 1986). However, a fern spike is not present at several apparently continuous K/T sections in southern Canada (e.g., Lerbekmo and St. Louis 1986; Lerbekmo et al. 1987).

Earliest Paleocene megaflores have been described from New Mexico, Colorado, and North Dakota. The megaflores from New Mexico and Colorado show a small increase in diversity and angiosperm dominance in the decimeters above the boundary, but the angiosperms are inferred to have been early successional taxa (Wolfe and Upchurch 1986, 1987b). Megaflores in this area continued to be of low diversity for at least the first million years of the Paleocene. This led Wolfe and Upchurch (1986, 1987a) to propose the process of "quasi-succession," a sequence of changes analogous to ecological succession but requiring several orders of magnitude more time because of the continental scale of the initiating disturbance. In contrast to the lengthy recovery phase in the southern Rocky Mountains, earliest Paleocene assemblages from western North Dakota show a more rapid increase in diversity, even though extinction levels at the K/T boundary were very high (K. R. Johnson et al. 1989; K. R. Johnson 1991; Johnson and Hickey 1991). In all probability the interregional differences in the expression of the fern spike and characteristics of the earliest Paleocene megaflores reflect differences in ecological recovery following the K/T extinctions that were induced by varying local sedimentary environments, local climatic differences, and/or taphonomic effects. These kinds of effects have been documented in Alberta, Canada,

where intraregional differences in Maastrichtian to early Paleocene climate exerted a strong influence on palynofloral composition and sedimentary characteristics (Jerzykiewicz and Sweet 1988).

Although earliest Paleocene pollen assemblages from near-shore marine environments in Japan show an increase in fern spores, as well as pine pollen, relative to latest Cretaceous palynofloras from the same area (Saito et al. 1986), the fern spike is not as pronounced as that seen in many sections in the Rocky Mountains. Furthermore, the increase in pine pollen may reflect taphonomic enrichment of this buoyant pollen type in marine sediments rather than a true increase in pine (Spicer 1989). The limited data from Japan are consistent with a less severe destruction of vegetation at the K/T boundary and more rapid recovery in the Paleocene. Southern Hemisphere palynofloras show even less dramatic patterns of change at the K/T boundary. Palynofloras from terrestrial sections in New Zealand show only moderate levels of turnover across the K/T boundary (Raine 1988), and palynofloras from near-shore marine sediments on Seymour Island off Antarctica show almost no extinction through the latest Cretaceous–earliest Paleocene interval (Askin 1988). These southern high-latitude early Paleocene assemblages represent coniferous forest vegetation (mostly Podocarpaceae) with ferns and a variety of angiosperms, including some *Nothofagus* (southern beech). Generally, southern high-latitude, Paleocene palynofloras are less diverse than those of the Late Cretaceous, but this probably reflects long-term cooling rather than destruction of vegetation at the K/T boundary (Askin 1988).

Whatever the local variations in the pattern of recovery in western North America were, it seems clear that K/T devastation of terrestrial biotas was less severe in other parts of the world. This is consistent with geological and mineralogical data indicating the bolide(s) struck the earth near North America, perhaps at the northern end of the Yucatan Peninsula, and/or in Iowa (Bohor et al. 1987; Hildebrand and Boynton 1990; Hildebrand et al. 1990; Izett 1990). There is now little disagreement that the K/T bolide impact(s) caused high levels of local-to-regional extinction and ecological disruption in western North America, but the longer-term effects of the event on terrestrial vegetation are less well understood. Evidence for a sharp but long-lasting transition to wetter climates over most of North America in the early Paleocene has been seen in many studies (e.g., Hickey 1984; Fastovsky and McSweeney 1987; Retallack et al. 1987; Wolfe and Upchurch 1987b; Lehman 1990), and Wolfe and Upchurch (1987b) have argued the shift may be a direct consequence of the K/T bolide impact. Wolfe (1987) maintained that preferential extinction of evergreen species at the K/T boundary (because they were less able to survive a short period of cold temperatures generated by the impact cloud) left Northern Hemisphere floras permanently enriched in deciduous lineages. Hickey (1980) argued that the high proportion of deciduous species in many Paleocene floras was a consequence of colder climate. Confir-

mation of Wolfe's hypothesis in particular awaits better independent documentation of paleoclimatic trends, because continental paleoclimate inferences for the Paleocene depend largely on physiognomic features of the vegetation, which Wolfe (1987) maintained were influenced by the K/T extinction.

5.2 Paleocene-Eocene Vegetation

Paleocene megafloral assemblages from high northern latitudes demonstrate the existence of forests dominated by deciduous conifers of the bald cypress family (Taxodiaceae), with an accessory component of ginkgos and deciduous dicots that probably grew in riparian habitats (e.g., Hickey et al. 1983). Eocene forests in the Canadian Arctic are preserved as standing trunk fields with in situ litter (peat) beneath them (Basinger et al. 1988; Francis 1991). Eocene swamp forests also were dominated by taxodiaceous conifers (*Glyptostrobus* and *Metasequoia*), but presumed evergreen species of *Pinus* (pine), *Picea* (spruce), and *Abies* (fir), as well as the deciduous *Larix* (larch), by then had become important in these settings. The swamp conifers had trunk diameters of 1.5 m or more, growth rings comparable to those of extant temperate-zone conifers, and inferred heights of up to 50 m (Basinger et al. 1988). The large overall size and thick growth rings of the trees imply a productive ecosystem. The Eocene high Arctic assemblages also contain *Ginkgo* and a number of dicot species in the Betulaceae (birch family), Juglandaceae (walnuts), Platanaceae (sycamores), and Fagaceae (oaks). The dicots probably grew in riparian areas (Basinger et al. 1988).

Throughout the Northern Hemisphere, early-to-middle Paleocene mid-latitude floras are known for their relatively low taxonomic diversity and homogeneity, for example, late Paleocene assemblages from Mongolia, China, the western United States, and Scotland have many similar forms (Brown 1962; Mukulbekov 1988; Guo 1985; Boulter and Kvacek 1989; Crane et al. 1990). As in contemporaneous Arctic assemblages, the dominants in wet or swampy areas were the taxodiaceous conifers *Metasequoia* and *Glyptostrobus* (e.g., Hickey 1980; Fastovsky and McSweeney 1991), although better-drained substrates supported a limited variety of most deciduous dicots (e.g., Hickey 1977, 1980). These floras may represent a rough equivalent to extant deciduous, hardwood forests, although the existence of some large herbaceous forms (e.g., *Zingiberopsis* in the ginger family) implies they were not subject to winter temperatures far below freezing. In southern North America, fossil leaf assemblages from swamp settings tend to be dominated more by dicots than by conifers (Wolfe and Upchurch 1987b), and silicified Paleocene trunks from fluvial swamp sediments in southern Texas are dicots (Wheeler 1991); but in more northerly areas, wood in such settings generally is coniferous.

By latest Paleocene times, evergreen broad-leaved angiosperms became

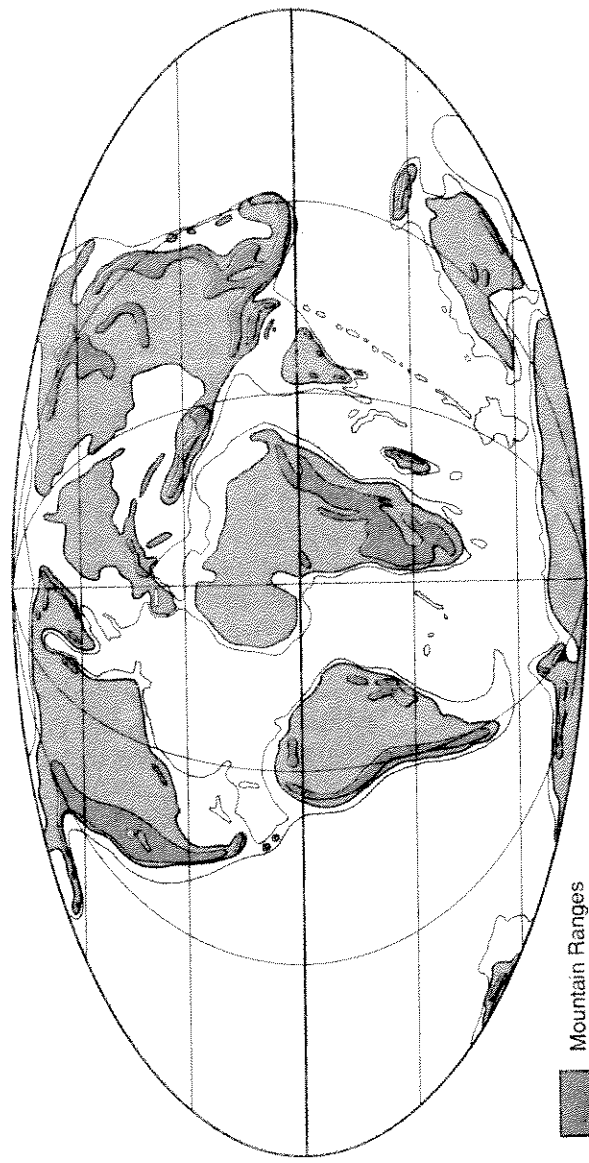
more common in many Northern Hemisphere floras (e.g., Hickey 1980; Wolfe and Upchurch 1987a). The earliest well-documented Tertiary fruit, seed, and wood assemblages are late Paleocene to early Eocene in age and indicate that there existed a wide variety of angiosperms with a "modern" range of seed sizes (Tiffney 1984; but see Knobloch and Mai 1986). These forms were broadly seral, and it is highly probable that the species with larger diaspores were biotically dispersed and capable of establishing and maintaining populations under a closed canopy forest.

Paleocene assemblages from 46 degrees S latitude in Argentina are thought to represent a suite of vegetational types including mangrove, swamp forest, tropical rain forest, montane rain forest, and savanna-sclerophyllous forest (Romero 1986). Few Paleocene floras from Australia have been described in paleoclimatic or paleoecological terms. However, a series of late Paleocene floras from southeastern New South Wales, at a paleolatitude of about 57 degrees S, includes both palynomorphs and fossil wood (Taylor et al. 1990). Podocarpaceous and araucarian conifers are the most abundant components of these palynofloras, although angiosperms are more diverse and include *Nothofagus* and members of the Proteaceae, among others. Taylor et al. (1990) suggest these palynofloras were derived from cool-temperate rain forests that had a coniferous canopy, and this is supported by the abundance of conifer wood relative to angiosperm wood. As in North American Late Cretaceous and Paleocene floras, conifers were particularly dominant in swamps and on peat substrates, although the Australian conifers were podocarps rather than bald cypresses.

The acme of tropicality and of angiosperm-dominated closed forest was probably during the early Eocene, when subtropical vegetation may have extended to 60 degrees N latitude, and full tropical, multistratal rain forests occurred as far north as 30 degrees N latitude (Wolfe 1985). (Fig. 6.5 shows reconstructed middle Eocene paleogeography.) In northern Europe, the fruit and seed assemblages from the Eocene London Clay record a diverse flora that was taxonomically, and perhaps vegetationally, most similar to those now occurring in tropical Southeast Asia. Vegetational types identified from the London Clay flora include mangrove swamp with abundant *Nypa* (Palmae) and associated *Ceriops* (Rhizophoraceae), as well as highly diverse, dense paratropical forest and probable gallery forest with diverse lianas of the families Menispermaceae and Icacinaceae (Collinson and Hooker 1987). However, the London Clay flora also retained members of typical Paleocene Holarctic lineages that are now temperate in their distribution, such as *Cornus* and Betulaceae (Collinson 1983). Animal and plant fossils characteristic of the mangrove biota also occur together in middle Eocene sediments of southern Texas (Westgate and Gee 1990).

Eocene megafloras from China have been summarized recently by Guo (1985). Eocene assemblages tend to be very diverse and to contain a high pro-

MIDDLE EOCENE (50 Ma)



- Mountain Ranges
- Lowlands
- Continental Shelf

Paleotopography

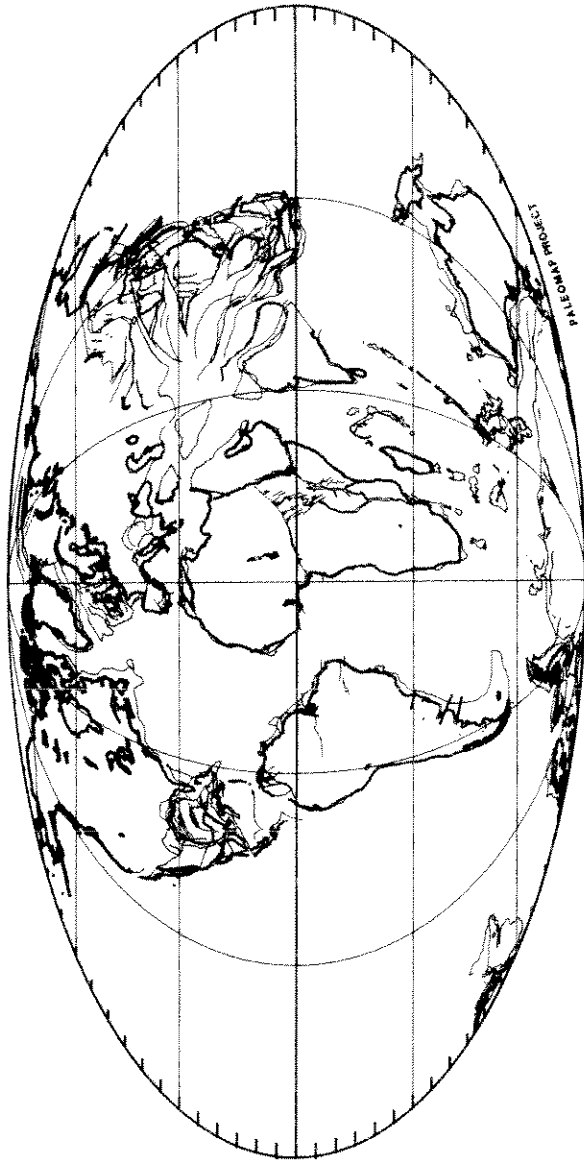


Plate Positions

Fig. 6.5. Generalized continental positions and orography in the middle Eocene. (Courtesy of C. R. Scotese and the PaleoMap Project, University of Texas, Arlington)

portion of broad-leaved evergreen forms. Generally the leaf physiognomy of Eocene floras suggests somewhat drier climate than during the Paleocene, although a variety of vegetational types have been recognized in different parts of China. Humid subtropical forests consisting of a mixture of deciduous and evergreen dicots, and deciduous conifers existed in the north, and these shared many taxa with coeval floras of North America: the ferns *Lygodium* and *Salvinia*, the conifers *Glyptostrobus* and *Metasequoia*, and a number of angiosperms, including *Cercidiphyllum*, *Cinnamomum*, *Alnus*, and palms. Dry subtropical forests characterized central China. These assemblages are somewhat less diverse than those from farther north, and leaf texture tends to be more coriaceous. Humid tropical forests occupied the southern part of the country. Over two-thirds of the species in these assemblages are broad-leaved evergreen forms, and there is particularly high diversity in the Lauraceae (laurel family). Conifers apparently were very rare in the humid tropical forests (Guo 1985).

During the Eocene, Australia, which was then between 30 and 60 degrees S, supported diverse, angiosperm-dominated, subtropical-to-tropical rainforest (Christophel and Greenwood 1989; Hill 1982). Megafossil assemblages from several middle Eocene localities in Anglesea, southeastern Australia, contain species with nearest living relatives now restricted to tropical rain forest in northern Queensland, including *Podocarpus*, the cycad *Bowenia*, and dicots in the Casuarinaceae and Proteaceae. Leaf physiognomic characteristics of these floras are also consistent with tropical or warm subtropical forests (Christophel and Greenwood 1989). Interlocality differences in floral composition at Anglesea suggest these forest were heterogeneous in species composition (Christophel et al. 1987). Eocene megafloras from Tasmania suggest somewhat cooler, though still subtropical, climatic conditions. Lowland rain forests in Tasmania included Araucariaceae, Casuarinaceae, and *Nypa* (Hill and Bigwood 1987), and vegetation from somewhat higher elevations included *Nothofagus* (Hill 1984).

Although Eocene floras from Argentina indicate subtropical to fully tropical forest, some taxa suggest seasonal dryness (Romero 1986). Beginning in the middle Eocene and continuing through to the Oligocene, decreases in the percentage of species with entire-margined leaves and in species with large leaves imply cooler and/or more seasonal climates in southern South America (Romero 1986). Africa appears to have suffered a restriction of wet tropical forests beginning in the middle Tertiary, though perhaps this did not affect much of the continent until the Miocene (Axelrod and Raven 1978). Late Eocene floras from northern Egypt suggest wet or seasonally wet tropical forest (Wing, unpublished data from Kasr El Sagha Fm.).

Drying and warming climate in the eastern Rocky Mountain region of North America during the middle and later Eocene resulted in the loss of conifers even in wetter habitats at lower elevations (Wing 1987), although pinateous conifers became important in montane forests in the Rocky Mountains

and farther west (Wolfe and Wehr 1987; Axelrod 1966). The increasing seasonal dryness suggests vegetation that was probably more open, more deciduous, and of lower stature (MacGinitie 1953, 1969; Leopold and MacGinitie 1972; Wing 1987), although it is not known whether herbaceous angiosperms were an important part of this vegetation. The geographic extent of the drying trend is as yet unknown, but it is clearly established that mesic tropical-to-subtropical forest persisted along the Pacific and Gulf coasts of North America throughout the Eocene (MacGinitie 1941; Wolfe 1978; Frederiksen 1988). A global decline in temperatures and increase in seasonality about 33 Ma resulted in a shift to more deciduous broad-leaved types of vegetation in coastal western North America (Wolfe 1978), and floral evidence from Europe also suggests a major drop in temperature at or near the end of the Eocene (Collinson et al. 1981; Cavelier et al. 1981; Collinson and Hooker 1987; Medus and Pairis 1990). The suddenness and synchronicity of the vegetational shift in Europe has not been precisely determined, although it appears to have been a fairly gradual process (Collinson 1991).

Mean seed size in later Tertiary temperate-latitude floras shows a slight decline, which perhaps reflects the increasing abundance and diversity of herbaceous angiosperms (Tiffney 1984). Although clear evidence for the development of grassland vegetation is not present before the mid-late Miocene, megafossils of grasses that are modern in appearance are known from the latest Eocene Florissant flora (MacGinitie 1953), and extant tribes apparently were established by the early Eocene (Crepet and Feldman 1989).

5.3 *Paleogene Faunas*

The fossil record suggests a continuous increase in the number of insect families throughout the Paleocene. The appearance of modern moths and butterflies (Monotrypsia and Ditrypsia) in the middle Eocene provided important new pollination agents for the angiosperms. Formicoid ants underwent a considerable radiation during the latest Cretaceous or earliest Paleocene (Wilson 1987).

The beginning of the Paleocene witnessed the rise of mammals. Mammalian diversity in western North America quickly rose from 20 to 45 genera within 250,000 years of the K/T boundary, and 2 million years into the Paleocene, it reached 70 genera (Archibald 1983). Placental herbivores were initially rather small and fairly similar to each other in overall appearance. Many had specialized anterior dentitions (large and/or procumbent incisors and canines and enlarged premolars), which implies they may have selected and processed small food items such as fruits, seeds, or small prey. Larger forms in these early Tertiary faunas, generally heavy-bodied, short-limbed Pantodonta, lacked conspicuous dental specializations; this suggests that they utilized a wide variety of vegetational resources. Specialized browsers were not a significant component of the fauna (Stucky 1990).

The transition from the Paleocene to the Eocene in North America is char-

acterized by a significant turnover in mammalian faunas due to immigrations of new taxa and declines in the diversity through extinction of archaic forms (Rose 1981, 1984; Stucky 1990). Many herbivorous groups with extant representatives made their first appearance in the fossil record across the Paleocene/Eocene boundary, including rodents at the end of the Paleocene. The early Eocene represented a period of major biotic interchange between North America and Europe, resulting in homogenization of mammalian faunas in the Northern Hemisphere (McKenna 1983). Both groups of modern ungulates, the even-toed Artiodactyla and the odd-toed Perissodactyla, appeared in the Northern Hemisphere at the beginning of the Eocene. A major radiation of these herbivorous mammals commenced in the early Eocene and was accompanied by a trend toward larger body size (Rose 1984; Stucky 1989). Artiodactyls were initially less numerous and diverse than the perissodactyls but underwent an extensive radiation later in the Eocene (Cifelli 1981). Development of cutting ridges (lophodonty) appeared in the early Eocene among perissodactyls but development of crescentic shearing crests (selenodonty) did not become common among artiodactyls until the late middle Eocene. Mammalian assemblages from the late Paleocene and Eocene of Patagonia are dominated by a variety of endemic ungulates, especially notoungulates (McKenna 1980), which are characterized by the pattern of lophs on their molar teeth and reach their maximum diversity in the Oligocene. In North America the highest alpha-diversity levels for mammals were reached during the Paleocene and in the early-middle Eocene interval; assemblages from the later Eocene and Oligocene have fewer species and are more likely to be dominated by single species, perhaps indicating the clumped distribution of animal populations that is today characteristic of open vegetation (Stucky 1990). The transition from the late Eocene to the Oligocene (Chadronian and Orellan Provincial Ages) is marked by major changes in the composition of mammalian faunas and continuing increases in cursoriality and lophodonty in many lineages (particularly those of Asian origin; Webb 1977). The Chadronian-Orellan faunal turnover in North America appears to correlate with the Eocene/Oligocene boundary as recognized in the marine realm and with the sharp increase in temperature seasonality seen in terrestrial floras (Swisher and Prothero 1990). However, the Chadronian-Orellan event does not represent a major extinction, but rather a continuation of the trend established in the late Eocene (Stucky 1989, 1990).

5.4 Paleogene Ecological and Evolutionary Trends

Starting in the middle-to-late Paleocene, fruit and seed assemblages document a great range of sizes of angiosperm diaspores; some of the larger ones were almost certainly biotically dispersed (Tiffney 1984). Paleocene and Eocene diversification in the Juglandaceae (Tiffney 1986b; Manchester 1987), and

possibly in the Fagaceae and Podocarpaceae, produced more species with diaspores suited to dispersal by small mammals. Beginning in the early-to-middle Paleocene and continuing into the early Eocene, the guild of small, omnivorous/herbivorous, arboreal/scansorial mammals began to show a high diversity of species with specialized anterior dentitions, generally featuring the hypertrophy of premolars or incisors, and crushing molar teeth (Peripitychidae, Plesiadapiformes, Paromomyidae, Microsyopidae, Carpolestidae, Rodentia, and Multituberculata).

The concomitant increase in the number of large, probably biotically dispersed angiosperms and the number of species of fruit- and seed-eating mammals could represent the initial coevolutionary radiation of what is now an extremely common and important kind of relationship, especially in tropical vegetation (Wing and Tiffney 1987). If this does indeed represent a coevolutionary spiral, then the relationship should be apparent when examined at finer temporal and geographic scales. Present knowledge of Paleocene fruit and seed floras is based on a small number of floras that are not well correlated with mammalian faunas. Late Paleocene and early Eocene biotas from southern England (Collinson and Hooker 1987), however, are consistent with this scenario, and similar data could be assembled for the western United States. If the coevolutionary explanation is correct, diaspore size and structure should show changes as early as the Puercan/Torrejonian boundary.

Another possible example of coordinated change in faunas and floras is seen in the late Eocene of the Rocky Mountain region of North America. Paleobotanical evidence suggests a shift toward an increasingly open savanna-like vegetation with plants of lower stature (MacGinitie 1969; Leopold and MacGinitie 1972; Wing 1987). There was a concurrent, initially quite subtle trend among mammalian herbivores toward increased body size, lophodonty, and cursoriality, and a decline of arboreal forms (Webb 1977; Stucky 1990). This may represent another case of diffuse coevolution, in which the development of more open vegetation (presumably the result of increased seasonality in mean humidity and annual temperature; Wolfe 1978) created opportunities for many lineages to develop features of open-country bulk feeders. Large herbivores, in turn, may have played a significant role in maintaining suitable conditions for weedy plants, particularly herbaceous angiosperms (Wing and Tiffney 1987). The generality of this pattern must be examined on a finer temporal and geographic scale. Floras on the Pacific and Gulf coasts of North America lagged behind those of the eastern Rocky Mountain region in this change, retaining closed semitropical vegetation. Therefore the faunas in this area should prove to be more "archaic" in their ecological characteristics. In fact, mammalian assemblages from Texas and California do appear to retain higher proportions of arboreal species later than those in the northern midcontinent (Stucky 1989, 1990).

It has been argued that Paleogene mammalian faunas in South America de-

veloped adaptations to open settings earlier than those in North America (Stebbins 1981), but more recent work on the chronology and composition of mammalian assemblages in southern South America suggests that, as in North America, open-country faunas were primarily a latest Eocene and later phenomenon (Marshall and Cifelli 1990). In Europe a different set of mammalian lineages also exhibited evolutionary trends congruent to those observed in western North America at roughly the same period of time. A prediction and test of the North American data is that the corresponding European floras should reflect the same types of vegetational change; some evidence suggests that this is indeed the case (Cavelier et al. 1981; Legendre 1987).

6 MESOZOIC AND EARLY CENOZOIC ECOLOGICAL CHANGES

Much of the preceding text has been an attempt to describe the structure of terrestrial communities typical of certain intervals in the past and to infer interactions such as herbivory, dispersal, pollination, and competition that occurred in those long-extinct communities. What follows is a summary of how we think some of these interactions have changed over the whole span of the Mesozoic and early Cenozoic.

6.1 *Changes in Herbivory*

The basic mechanisms of arthropod herbivory (chewing, leaf mining, sucking, etc.) seem to have been established during the late Paleozoic (see chap. 5). At present, limited data prevent us from seeing patterns of change or stasis in arthropod damage is known from the fossil record, including leaf mines (e.g., Crane and Jarzembowski 1980), galls (Larew 1986), and chewed leaves (e.g., Grande 1984), which should permit changes in arthropod feeding types to be compared with changes in observed damage through time.

Through the Mesozoic and early Cenozoic, there were substantial changes in the body-size distribution of herbivorous tetrapods, the height above ground at which they fed ("browseline" of Coe et al. 1987), and the characteristics of their food-processing structures (e.g., Weishampel and Norman 1989). Mesozoic herbivore faunas characteristically seem to have had a high proportion of their diversity in larger body-size categories, but species richness overall was much less than in Cenozoic assemblages. This pattern began to change in the Late Cretaceous, and during the Paleocene and Eocene small herbivores were much more diverse than large ones. Not until the latter half of the late Eocene did very large herbivores again become a diverse faunal element, but body size did not approach that of the dinosaurian megaherbivores

of the Mesozoic. Changes in feeding height roughly followed those in body size, although feeding above 1 or 2 meters did not develop until the Late Triassic. The browse line was pushed to perhaps as much as 10 or 12 meters above the ground during the Jurassic. During the Late Cretaceous, the diversity and abundance of high-browsing herbivores diminished in the Northern Hemisphere, while tetrapods feeding between 1 and 3 meters above the ground became more abundant and diverse. From the K/T boundary until the mid-Cenozoic there were no high-browsing herbivores. Terrestrial browsers feeding at or above 2 meters did not reappear until the Oligocene.

These changes in herbivore body-size distribution and in masticatory and locomotor characteristics are consistent with an overall pattern of: (1) browsing herbivory through much of the Mesozoic; (2) a shift to more frugivory-granivory in the Paleocene-Eocene, following the extinction of large browsers at the K/T boundary; and (3) a partial return to browsing in the mid Tertiary. Herbivores of larger body size tend to respond to vegetation as a finer-grained resource than do small herbivores (Peters 1983; Crawley 1983) and thus would be expected to create a different kind of selective regime for plants. In particular, large herbivores eat a broader range of plant tissues, including those with low unit energy, and are more likely to cause significant damage to the plant in a single feeding episode (e.g., Croze 1974). These feeding habits may favor a variety of plant traits including mechanical defenses such as thorns (Janzen 1986), strong compensatory growth (Stebbins 1981; McNaughton 1984), and secondary compounds. Most small vertebrate herbivores are selective folivores (e.g., McNab 1978), frugivores-granivores (Fleming et al. 1987), nectivores, gummivores, or omnivores and are therefore more likely to view plant resources in a coarse-grained manner and to be particularly interested in tissues with higher unit energy. Herbivory by small vertebrates might be expected to elicit a broadly similar set of plant defenses, but probably with a greater emphasis on protection of seeds and less emphasis on compensatory growth.

6.2 Changes in Dispersal

The wide taxonomic distribution of animal dispersal among seed plants, as well as direct and indirect evidence from the fossil record, suggests that fruits and seeds have been a significant food resource for tetrapods since at least the Late Permian. Vertebrate dispersal, seed morphology consistent with vertebrate dispersal, or seed remains in vertebrate coprolites are known among living and/or fossil members of Ginkgoales, Cycadales, Caytoniaceae, Bennettitales, and Gnetales (Hill 1976; Van der Pijl 1982; Weishampel 1984b; Tiffney 1986a; Crane 1987; Norstog 1987). Some Mesozoic conifers were probably animal dispersed (Tiffney 1986a), as is true of a number of distantly related species of extant conifers (e.g., species of *Pinus*, *Juniperus*, and

Podocarpus). Indeed, animal (fish?) dispersal may have been characteristic of some pteridosperms and cordaites as early as the Carboniferous (Tiffney 1986a). Facultative animal dispersal is primitive for many branches of the seed-plant clade above the level of Lyginopteridales (cycads, conifers, ginkgos, many angiosperm lineages, and various Mesozoic "seed fern" groups); this implies that the interaction is easily developed in one form or another.

Although some form of frugivory and dispersal may have been common in terrestrial ecosystems from the Late Permian onward, evidence from the fossil record strongly indicates major differences in the type of frugivory and animal dispersal characteristic of the Mesozoic versus the Cenozoic. Direct evidence for animal consumption of seeds is extremely rare in the fossil record, and even then such evidence only proves that the seeds were eaten by an animal, not that they were dispersed by one. Therefore changes in dispersal must be inferred from morphological correlates in plants or their possible dispersers. For plants the correlates include diaspore size (large diaspores generally being biotically dispersed; see Primack 1987 and references therein), evidence for fleshy tissue around the seed (endozoochory), hooks or barbs (epizoochory), and wings or hair tufts (anemochory). For vertebrates the correlates include body size (see preceding discussion on herbivory) and dental specializations. On the basis of these traits, Tiffney (1986a) argued that dispersal during much of the Mesozoic was largely by abiotic means or as a result of generalized endozoochory carried out by large herbivores as a by-product of foliage browsing. Tiffney also suggested that the kind of dispersal typical of living birds and mammals in tropical forests, in which dispersers consume a fleshy fruit enclosing a few large seeds or a number of small seeds, was not common until the early Cenozoic. Such dispersal interactions are of major importance in modern tropical forests; 50–90% of shrubs and trees rely on vertebrate dispersers, and up to 80% of mammalian and avian biomass can consist of frugivores (Fleming et al. 1987).

6.3 Changes in Pollination

As with animal dispersal, insect pollination is taxonomically widespread in extant seed plants, most certainly was present in several Mesozoic groups, and may have been present as early as the Carboniferous (Dilcher 1979; chap. 5). Of the Mesozoic groups, some, perhaps most, Bennettitales were insect pollinated (Crepet 1972; Crepet and Friis 1987). Gnetales, which were diverse and abundant in low-latitude floras in the Early Cretaceous (Doyle et al. 1982; Crane and Upchurch 1987; Lidgard and Crane 1990), probably included many insect-pollinated species, judging from the widespread occurrence of insect pollination in extant species. Similarly, living cycads are known to have elaborate insect pollination systems (Norstog 1987), and it seems likely that Mesozoic cycads were insect-pollinated. Ginkgos and conifers are the only

major groups of seed plants common in the Mesozoic that generally lack features consistent with insect pollination. The apparent absence of insect pollination in ginkgoaleans may reflect the present low diversity of the clade and incomplete knowledge of the extinct species. In contrast, there exists no evidence for insect pollination in the moderately diverse living conifers or in fossils of this group.

Given that insect pollination is ancient and taxonomically widespread, it seems probable that it was a common interaction in preangiosperm Mesozoic vegetation. The insect groups implicated in preangiosperm pollination were beetles, sawflies, flies, or other ancient groups (Crepet and Friis 1987). In the context of the pollination biology of extant angiosperms, these insects, especially beetles, are usually considered to be "primitive" pollinators (e.g., Crepet 1984). However, some beetles may participate in rather sophisticated pollination interactions of the kind typical of more "advanced" pollinators (e.g., Young 1988). The presence of advanced pollination interactions in older insect groups at least raises the possibility that complex and sophisticated pollination could have arisen prior to the Late Cretaceous (even though there is little direct evidence), but it would not necessarily have conformed to the modes of advanced pollination seen in living angiosperms.

6.4 Changes in Plant Competition

Mesozoic vegetation has been reconstructed as low-statured and open, perhaps because of seasonal rainfall and fires. A diverse fauna of large herbivores represents an additional element that could have increased the frequency and scale of disturbance, analogous to the role of elephants in some present-day African forests (Jones 1955). Clearly, habitat openings had to be more extensive during the Jurassic and Cretaceous than in the Paleogene, given the large body size of dinosaurian herbivores. If disturbance events in the Mesozoic tended to be more frequent and of larger spatial scale than in many contemporary forested areas, direct plant-plant competition could have been reduced and mediated by selective removal of individuals less resistant to large vertebrate herbivory or damage by fire.

It is not clear what effects such a disturbance regime would have had on the species diversity of late Mesozoic vegetation. It has been proposed that over ecological time, selective herbivory can maintain the richness of a plant community by preventing competitively superior species from excluding those that are slower-growing but less appetizing (the "intermediate disturbance hypothesis" of Grime [1973] and Connell [1978]). We do not know to what degree dinosaurian herbivory was selective. It may be inappropriate, furthermore, to apply an ecological-time theory to geological-time observations. For instance, in modern dry-country grasslands with an evolutionarily long history of grazing, competition seems to be little reduced by current grazing, because most plant species have similar growth habits and response to damage. In con-

trast, in "subhumid" grasslands (where a wider variety of life-forms is present), competition is reduced and diversity is increased at intermediate levels of herbivory (Milchunas et al. 1988). These observations suggest that the effects of herbivory on plant competition and diversity may depend as much on the evolutionary history of the particular system as on the actual amount or kind of herbivory.

The loss of large herbivorous tetrapods at the K/T boundary should have substantially affected disturbance regimes of many kinds of vegetation. Increased rainfall (Retallack et al. 1987; Wolfe and Upchurch 1987b; Lehman 1990) also would have reduced disturbance created by fire, although rainfall can increase the rate of formation of small tree-fall gaps (Brokaw 1985). These rapid decreases in the frequency and scale of disturbance could well have increased the importance of direct competitive interactions between plants. Removal of vertebrate herbivores has been demonstrated to have strong short-term effects on vegetational structure (McNaughton 1979; Thornton 1971; Hatton and Smart 1984), and strong long-term effects also have been inferred (Owen-Smith 1987). Although the effects of insect herbivory and tree falls might have remained constant or even increased following the K/T extinctions, it seems likely that in many environments there would have been an initial decrease in diversity as species with greater competitive abilities excluded those that invested more energy in defending against nonexistent large vertebrate herbivores or rare fire. Over "evolutionary" time, the lowered disturbance regime and presumed increase in competition might have favored a wider range of competitive and "stress-tolerant" strategies (*sensu* Grime 1977), leading to larger seeds, greater shade tolerance, and more "quantitative" chemical defense (Denslow 1987; Coley et al. 1985).

7 DISCUSSION AND CONCLUSION

In this final section, we use examples to elucidate the connection between environmental conditions and inferred community structure, the implications of change in community structure and dynamics for the evolution of individual lineages (and vice versa), and the way in which large-scale perturbations might affect ecological structure and evolutionary opportunities.

7.1 Precipitation, Diversity Gradients, and Vegetational Structure

Richness and standing biomass of living terrestrial vegetation is strongly influenced by four kinds of environmental variables: precipitation, temperature, light, and nutrients. Nutrient levels often vary on quite small spatial scales and are difficult to estimate for fossil floras (although low available nutrients are characteristic of many peat-forming environments), but estimates of the other factors are frequently available. In the present day, seasonal fluctuations in light and temperature increase strongly with higher latitude, making it dif-

difficult to separate their effects. However, both are probably major factors in strongly depressing alpha species richness at higher (particularly polar) latitudes.

Recently much emphasis has been placed on the role of temperature fluctuation as a causal factor in extinctions and other long-term biotic changes in the marine realm (Stanley 1984). The record of terrestrial life during the Mesozoic, however, strongly documents the importance of rainfall. This is partly because the Mesozoic and early Cenozoic were times of relatively low equator-to-pole temperature gradients, but it also reflects the importance of rainfall in determining the productivity and structure of terrestrial ecosystems.

Rainfall is high and relatively aseasonal in many equatorial regions as well as in some midlatitude areas that have moderate seasonality of light and temperature. The most diverse vegetation is found in tropical forests, where rainfall, light, and temperature are high with little seasonal fluctuation. The vegetation also has high standing biomass. Vegetation growing under high, aseasonal rainfall but seasonal light and temperature (i.e., temperate rain forest) can achieve exceptionally high biomass but has relatively lower diversity (Franklin 1988). In tropical latitudes where light and temperature are high with low seasonal fluctuations, areas with low or highly seasonal rainfall support vegetation of reduced standing biomass and reduced richness (deciduous forest to savanna to grassland).

The Mesozoic to early Cenozoic interval differed strongly from the present in that temperatures were warmer, especially at the poles (e.g., Parrish 1987). Furthermore, the existence of Pangaea, with its attendant monsoonal circulation, and the absence of polar fronts that would have confined the Intertropical Convergence Zone to equatorial regions created a global climatic regime where the low-to-mid-latitude regions of the earth experienced persistently to seasonally arid conditions for essentially the whole Mesozoic and early Cenozoic (Robinson 1971; Frakes 1979; Parrish et al. 1982; Ziegler et al. 1987; Parrish and Peterson 1988). (Monsoonal circulation was reduced in the later Jurassic in Laurasia and in the Early Cretaceous in Gondwana [Parrish et al. 1986; Parrish and Peterson 1988].) Coal deposition, and by inference wetter climates, returned to many midlatitude areas in the Late Cretaceous and Paleocene, but evidence for such climates in the equatorial zone is not widespread until the mid-Tertiary (Ziegler et al. 1987).

Thus, in contrast to the modern situation in which warm temperatures and high levels of precipitation and light are found generally in the equatorial regions, the equatorial region would have been drier during most of the Mesozoic-early Cenozoic. Rainfall would have been higher (and presumably evapo-transpiration somewhat lower) at midlatitudes, but even in an ice-free world, temperatures would have been lower, and light seasonality would have had the same gradient as today (Axelrod 1984). Thus, productivity of terrestrial vegetation was probably lower near the equator than it was at midlatitudes (Ziegler et al. 1983). Given the interaction of rainfall, temperature, and light in

the Mesozoic world, both richness and standing biomass probably reached a maximum in midlatitudes, with the stature and diversity of equatorial vegetation reduced by low or highly seasonal rainfall, and that of high-latitude (polar) vegetation reduced by light seasonality and cool temperatures. Limited evidence from Late Triassic floras supports a high midlatitude diversity hump. The most species-rich vegetation of the Mesozoic might be expected to be less diverse than present tropical rain forest, because the tropical areas of the earth's surface, which had the highest levels of temperature and light, were receiving less rainfall than today; and the midlatitude areas with high rainfall had lower temperatures and seasonal illumination.

7.2 Long-Term Effects of Precipitation on Plant-Herbivore Dynamics

The nature of plant-animal interactions and the trophic characteristics of herbivore faunas are influenced strongly by climate through the intermediary of vegetational structure and productivity. Where mean annual temperature and/or precipitation are low or strongly seasonal, individual plants tend to be small in stature and vegetation has low standing biomass (there is a more than 500-fold difference in above-ground standing biomass between some tundras and forests in North America; see Franklin 1988 and Bliss 1988). Although low or highly seasonal temperature and precipitation have an enormous effect on standing biomass levels, they have less effect on net productivity of vegetation, particularly net productivity of leaves. For example, the standing biomass of dense, *Prosopis*-dominated, Sonoran desert scrub is one-tenth to one-hundredth that of most eastern deciduous forests, but its annual production of foliage is less by only about one-third to one-fifth (MacMahon 1988; Greller 1988). Jordan (1971) compared a number of vegetation types worldwide and noted that the maximum efficiency of energy storage in short-term structures (i.e., leaves) was achieved in systems where the major primary producers were annual plants, even though the highest overall rates of productivity were in tropical forests. Much of this difference between overall productivity and productivity of leaves is accounted for by the greater proportion of energy devoted to wood production in forest vegetation.

A number of the vegetational variables influenced by climate are significant to herbivores: the productivity of leafy tissue, the proportion of wood to leaves, the height above ground of the canopy, the total standing biomass, and the size of spatial openings in the vegetation. Since wood is not digestible to vertebrate herbivores, these aspects of vegetation in turn have a particularly large influence on the characteristics of vertebrate herbivore faunas. For example, in the present day, areas with a high biomass and diversity of large vertebrate herbivores also have highly seasonal climate (Coe et al. 1976; Coe 1983). This is presumably because vegetation under this kind of climate is usually low in stature, dominated by herbaceous species, and produces large

quantities of leafy tissue, thus providing a large resource pool for herbivores restricted to feeding within a few meters of the ground. Large grazing or browsing herbivores may have a reciprocal effect on vegetation (McNaughton 1984), favoring the success of plant species with a "ruderal" (Grime 1977) to "large gap" (Denslow 1987) strategy, i.e., those with fast growth rates, many small seeds, and high reproductive capacity. Furthermore, Oksanen (1988) argued that herbivores have their most profound influence on vegetational structure in ecosystems with moderate-to-low total productivity (e.g., tundra, grasslands), because under these conditions predator populations may be insufficient to regulate herbivore numbers effectively.

In contrast, high, aseasonal rainfall favors a large standing biomass of plants, much of which is woody support tissue that does not provide a direct resource for large herbivores. In dense forest vegetation, it is small, arboreal, frugivorous and insectivorous vertebrates rather than large terrestrial ones that are diverse and abundant. This is consistent with an ecosystem in which primary productivity is available largely in the canopy or after being cycled through populations of arthropod detritivores and herbivores.

As we have seen, many of the observed or inferred characteristics of low-to-mid-latitude Triassic through Early Cretaceous terrestrial organisms and ecosystems are consistent with dry or seasonally dry climates: plants with xeromorphic features of foliage and cuticles, increasing dominance of seed plants over pteridophytes, little evidence for closed-canopy vegetation, importance of fusainized plant material in many fossil deposits, declining importance of amphibians, diversification of tetrapod groups excreting uric acid rather than urea, and evolution of large body size in many groups of herbivorous tetrapods. The general similarity of Triassic (perhaps even Late Permian) through Early Cretaceous terrestrial communities in these features suggests that rainfall may have been a controlling factor in terrestrial community structure during the Mesozoic. Dry or seasonally dry conditions favored savanna-like rather than rain-forest-like interactions between plants and herbivores.

The low diversity of large herbivores and the importance of closed vegetation types during the early Paleocene stand in stark contrast with the situation in the Mesozoic. From a paleoecological perspective, this appears to be the most dramatic structural shift to take place in terrestrial ecosystems from their full establishment in the mid-Permian to the present day. Throughout the Paleocene and into the Eocene, the characteristics of most terrestrial biotas (at least in the well-studied midlatitude regions) are consistent with a dense forest vegetation, as are the inferred interactions of herbivores and plants. Precipitation appears to have been high in the mid-to-high latitudes, but the equatorial area is thought to have remained drier until the mid-Tertiary (Ziegler et al. 1987). It is unfortunate that Paleogene floras and faunas of equatorial regions are poorly known because these would provide an important test of the effect of rainfall on vegetational structure and plant-herbivore interactions.

7.3 *Coevolutionary Limits on Vegetational Richness*

The development of animal pollination and dispersal of plants has played a major role in theories developed to explain changes in vegetational richness through time. These ideas have been formulated explicitly by Niklas et al. (1980) and Knoll (1986). Knoll used number of species per described flora as a proxy for alpha species richness and found that *mean* richness had increased substantially through time, but with long plateau periods prior to the development of seeds in the Late Devonian and the major diversification of flowering plants in the Late Cretaceous. Knoll (1986) hypothesized that these plateaus were broken by the evolution of the seed habit and of advanced insect pollination, respectively. Crepet (1984) also highlighted the importance of insect pollination in the radiation of the angiosperms.

Number of species per described flora may be a poor proxy for alpha diversity for a number of reasons, including the large effect of sampling intensity on number of species (Burnham et al. 1990). Even assuming that the described pattern of change in *mean* alpha richness is correct, Knoll's causal explanation is called into question by the data presented on *maximum* species number per flora. If the rarity of the seed habit in Paleozoic floras and less-elaborate insect pollination in Mesozoic floras limited alpha richness levels, then it is difficult to explain why the most diverse floras from the Late Carboniferous and Late Triassic are nearly as diverse as the most diverse Late Cretaceous floras. Biotic limitations should affect maximum diversity as much as or more than mean diversity, so the very great richness of even a few Late Carboniferous and Late Triassic floras is not consistent with a biotically determined ceiling on alpha richness. Explanations of diversity change that rely solely on biotic interactions and innovations ignore the potential role of climate. Given that seasonally dry climates prevailed for most of the Mesozoic in the low latitudes, and given the strong influence of moisture on alpha diversity (e.g., Gentry 1988), it is possible that the Mesozoic plateau in mean diversity is related more to climatic than biotic limitations (although clearly these are not independent factors). Furthermore, the problems involved in estimating alpha diversity of past vegetation and the unknown strength of the climatic effect make it premature to use lower levels of alpha diversity to argue that Mesozoic plant-animal interactions were less intricate or less likely to enhance diversity than those of the present.

7.4 *Comparative Paleocology of Mass Extinctions*

Seven significant Mesozoic–early Cenozoic extinctions were identified by Raup and Sepkoski (1986) in an analysis of marine animal families: Permian/Triassic (actually Dzhulfian), Triassic/Jurassic, Early Jurassic (“Pliensbachian”), Jurassic/Cretaceous, mid-Cretaceous (Cenomanian/Turonian), Cre-

taceous/Tertiary (Maastrichtian), and terminal Eocene. The "Pliensbachian" extinction is probably regionally confined and actually a Toarcian marine event (A. Hallam, pers. comm., 1986). Likewise, significant faunal changes in the marine realm at the Cenomanian/Turonian (Raup and Sepkoski 1986) and at the end of the Eocene (Stucky 1990) do not appear to be paralleled by comparable changes in terrestrial biotas. The remaining periods do represent times of increased extinction and turnover on land, although with the exception of the K/T boundary, correlation with the marine extinctions is rather imprecise. Further refinement in the data, especially at the substage level, will certainly permit more accurate documentation of the patterns of extinction. Traditionally mass extinctions have been compared on the basis of their magnitude and duration, with less consideration of their selectivity in an ecological sense (but see Jablonski 1986 and Raup 1986). Below we summarize briefly the ecological signatures of the Permian/Triassic, Triassic/Jurassic, Cretaceous/Tertiary, and terminal Eocene extinctions.

Particular emphasis is placed on the fate of large herbivorous tetrapods during these periods of extinction. Such animals should be particularly sensitive even to short-term cessation of primary productivity, such as is predicted by impact models of mass extinction, because large herbivores are especially dependent on a continuous supply of low-unit-energy plant food (e.g., Demment and Van Soest 1985), and because physiologically and mechanically they are poorly equipped to shift to alternative food sources (e.g., carrion, insects, detritus). Periods of climatic deterioration (i.e., more seasonally dry or cool climate) may actually increase habitat and resources for large herbivores by favoring ruderal plants, so (in contrast to an impact-generated halt in primary productivity) they should not necessarily lead to preferential extinction of large herbivores.

For terrestrial plants, the Permian/Triassic extinction might be better described as the Permian-Triassic transition—a long period of turnover (Late Carboniferous and much of the Permian) during which there was extensive replacement of higher-level taxa. The demonstrated diachroneity of the transition in a time frame of millions of years and its relation to large-scale continental movements probably indicate a climatic origin (Knoll 1984; Ziegler 1989). Although the *Dicroidium* flora replaced the *Glossopteris* flora in Gondwana, much of the shift toward gymnosperm dominance had already taken place by the Permian/Triassic boundary. The vegetational consequences of taxonomic change in terrestrial floras at the Permian/Triassic boundary are hard to reconstruct but do not seem to have been profound. At present there is no evidence for a pulsed plant extinction event in the Late Permian or at the Permian/Triassic boundary. It has been claimed that tetrapod extinctions were more severe (Benton 1985; Padian and Clemens 1985), but ecological characteristics such as size distribution and inferred trophic adaptations of herbivores were similar across the Permian/Triassic boundary. The general similarity of

Late Permian and Early Triassic terrestrial biotas may reflect similar global climatic regimes during those time intervals.

The Triassic/Jurassic vertebrate extinctions were severe and were apparently confined to a relatively short (< 1 My) interval (Olsen and Sues 1986; Benton 1986; Olsen et al. 1987). Observation of a fern spike at the Triassic/Jurassic boundary throughout the Newark Supergroup in eastern North America has led to the hypothesis of a mass-kill event and interruption of terrestrial productivity analogous to that hypothesized for the K/T boundary (Fowell 1990). Furthermore, palynofloral turnover at the Triassic/Jurassic boundary is sharp and substantial, and the dramatic increase in the importance of Cheirolepidiaceae in the Early Jurassic indicates vegetational differences between the two periods. To some extent, smaller herbivorous tetrapods may have had higher survival rates than large ones. However, at least two groups of prosauropod "megaherbivores" are known from both the Late Triassic and the Early Jurassic. Given the sensitivity of large-bodied herbivores to disturbance in primary productivity, the survival of these prosauropods and many other tetrapods may place limits on the severity of the effects of the bolide impact hypothesized by Olsen et al. (1987). As with the Permian/Triassic boundary, global climate does not seem to have undergone a major transition during this interval, although monsoonal conditions may have reached a peak in the Late Triassic (Parrish and Peterson 1988).

The K/T extinction is the only event of the Mesozoic and early Cenozoic that has an unmistakable ecological component: total extinction of large terrestrial vertebrates and radical changes in body-size distribution among herbivorous vertebrates, in herbivore trophic adaptations, and in angiosperm diaspore size, lasting for many millions of years following the extinction event. Furthermore, it is almost certain that devastation of vegetation in western North America and the subsequent appearance of early successional vegetation directly above the K/T boundary were causally related to the impact of an extraterrestrial object. The notion of a bolide impact, first advanced by Alvarez and others, is increasingly supported by geochemical anomalies and features such as shocked quartz in boundary strata. Important questions remain, however, about its long-term consequences and the relative importance of the direct physical consequences of the impact as opposed to climatic changes (independent of, induced by, or enhanced by the bolide) and ecological reorganizations resulting from extinction and evolutionary re-radiation of terrestrial organisms.

The unique combination of rapid, major extinction in many groups of terrestrial organisms, especially dinosaurs, and the appearance of structurally very different terrestrial ecosystems following the extinctions imply that the K/T extinction had a unique cause or combination of causes. Climatic change may have been involved in the long-term changes. Increased coal deposition in the mid-to-high latitudes during the Late Cretaceous suggests more (or

more evenly distributed) annual rainfall (Spicer et al., 1990), and coal deposition in inland areas increased again in the Paleocene. The additional rainfall may have been one cause for the spread of denser, closed-canopy forests, the greater abundance and diversity of small herbivores, and the decreased diversity of large herbivores.

Many important issues remain unresolved: How long did it take terrestrial ecosystems to re-equilibrate? What was the role of changed climatic conditions in creating new types of ecosystems? Which effects of the bolide impact were most likely to have reverberated for periods of millions of years? The concept of quasi-succession (Wolfe and Upchurch 1986, 1987b) draws a direct analogy between ordinary ecological succession and processes that took place over millions of years following the K/T bolide impact. Wolfe (1987) also argued that the dominantly deciduous vegetation of the northern Rocky Mountains during the Paleocene resulted from higher survival of deciduous species at the K/T boundary. These ideas emphasize the direct effects of the bolide impact. An alternative (though not mutually exclusive) idea is that K/T extinctions forced the development of new ecological relationships between plants and animals, resulting in long-term evolutionary and ecological changes (e.g., Wing and Tiffney 1987).

A layer with anomalously high iridium concentrations and levels containing microtektites demonstrate an unusual input of extraterrestrial matter to the earth near the Eocene/Oligocene boundary (Ganapathy 1982; Alvarez et al. 1982). It is now clear, however, that there were several separate impact events during which microtektites were deposited, and that all of these events occurred around 35–36 Ma, thus predating the Eocene/Oligocene boundary (Miller et al. 1991), as well as the temperature decline observed in terrestrial floras (Wolfe 1978). Furthermore, the ecological and temporal pattern of terrestrial vertebrate extinctions in North America is not consistent with a bolide-induced extinction. Much of the terrestrial extinction attributed to the Eocene/Oligocene boundary appears to have taken place over an extended interval, rather than at the boundary itself (Prothero 1985; Stucky 1990), and diversity of large browsing and grazing herbivores increased during this time (Stucky 1990). Extensive penecontemporaneous faunal interchange also has been reported in Europe, where changes in the distribution of vertebrate body sizes associated with the extinctions have been interpreted as evidence for a shift to more open, drier habitats (Legendre 1987). Floras from the interval between 30 and 35 Ma indicate a great increase in deciduous, temperate species on the Pacific coast of North America, which is believed to reflect a substantial decrease in temperature and increase in temperature seasonality at about 33 Ma (Wolfe 1978). This temperature change in the terrestrial realm is approximately synchronous with oxygen isotope and marine faunal evidence for decreasing ocean temperatures, which probably resulted from the establishment of the Antarctic ice cap (e.g., Kennett 1977). Although major

changes in world climate and the structure of terrestrial ecosystems seem to have been concentrated during a five-million-year period from about 36 to 33 Ma, there is no good evidence for catastrophic change at or near the Eocene/Oligocene boundary.

7.5 *Ecological Context and Evolutionary Opportunity*

It is widely accepted that a major perturbation can “clear” ecological space and permit the explosive adaptive radiation of formerly unimportant groups through a mechanism analogous to ecological release (e.g., Van Valen 1978; Erwin et al. 1987). Following the origin of the largest-scale evolutionary innovations, similar events may have occurred, for instance, the “Cambrian explosion” of marine metazoan life has been attributed to a breakthrough into previously unexploited modes of life (Erwin et al. 1987). Perhaps similar events occurred following the first invasions of land. As shown in chapter 5, a number of evolutionary-ecological breakthroughs continued to occur in terrestrial biotas through much of the Paleozoic. However, the increasingly crowded world of the Mesozoic and Cenozoic may have been rather different. To what degree have evolutionary radiations followed upon evolutionary innovations that broke the existing ecological order? To what extent has external disruption of the ecosystem been necessary before evolutionary innovations could be “captured” by a subsequent radiation? How different is diversification within an unperturbed ecosystem from diversification in a decimated one? To what degree is morphological innovation the cause, and to what degree is it the result, of changes in ecological interaction?

Answering such questions will require a high level of temporal resolution, an understanding of the branching sequence of the evolutionary radiation, and knowledge of its ecological context. In the absence of these we can cite what may be end members of a spectrum. For example, the Early-to-mid-Cretaceous diversification of angiosperms appears to have taken place in a relatively intact ecosystem. The paleoecological indicators used by us suggest that, in general, Early Cretaceous terrestrial ecosystems were similar in many ways to those of the Jurassic and Triassic. In contrast, the Paleocene diversification of mammals was an event unprecedented in the previous 150 My of mammalian history, and it occurred immediately following a major disruption of vertebrate communities at the end of the Cretaceous. Both of these radiations rapidly produced a large number of species (angiosperms: Lidgard and Crane 1988, 1990; mammals: Van Valen 1978; Archibald 1983). Even though both groups are now major components of most terrestrial communities, the mammals appear to have become ecologically diverse and important far more rapidly (1–5 My?) than the angiosperms (10 My?). The rapid evolutionary radiation of mammals into different ecological roles may have been a consequence of the relatively unoccupied adaptive landscape in the earliest Paleocene.

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