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Arthur Cronquist
The New York Botanical Garden, Bronx, New York 10458

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THE BIOTA OF THE INTERMOUNTAIN REGION IN GEOHISTORICAL CONTEXT

Arthur Cronquist

ABSTRACT.—The present Great Basin Floristic Province had achieved roughly its present topographic conformation by some time in the Miocene epoch and had a climate not too different from the present one, though probably a little warmer, moister, and less continental. Both the flora and the fauna took on a fairly modern aspect during the Miocene, as a result of worldwide evolutionary changes and more specific adaptation to the conditions of the region. Changes in the biota since that time mainly reflect evolution and migration at the level of species and, to a lesser extent, genera, in response to regional conditions and the repeated fluctuations in climate. The climatic reversals of the Pleistocene caused repeated inverse migrations of more northern, mesophytic elements in the flora, on the one hand, and more southern, xerophytic elements on the other. These expansions and contractions of range favored hybridization and genetic mixing among related plant species. The fauna of the region, dependent eventually on the flora, must have been subjected to basically the same set of repeated changes in range and local distribution during the Pleistocene. About 10,000 years ago many of the large mammals in the Intermountain Region, as elsewhere in North America, rapidly became extinct, perhaps largely through overkill by primitive man.

A proper understanding of the present is always facilitated by some knowledge of the past. Therefore I want to say something about the geological and biological history of the Intermountain Region, to help provide a proper setting for the other papers of this symposium. Nearly everything that I have to say is already in the scientific literature somewhere, but the particular synthesis may be in part new.

As a first approximation of the truth, one may say that the aspect of the vegetation of any region is controlled by the climate, and the taxonomic composition of the flora is determined by the climate and the history. The general nature of the fauna is in turn determined by the vegetation, and the taxonomic composition of the fauna is determined by the vegetation and the history.

It is, of course, also true that the fauna influences the flora. One of the reasons that grasses predominate in certain climates is that they are better adapted to withstand grazing than are most other herbaceous plants. Furthermore, evolution of floral structure is to some extent correlated with the evolution of pollinating insects (Leppik 1957), and particular species of plants may become dependent on particular pollinators. A notable example that may be familiar to many readers is provided by Yucca and the Tegeticula moth. Some of the importance of the influence of the fauna on the flora is also shown by the devastating effect of the introduction of goats to some of the islands off the Pacific Coast of southern North America. More complex interactions between plants and animals also occur. Yet the preponderant control is that exerted by the food makers (plants) on the food eaters (animals). Therefore it is reasonably possible to consider the vegetation and flora of a region with only secondary attention to the fauna, whereas any proper consideration of the fauna must be grounded in a knowledge of the vegetation. These facts, or what I take to be facts, are fortunate for me, because I know a lot more about plants than I do about animals.

The Intermountain Region may be variously delimited. For purposes of this discussion, I take its limits to be those of the

Great Basin Floristic Province, as defined by Gleason and Cronquist (1964). In large part these limits are the same as those of the Intermountain Flora (Cronquist et al. 1972), but the Great Basin Floristic Province extends somewhat further south into Arizona and also includes a part of northwestern New Mexico as well as a sliver of western Colorado. In addition to the hydrographic Great Basin, the area under consideration also includes the Snake River Plain and the more westerly segment of the Colorado Plateau. The region has a continental climate, with fairly hot, dry summers, and cold, snowy winters. The lowlands and foothills are largely desert and semidesert; a more mesophytic flora often occupies the upper elevations. South of the Intermountain Region lie hotter deserts, marked especially by milder winters. These southern deserts have a rather different flora, and the plant communities are often dominated by *Larrea*. The southern deserts are not a part of the Intermountain Region as here defined.

**Geologic History**

We shall start our consideration of the intermountain biota with a summary of the geologic history of the region from the Cretaceous period to the present. Much of the information in this section comes from papers by Bateman (1968), Eardley (1968), and Roberts (1968).

The present Intermountain Region has been at middle latitudes since before the beginning of the Cretaceous. North America has drifted westward, with respect to Europe and Africa, throughout that time, but the latitude of our area has changed relatively little (Dietz and Holden 1970, Smith et al. 1973).

Our region has been subjected to repeated and almost continuous tectonic disturbance, leading to uplift and erosion, from the beginning of the Cretaceous to the present. The terrain throughout that time has been highly varied, doubtless producing a diversity of habitats. The Upper Cretaceous, in particular, was a time of great and prolonged uplift in western Utah and eastern Nevada. There was a large interior drainage basin in north-central Nevada even in the late Upper Cretaceous, and in mid-Eocene time there appear to have been high mountains and large lake basins throughout most of the present hydrographic Great Basin. In Oligocene time these lake basins were considerably elevated and themselves subjected to erosion.

The present Rocky Mountains and Colorado Plateau began to rise early in the Tertiary, and they have continued to rise at varying rates until the present. The Sierra Nevada, bounding the Great Basin on the west, also has a long history. After a relative quiescence during the Oligocene, the tilt-uplift of the Sierra Nevada was considerably accentuated during the Miocene. The concurrent uplift of the Rocky Mountains and Colorado Plateau shaped the Great Basin. By some time in the Miocene, it appears that "basin and range topography extended from the Wasatch Mountains to the Sierra Nevada, and most of the area drained into interior basins" (Roberts 1968). There is some difference of opinion on the timing, however, and Axelrod (1950) believes that the present interior drainage of the Great Basin dates from near the close of the Pliocene.

The Snake River Plain, forming a broad crescent across southern Idaho, belongs to the Great Basin floristic province but is geologically distinctive. The Upper Cretaceous uplift in western Nevada and eastern Utah extended across the present Snake River Plain as well. During Eocene time the present Snake River Plain was buried by lava in a major and prolonged tectonic disturbance that formed a volcanic plateau extending from western Wyoming across southern Idaho and probably into eastern Oregon. In Oligocene time the Snake River basin took shape, possibly "as a tension rift in the lee of the Idaho batholith" (Axelrod 1968), which began to drift north. Sub-
sidence of the basin and outpouring of new lava flows have continued until the present time. The youngest deposits in the Craters of the Moon region at the north edge of the Snake River Plain are probably only a few hundred years old.

It is thought that for most of the Cretaceous period the climate of the world was relatively warm and equable, and that tropical and subtropical climates entirely suitable for the growth of forests extended from about 60 degrees north to about 60 degrees south (Barnard 1973). As late as the Eocene, the London Clay flora, at 35 degrees north, is definitely tropical (Hughes 1973). One may reasonably have some doubt about how humid the climate may have been in Nevada during the Upper Cretaceous, because of the presence of an interior drainage basin, but such Cretaceous fossil floras as we have from the western United States suggest the presence of adequate moisture.

The frequent presence of interior drainage basins in the Intermountain Region for many millions of years past tells us something about the climate. The precipitation/evaporation ratio for much of the region much of the time must have been something less than 1. At a p/e ratio of more than 1, lake basins fill and spill over, finding external drainage. It is generally considered that a p/e ratio of not less than about 1 is required to support a forest. Therefore, for much or most of its span of existence the Great Basin is not likely to have been widely forested. Other parts of the Intermountain Region appear to have had a similar climatic regimen.

Island Topography

The topographic diversity of the Intermountain Region, with its associated differences in temperature and moisture, effectively converts the habitats for many species of plants and animals into a series of islands. Not only the mountains, but also the valleys, form such islands for species without good means of dispersal. Birds can travel from one island to another, but small mammals frequently cannot. Different kinds of plants likewise differ in the ability to pass the inhospitable stretches between islands.

On the other hand, these islands do not have the relative permanence of oceanic islands. The various island habitats in the Intermountain Region have expanded and merged, contracted and broken up, disappeared and reappeared, during Pleistocene and post-Pleistocene time because of changes in the climate. The principles of island biogeography, as expounded for example by MacArthur and Wilson (1967), are pertinent to the Intermountain Region, but their effect is limited by the climatically controlled changes in island area.

Early Angiosperm Evolution

The angiosperms appear to have originated early in the Cretaceous. Since we do not have fossils to connect the angiosperms to their necessarily gymnospermous ancestors, we cannot say with certainty that they did not originate somewhat earlier. The fossil record does make it clear that the evolutionary diversification of the group did not get well started until the Cretaceous. Angiosperms enter the fairly early Lower Cretaceous fossil record as an uncommon and not highly diversified group. Many of these early angiosperm fossils were at first optimistically identified with modern genera, leading to the widespread belief that the angiosperms entered the fossil record full-blown. We can now say with some assurance that the reverse is true. The pollen record speaks eloquently to the relative homogeneity of the early angiosperms, and a reexamination of the megafossils shows that their identification with modern genera was disastrously incorrect. The purportedly Jurassic palm from Utah (Tidwell et al. 1970) is clearly a palm, but it is not Jurassic. The stratigraphy of the site where it was collected is complex, and subsequent careful study shows that it is of Tertiary age (Scott et al. 1972).
The comments made in this paper on angiosperm evolution in general are heavily influenced by studies in the past decade by Dilcher (1969, 1973), Doyle (1969), Hickey (1973), Walker and Doyle (1975), Doyle and Hickey (1976), Hickey and Wolfe (1975), and Wolfe et al. (1975), who are in the forefront of the ongoing reevaluation of the early angiosperm fossil record. Their published work and my conversations with them have helped to shape my views, and I am particularly indebted to Dr. Leo Hickey for advice and counsel during the preparation of this paper. Within the Intermountain Region, the work of Axelrod (1948, 1950, 1952, 1956, 1958, 1964, 1966, 1968, 1975) is of course preeminent. Without it, our knowledge of the fossil flora would be scanty indeed. The interpretation presented is, as always, my own; those who helped me are not to be held responsible for what I might say.

The place of origin of the angiosperms is still uncertain. It is clear that they are basically a tropical group, but beyond that the situation is debatable. We can say that as early as the Aptian stage of the Lower Cretaceous, 125 million or more years ago, they were well scattered in both Gondwanaland and Laurasia, including North America, but that they did not begin to dominate the landscape until the Upper Cretaceous. There is no reason to suppose that the Intermountain Region had anything to do with the origin of the angiosperms, but at the same time it is clear enough that it has supported some angiosperms at least from the Albian stage of the lower Cretaceous to the present.

Unfortunately we can not yet see a historical connection between the Cretaceous and Tertiary angiosperm floras of the Intermountain Region, or indeed of most other parts of the world. Most of the Cretaceous genera did not persist long if at all into the Tertiary, and the limited fossil record does not show whether our early Tertiary genera originated in situ from the Cretaceous ones or migrated in from elsewhere. One of the few Upper Cretaceous fossil floras definitely known from within the Intermountain Region is in the Blackhawk formation in central Utah, a member of the Mesa Verde Group (Parker 1968, as reported by Tidwell et al. 1972). This flora included some palms and a number of woody dicotyledons and is thought to indicate humid lowland conditions under a warm-temperate to subtropical climate. This is in general harmony with views of the Cretaceous climate of the region based on other data (e.g. Axelrod 1950).

Beginning with the Paleocene, we have a more nearly continuous history of the Intermountain flora, but even so there are some considerable gaps. Well over half of the Paleocene genera of angiosperms in the world flora are now extinct, and the fossil record as studied to date rarely shows the origin of modern genera from the more archaic ones. It appears that in the Paleocene the climate of the Intermountain Region was still reasonably warm and moist, subtropical or warm temperate, as it had been in the Upper Cretaceous.

**Evolution of Floristic Groups in the Intermountain Region**

By the middle of the Eocene, some 50 million years ago, the climate in the Intermountain Region had begun to dry out. The first indication of this in the fossil record comes in the Eocene Green River flora of northwestern Colorado and northeastern Utah (Axelrod 1950, MacGinitie 1969). This resembles the early Oligocene Florissant flora from Colorado (MacGinitie 1953) and like it may have been a subtropical savanna-woodland. No closely similar flora exists today.

Drying of the Intermountain climate continued, with some fluctuations, throughout the Tertiary. By early Oligocene the mean temperature of the world, at least in presently temperate regions, had begun to drop (Bowen 1966), and in late Oligocene it dropped markedly (Wolfe and Hopkins
1967); it never again regained the Cretaceous levels. Concomitant with increasing aridity and decreasing mean temperature in the Intermountain Region was a gradual trend toward a more continental climate, with hot, dry summers and cold, somewhat moister winters, continuing until about the middle of the Pliocene.

Floristic changes in the Intermountain Region were, of course, related to the evolutionary diversification of the angiosperms throughout the world. The monocotyledons evidently diverged from primitive dicotyledons shortly after the appearance of angiosperms in the fossil record, during the Lower Cretaceous. Palms became important elements of the world flora during the Cretaceous, and grasses in the Oligocene or earlier. Dicotyledonous herbs were rare throughout the Cretaceous and on into the Paleocene and Eocene. They began to become more abundant in the Oligocene, and they increased dramatically at the beginning of the Miocene, some 25 million years ago. During Miocene time the flora of the world began to take on a fairly modern aspect, with a great many genera that still exist today. The increase in dicotyledonous herbs in the mid-Tertiary is thought to reflect at least in part the increasing aridity of the climate throughout much of the world, enlarging the area not suitable for forests.

It is evident that during the drying of the climate in western North America the Tertiary flora sorted itself out into a more northern, mesic flora dominated by trees, and a more southern, xeric flora with few if any trees. Fossil floras from near the Oligocene-Miocene boundary in southwestern Montana suggest a mainly forest vegetation, with some elements from the drylands to the south (Becker 1969). Within the dryland flora there was a further differentiation into a more northern segment adapted to cold winters, and a more southern segment adapted to a warmer climate. The present Great Basin Floristic Province, representing the more northern of these two dryland floras, evidently took shape in the Miocene. Indeed the Miocene boundary between the Great Basin flora and the Mohave Desert (a part of the more southern flora) may have been about where it is now (Axelrod 1950).

It is not clear how much of the differentiation of the intermountain flora during the Tertiary represents evolution in situ, and how much of it reflects immigration from other regions. Certainly both processes occurred. A similar sorting out occurred in other parts of the world, and in Eurasia this involved many of the same families and even genera. It is not likely that the same taxonomic groups originated independently in North America and Asia. There must have been some interchange.

The genus Artemisia might be considered in this regard. Although Artemisia tridentata Nutt. and its immediate allies dominate the scene in much of the Intermountain Region, Artemisia is not of American origin. The tribe Anthemideae of the family Asteraceae (Compositae), to which Artemisia belongs, is basically an Old-World tribe, and most of the species of Artemisia itself occur in the Old World rather than in the new. Artemisia and Juniperus characterize the landscape in parts of Armenia, for example, as well as in the Intermountain Region. Artemisia in the western United States is an immigrant, although the particular species we now have may well have originated here from immigrant ancestors.

Some other members of the Asteraceae are definitely American. The whole tribe Heliantheae is clearly so. Its present center of diversity is in the arid highlands of central Mexico, and it seems reasonable to suppose that the tribe is of Mexican or western American dryland origin. Many members of the group here will probably be acquainted with species of Balsamorhiza, Chaenactis, Enceliopsis, Eriophyllum, Viguiera, and Wyethia, all members of the Heliantheae, that grow in the Intermountain Region. The large genus Haplopappus, in the tribe Astereae, is strictly American (North and South), with one center of diversity in western North America and another in
Chile. *Erigeron* is another large genus of the Astereae that has its principal center of diversity in western North America and appears to have originated there. I am not suggesting that these several genera of Heliantheae and Astereae originated in the Intermountain Region, but they probably did not have far to come to get here.

*Atriplex*, another important genus in the Intermountain Region, has more species in the Old World than in the New. The family Chenopodiaceae, to which *Atriplex* belongs, has considerable concentrations of species in the Mediterranean region, in western and central Asia, in South Africa, and in Australia, as well as in the drier parts of both North and South America.

The Boraginaceae appear to be tropical and woody in origin, but they are well represented by numerous herbaceous genera and species not only in our arid West but also in the Mediterranean region and in central Asia. To what extent did our boragineous intermountain herbs originate in North America from tropical woody ancestors, and to what extent do they reflect immigration of herbs from the Old World? Certain genera, such as *Cryptantha* and *Plagiobothrys*, are clearly American now, whatever their eventual origin, but others, such as *Lithospermum*, are well developed in Eurasia and may well be immigrants in North America.

The Brassicaceae are well represented in the Intermountain Flora, but they are even more numerous and diversified in the arid region from central Asia to the Mediterranean, and the family as a whole is probably of Old World origin. Such familiar genera as *Lesquerella*, *Physaria*, *Stanleya*, *Streptanthus*, and *Thelypodium* are strictly American, whatever the origin of the family as a whole. *Cardamine*, *Lepidium*, and *Roripa*, on the other hand, are well represented in the Old World also.

A few families, such as the Hydrophyllaceae and Polemoniaceae, evidently have their principal center of diversification in western North America, even if the region of their ultimate origin is not yet clearly established. Such genera as *Phacelia*, in the Hydrophyllaceae, and *Gilia*, in the Polemoniaceae (Grant 1959), are clearly at home in the Intermountain Region. There is no reason to suppose that they came in from some other continent.

Axelrod and Chaney have in various papers (e.g., Axelrod 1958) promoted the thought that the Tertiary flora of the western United States can be divided into an Arcto-Tertiary and a Madro-Tertiary segment. The Arcto-Tertiary geoflora, dominated by deciduous trees, is considered to have been very wide-spread, extending across most of northern North America and northern Eurasia. The deciduous forest of the eastern United States is considered to be the nearest modern American counterpart and a lineal descendant of the Arcto-Tertiary geoflora. The Madro-Tertiary geoflora, on the other hand, was adapted to drier, warmer conditions, with many xeromorphic shrubs, the trees being restricted to favorable habitats, or completely wanting. The Madro-Tertiary geoflora as so conceived was geographically more restricted than the Arcto-Tertiary, being confined to northern Mexico and the southwestern United States. The “Madro” part of the name comes from the Sierra Madre Occidental in northwestern Mexico. The Madro-Tertiary flora is considered to have originated in situ from subtropical western American plants that gradually became adapted (through evolution) to xeric conditions.

The concept of Arcto-Tertiary and Madro-Tertiary floras has recently been challenged by a number of authors, notably Wolfe (e.g., 1969), and is now in some disrepute. The problem, to my mind, is that some useful generalizations have been taken too literally and interpreted too rigidly. I am reminded of Gleason’s challenge (1926) to Clementsian concepts of plant associations. Most modern ecologists agree with Gleason that the association is a mental construct that can be defined only arbitrarily. The idea that the community is an
organism is a good aphorism, but it can lead to serious misunderstanding if it is taken literally. Likewise the concept of an Arcto-Tertiary and a Madro-Tertiary geoflora is useful if one conceives of these floras broadly and loosely and recognizes that each of them encompasses a considerable amount of diversity, that some elements were common to both, and that there was continuous interchange between them. It is helpful to think in terms of floristic groups, but we should keep it constantly in mind that each species has its own limits of ecological tolerance, its own means of migration, and its own evolutionary potentialities, the last being influenced also by hybridization with related species. The species that make up any floristic group have entered that group, through immigration or through evolution in situ, at various times in the past, and species that are now associated may not remain associated under some future climatic regimen.

I can easily agree with Axelrod that the modern desert flora of the western United States and northern Mexico probably "developed during the Tertiary period by gradual adaptation of more mesic plants to slowly expanding dry climate" (Axelrod 1950). It seems perfectly logical to suppose that the present flora of the warm deserts south of the Intermountain Region is a linear descendant of a Madro-Tertiary geoflora that differentiated originally from American plants adapted to similarly warm but more mesic climates. There is no other likely source. Some of them doubtless originated instead by adaptation of Arcto-Tertiary taxa to warmer, drier climates, and some of these that entered the warm deserts from the north doubtless take their origin eventually in Asia, but it strains credulity to derive the bulk of the Madro-Tertiary flora in such a way.

The origin of the Arcto-Tertiary flora is a more difficult question. Obviously it represents an adaptation of tropical or subtropical plants to a cooler but still moist climate. Since it extended across both North America and Eurasia, one cannot a priori assume that it came principally from either an Old-World or a New World source. It seems logical to suppose that the Arcto-Tertiary flora originated from the Cretaceous tropical and subtropical Laurasian flora, but at the present time that is pure speculation. We have noted that the angiosperm fossil record as presently understood does not provide a good connection between the Cretaceous and the Tertiary. The problem is complicated by the fact that during the Mesozoic era and most of the Tertiary period North and South America appear to have been separated, not contiguous. South America was part of the southern continent, Gondwanaland, whereas North America was part of the northern continent, Laurasia. North America drifted away from Europe during and after the Cretaceous, but, until recently, it has mostly been well separated from South America. I say "mostly," because the geologic history of the Caribbean is complex and insufficiently understood, and the possibility of a direct connection between North and South America at some time during the Cretaceous or early Tertiary cannot be completely discounted.

At the present time the tropical part of the flora of North America (as represented by southern Florida, the West Indies, southern Mexico, and Central America) is clearly allied to the flora of South America. If there is any surviving Laurasian element in the present tropical North American flora, it is so thoroughly amalgamated into the Gondwanaland, South American flora that no one has yet been able to recognize it. In making this statement I exclude from consideration some primarily temperate-zone species and genera that extend into the tropics at the southern limit of their range.

Although the vegetation of most of the Intermountain Region is rather similar in aspect to that of the deserts farther south, it is very different in floristic composition. As Axelrod (1950) has pointed out, some of the dominant genera in the Intermountain Region, such as Artemisia, Atriplex, and Cera-
toides (*Eurytia*), apparently relate to the Arcto-Tertiary rather than the Madro-Tertiary flora. Likewise *Astragalus*, one of our largest genera in terms of number of species, has an even larger number of species in dryland Eurasia. Even if one prefers to avoid the terms Arcto-Tertiary and Madro-Tertiary, these genera still relate to Asian desert plants, presumably by way of a Beringian connection, rather than to plants from farther south in western North America. On the other hand, such large genera as *Penstemon* and *Eriogonum* are strictly American, best developed in arid western North America, without any obvious indication of a more southern (Madro-Tertiary) origin. *Haplopappus* may well be from the Madro-Tertiary, as Axelrod suggests, but its derivative *Chrysothamnus* centers in the Great Basin. We have already noted that some of the common genera of Heliantheae in the Intermountain Region may well be of Madro-Tertiary affinity. Thus it is not possible to assign the characteristic flora of the Great Basin province to either a chiefly Madro-Tertiary or a chiefly Arcto-Tertiary origin. Both of these Tertiary floras clearly contributed to the present flora of the region.

Thus, by some combination of differentiation from native elements, immigration from near and far, and proliferation of the immigrants, the Intermountain Flora acquired its special character during the Miocene epoch. Xerophytes predominated especially at lower elevations, but mesophytes survived in the moister habitats, often at higher elevations. These two types have been in continuous competition in the Intermountain Region since that time.

**Tension between Mesophytic and Xerophytic Communities**

Although the Great Basin floristic province took shape in the Miocene, it was not immediately so dry as it is now. Axelrod (1948) considers that open environments extended through the region in the Middle Pliocene, but that the plant community was predominantly grassland, with semidesert shrubs on the drier slopes. In Miocene and Pliocene time the presently desert regions supported species comparable to those in the pinyon-juniper woodland and oak woodland that now occur at slightly higher elevations or around the borders of the desert.

Axelrod (1950) considers that the trend toward a drier, more continental climate in the Intermountain Region, begun early in the Tertiary, culminated in Middle Pliocene time, perhaps 4 or 5 million years ago. Later in the Pliocene the climate probably became a bit cooler and moister. The Pleistocene, as we all know, was marked by alternating glacial and interglacial stages. From a long-term geohistorical viewpoint, the present time may be merely another Pleistocene interglacial. Actual glaciers in the Intermountain Region were largely restricted to upper elevations in the mountains; the continental ice sheet did not reach that far south in western North America.

The glacial periods were times of relatively lower temperatures and higher p/e ratio in the Intermountain Region, cooler and more mesic than the interglacials. During the glacial periods, the mesophytes, many of them of northern floristic affinities, expanded their distribution at the expense of the xerophytes; in the interglacials the process was reversed. The great differences in elevation, together with the strong local differences in moisture relations according to slope and edaphic factors, combined with the repeated shifts in climate to keep the species populations in constant turmoil throughout the Pleistocene. T. M. Barkley (personal communication) has suggested that the blurred boundary between *Senecio streptanthifolius* (a highland species) and *Senecio multilobatus* (a lowland, more xerophytic species) in Utah reflects such hybridization. Local polyploidy helps such hybrids and hybrid segregates to persist in appropriate habitats.

Another example of the advance and re-
treat of species in the Intermountain Region due to climatic changes is provided by the oaks. In north-central Utah there exist today clones of oak that have been conclusively demonstrated to be hybrids between \textit{Quercus gambelii} and \textit{Q. turbinella}. \textit{Quercus gambelii} is common in the area today, but \textit{Q. turbinella} reaches its present northern limits more than 250 miles to the south of these hybrids. It is reasonably believed that, during the postglacial hypsithermal period, some five or six thousand years ago, the range of \textit{Q. turbinella} extended north into north-central Utah, permitting the formation of the hybrids (Cottam et al. 1959).

Alpine fir, \textit{Abies lasiocarpa}, provides an example in the reverse direction. According to Cottam et al. (1959), fossils discovered in 1957 by D. J. Jones demonstrate that alpine fir grew along the shores of Lake Bonneville at a time when the lake level stood well below the Provo stage. Recent fluctuations in the level of Great Salt Lake remind us that p/e ratios in the Intermountain Region continue to fluctuate, but up until now the climatic changes during the relatively short time for which we have formal, written records do not approach the magnitude of the changes that occurred during geologic time.

**PRESENT-DAY CORRELATION OF ELEVATION WITH FLORISTIC GROUPS**

Elevation is closely correlated with moisture relations as well as with temperature in the Intermountain Region. As one goes higher into the mountains, the temperature drops and the p/e ratio increases, and one finds a progressively more northern element in the flora. Many years ago I read somewhere that in the western United States one can roughly equate one mile of latitude with four feet of altitude. In my own experience, this conversion factor works fairly well, although there are, of course, always modifying factors to be taken into account. At moderately high elevations in the mountains, one finds many species similar or identical to those of the northern coniferous forest, and above timberline one finds many species similar or identical to those of the modern circumboreal arctic flora. The spruce-fir forests of midupper elevations in the Intermountain Region represent a southern extension of the northern coniferous forest. Even though the dominant species are different, they compare closely with species from the northern forest. \textit{Abies lasiocarpa} compares with \textit{Abies balsamea}, \textit{Picea engelmannii} and \textit{P. pungens} compare with \textit{P. glauca}, and \textit{Pinus contorta} compares with \textit{P. banksiana}. \textit{Pseudotsuga menziesii}, on the other hand, does not have a boreal equivalent.

North of the Intermountain Region, in the northern Rocky Mountains of Canada and the northwestern United States, a very large proportion of the high-mountain species can be related directly to something from the holarctic or the northern coniferous forest. As one goes progressively southward, a larger and larger proportion of the alpine species are evidently highland derivatives from common lowland elements. In the Intermountain Region both of these types are well represented at upper altitudes. Alpine and subalpine species of \textit{Arctostaphylos}, \textit{Gentiana}, \textit{Myosotis}, \textit{Pedicularis}, \textit{Ranunculus}, and \textit{Saxifraga} are likely to have boreal affinities. On the other hand, montane species of \textit{Allium}, \textit{Eriogonum}, \textit{Hulsea}, \textit{Hymenoxys}, \textit{Lomatium}, and \textit{Penstemon}, even at the highest elevations, generally relate to species of lower elevations, often of dry habitats. Some common montane genera, such as \textit{Erigeron}, do not fit into either of these patterns. \textit{Erigeron} is best developed in the western American cordillera, but the species of the dry lowlands are evidently advanced, and the more primitive species are distinctly mesophytic.

**EVOLUTIONARY HISTORY OF MAMMALS**

The evolutionary history of the mammals parallels in many ways that of flowering plants. Although the group takes its origin
from therapsid reptiles in the Triassic period, the placental mammals do not enter the fossil record until late in the Cretaceous. Placental mammals diversified explosively during the Paleocene, and they have been the dominant animals in terrestrial ecosystems since that time. Evolution of mammals in North America is closely correlated with that in Eurasia, but not well correlated with that in South America, because of the essential separation of North and South America until relatively recent times.

The animals that may have had the most important influence on the plants during the Tertiary period were the grazing animals—ungulates, in the broad sense. Grazing mammals began to evolve in the Paleocene or Eocene, and they reached full flower in the Oligocene and Miocene (Jones and Armstrong 1973). One may reasonably suppose that there is a relationship between the evolution of grazing mammals and the rise of grasses during the same general time. Grasses originated no later than the Oligocene, and by Miocene time they were common. The intercalary meristem of the grass leaf can reasonably be interpreted as an adaptation to grazing pressure. Thus, although it may be true that at any given time the nature of the fauna is more dependent on the flora than vice versa, in the long run the evolution of plants is strongly influenced by animals.

The most startling feature of the evolutionary history of mammals in North America was the rapid extinction of a great many of the large mammals about ten thousand years ago. There is no real parallel in the evolutionary history of plants. Similar extinction occurred to varying degrees in other parts of the world, least of all in Africa. Both climatic changes and the influence of early man have been invoked to explain the massive extinctions. In North America, the case for the predominant influence of man is very good (Martin 1967), although the subject still evokes considerable debate and difference of opinion (Axelrod 1967). The large mammals had survived much more extensive climatic changes during the Pleistocene, and their disappearance from the scene appears to be closely correlated with the spread of man. Human hunters killed the large herbivores, and many of the large predators disappeared along with their prey. Bison, camels, elephants, and horses were abundant in the Intermountain Region during the Pliocene and Pleistocene (Axelrod 1950), but of these only the bison survived the human onslaught. It is clear enough that horses, at least, are well adapted to modern conditions in the Intermountain Region, and burros do very well a little farther south. On the other hand, the camels introduced into our southwest more than a century ago did not make the grade, although they might well have done so in the absence of man.

**Evolutionary History of Birds**

The birds apparently originated in the upper Jurassic and began to radiate in the Cretaceous, but nearly all the Cretaceous families are now extinct. After the extinction of the dinosaurs and before the evolution of large carnivorous mammals, there were some large flightless birds, which played the ecological role later taken over by large mammalian carnivores. In the northern hemisphere these birds were common from the Upper Paleocene to the middle of the Eocene. An ecologically similar but taxonomically distinct group of large, flightless, predatory birds was common from early Eocene to middle Pliocene time in South America, an area into which the large carnivores made a relatively late entry. Again the geographic separation of North America from South America during most of the time from the Cretaceous until late in the Tertiary had a profound effect on evolutionary patterns.

By the end of the Eocene the birds were highly diversified, and all living families and orders can be traced back at least that far. In Miocene time the avifauna began to take on a more modern aspect, and most of the
modern genera had come into existence by Pliocene time (Storer 1974). There was no great wave of recent extinction comparable to that of the large mammals.

The avifauna of the Intermountain Region has no endemic species and is distinguished mainly by what isn’t there. The species are all more or less widespread. Distinctively Californian, southern Rocky Mountain, and Mohavean species mostly do not extend into the Intermountain Region (W. H. Behle, this symposium).

EVOLUTIONARY HISTORY OF INSECTS

The evolutionary radiation of insects, like that of flowering plants, mammals, and birds, goes back many millions of years. The Coleoptera (beetles) are well known as fossils as far back as the Permian period. The Diptera and Hymenoptera date from the Jurassic period, but only in forms such as midges and crane flies (Diptera) and saw flies (Hymenoptera), which are not and presumably never were important pollinators. The bees and the higher Diptera, which are now important pollinators, first appear in the fossil record in early Tertiary time, although they may well have originated somewhat earlier (Carpenter 1953, Baker and Hurd 1968). Most or all of the early Tertiary bees belong to extinct genera, and one may legitimately speculate that the evolution of modern bees was intimately related to the evolution of structurally complex, bee-pollinated flowers during the Tertiary. The Lepidoptera originated no later than the late Cretaceous (MacKay 1970) and had already diversified to some extent in early Tertiary time, but here again the important pollinators are apparently not ancient types. Drawing upon the recent discoveries of Cretaceous fossil insects reported by Rodendorf and Zherikhin in 1974, Doyle (1976) visualizes “major extinctions of ‘Jurassic’ groups within a relatively brief interval of the Late Cretaceous, and a somewhat slower rise of groups now associated with angiosperms.” The coevolution of structurally complex flowers and insects capable of recognizing complex patterns represents another example of major evolutionary interaction between plants and animals (Leppik 1957, Baker and Hurd 1968).

The faunistic differentiation between Laurasia and Gondwanaland shows up at least in the aquatic insects of the Intermountain Region. Species of Gondwanaland ancestry occur mostly in the warmer waters, or their eggs hatch relatively late in the summer. Some species of Laurasian affinity connect to Eurasia through Beringia, and others through Europe (G. F. Edmunds, personal communication).

LITERATURE CITED


GREAT BASIN NATURALIST MEMOIRS


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