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Wisconsin Climate and Life Zones in North America

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In attempting to understand some speciation problems revolving around certain North American beetles, I discovered a need for more detailed information concerning the climatic and biogeographic conditions that prevailed at the maximum of the last glacial period. Although many recent studies of isolated localities —especially in the form of pollen analyses of peat bogs—were found, there appeared to be no broader study available that presents the over-all picture. The present paper (*1*) is an attempt to reconstruct more concretely the conditions indicated from the admittedly rather scanty data at hand.

Climate of Ice Sheets

Since it is natural to think of ice sheets as occurring in regions of the most intensive winter cold, it is somewhat of a surprise to discover that lower cold-month mean temperatures exist in areas that have no permanent ice cover than in those that have. In central Asia, for example, there is an extensive area that has a January mean of −50°F, according to Haurwitz and Austin (*2*); surrounded by an equally extensive belt with a corresponding mean of −40°F; nevertheless, the entire region, except in the high mountains, is unglaciated. In contrast, on the Greenland icecap and on Antarctica, which is nearly entirely glaciated, we find cold-month means that are considerably milder, between −20°F and −30°F.

Since extremely cold winters alone, then, do not satisfactorily explain the presence or absence of ice cover, we turn next to annual precipitation as an index to ice formation, for perhaps the steppes of Siberia and Inner Mongolia are too dry to permit formation of an icecap. But this too fails to appear as the limiting factor, for, while Greenland and Antarctica have less than 10 inches of precipitation annually, much of central Asia has well over that figure—in fact, up to 20 inches in a broad part of the region. Nevertheless, a study of the rather scanty climatic data that are presently available reveals that the annual precipitation, understandably enough, is of great importance. In Antarctica, where the annual mean is 7½ inches (at Little America), the ice sheet is diminishing rather rapidly, while in Greenland, where the mean is closer to 9 inches, the diminution is somewhat slower. Hence, it might be postulated that a minimum annual mean of 12 inches is essential for the maintenance of an ice sheet and that more than this is essential for the formation and growth of an ice sheet on a continental basis.

However important annual precipitation may be as a contributing factor for glaciation, the delimiting factor must be sought elsewhere, perhaps in the melting that is possible during the warm season. Examination of warm-month means seems to point quite obviously to a maximum mean of 45°F as the factor that restricts ice sheet formation, for no present continental glaciation occurs anywhere in the world where the warm-month mean exceeds this; nor, as far as figures are available, do the snow lines of mountains extend into regions with higher temperatures. For example, all except one major glacier of eastern Canada and the whole of the icecap of Greenland lie north of the July mean of 40°F, and this sole exception lies far north of the corresponding mean of 45°F. Antarctica lies far south, similarly, of the January mean of 40°F, and, in fact, mean daily temperatures rarely go above freezing anywhere on that continent. On the other hand, the great plateaus of central Asia, with their very low winter temperatures and fairly abundant rainfall, have July means of 50°F or more, and hence appear to be unable to maintain extensive, permanent glaciation.

From Fig. 1, it may readily be observed that the farthest advance of the Wisconsin ice sheet (*3*) extended, except in the central plains and Pacific Coast regions, not greatly beyond the present isotherms of mean July of 70°F and mean January of 20°F, a range of 50°. Assuming a similar range for the latitude during the last ice age and accepting the foregoing discussion as essentially correct, it is possible to postulate that these isotherms could have had values of 45°F and −5°F, respectively—a total decrease for the upper latitudes of 25°F. Furthermore, until the time when continental glaciation had progressed in North America as far south as the present belt of 15 or more inches of rainfall, we must also postulate some increase in annual precipitation. Once that point had been reached, the conditions prevailing at the present time would be ample for continued growth insofar as moisture is concerned.

Climate of Unglaciated Regions

If, then, the temperatures of the polar climates decreased, as it would appear, a total of 25°F, does it follow that those of the remainder of the continent diminished to the same extent at the maximum period? The evidence, scanty as it is, seems to indicate otherwise.

In the eastern part of the continent, most of the evidence, based as it is largely on palynological studies of peat deposits, is biogeographic in nature and hence indirect. In the western portion, however, the presence of ancient snow lines and glacial moraines on the mountain peaks provides much more direct information on the depression of temperature that occurred during the Wisconsin period. Ernst Antevs (*4*), in a recent study of a north-south series of peaks along the 105th meridian in the southern half of Colorado and in northern New Mexico, deduces a general depression of tempera-

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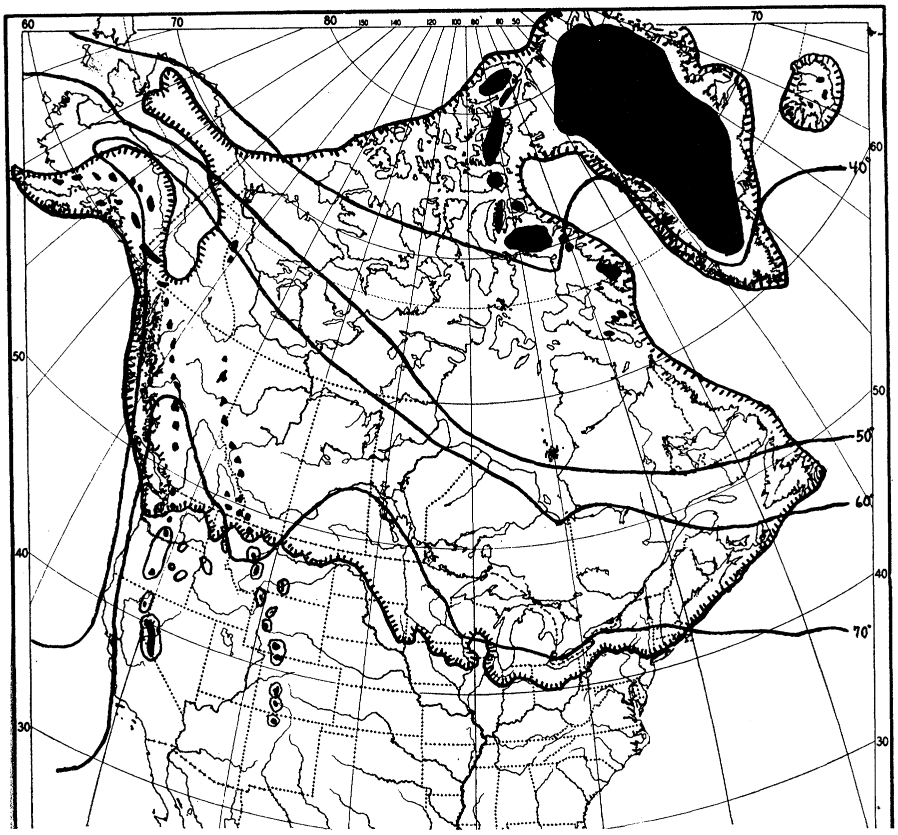


Fig. 1. Glaciation of the Wisconsin ice age compared with that of the present. Black areas, existing glaciation; hachured outline, Wisconsin glaciation. Isotherms are July means in degrees Fahrenheit.

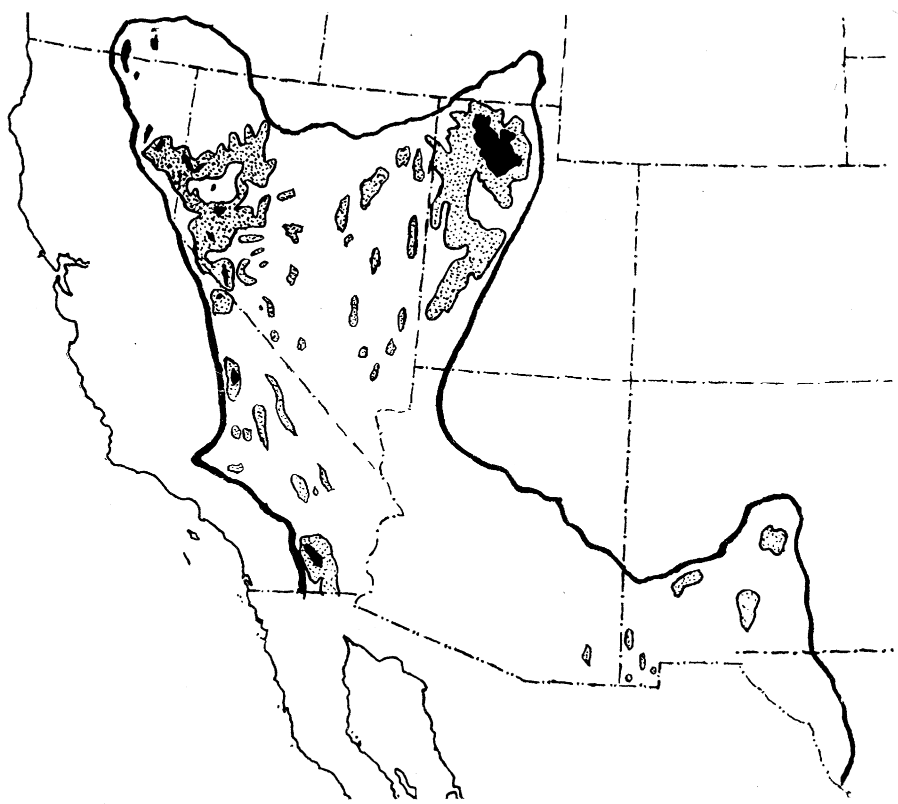


Fig. 2. Basin and Range region. Present pluvial lakes are shown in solid black; extinct pluvial lakes are indicated by stippling.

ture for the area of only 10°F. In this same paper, as well as in a similar study that was published earlier (*5*), he finds that the maximum of former very extensive lakes of the Basin and Range region (see Fig. 2) was reached simultaneously with that of the Cary substage; and he concludes that there was an increase in rainfall of 9 inches per year for the area. However, his conclusions are based on the assumption that no increase in rainfall occurred in the Pikes Peak area and may be in error to some extent. Nevertheless, his estimate of the temperature drop is in close accord with that of other workers (*6*) for regions of comparable present-day climates, such as southern Europe and Japan.

For latitudes farther north or south, there are no available data of this sort for North American localities. However, Meyer (*7*) found a depression of about 5° to 6°F for the equatorial Andes at the Wisconsin maximum.

In summary then, there appears to have occurred at the period of maximum glaciation a clinal depression of mean temperatures that amounted to 5°F at the equator, to 10°F at latitudes 35° to 40°N, and to 25° at the edge of the ice sheet. If one keeps in mind the curvature of the earth's surface in relation to the angle of the solar rays, such a cline does not seem illogical. On the other hand, the only apparent alternate hypothesis—that of a uniform depression of the mean temperature of, say 10°F—would suggest a July mean of 60°F for the ice sheet's lower boundary, which is similar to that of present-day England or northern Germany, or of the state of Maine, but with somewhat colder winters. Since no glaciers or permanent snow fields are known to exist today under such relatively mild climates, it seems scarcely likely that they could have done so in former times.

With the advent of the huge stretch of ice covering the upper half of the continent, it appears probable that a mean annual low-pressure system would have developed over the glaciated region. As a result, the mean annual cyclonic path, which at present enters the continent at about the latitude of Oregon, would have been displaced to the south so as to strike just above the middle California coast. From there it would have continued across the southern Rocky Mountains, leaving the east coast perhaps in the vicinity of South Carolina. Despite a slight decrease of evaporation in the equatorial regions owing to the temperature drop, the net effect of these changes would have been an increase in precipitation—as the result of increase in violence of the interactions of cold and warm air masses—in much of a southern belt across the nation. Therefore, we

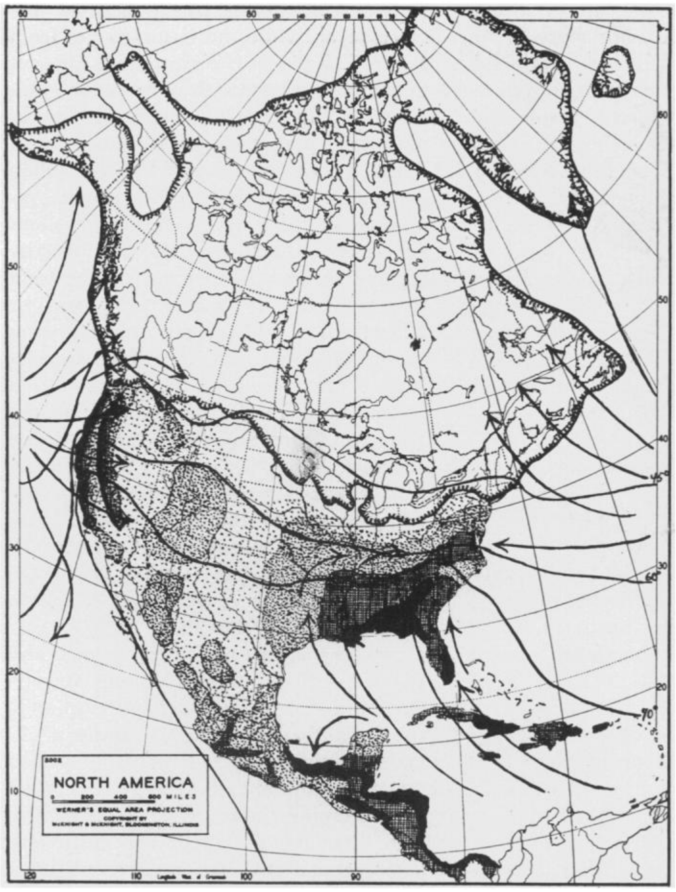


Fig. 3 (left). Hypothetical mean annual rainfall at the maximum of the Wisconsin glaciation. White areas, regions with less than 10 inches; lightly stippled areas, regions with 10 to 20 inches; heavily stippled areas, regions with 20 to 40 inches; crosshatched areas, regions with 40 to 60 inches; black areas, regions with more than 60 inches. Isotherms are July means in degrees Fahrenheit. Fig. 4 (right). Present mean annual rainfall. Legend same as that for Fig. 3. The arrows indicate the sources of atmospheric moisture.

might postulate a much more moist climate for the southwestern portion of the present United States as well as for the southeastern part, perhaps not too unlike the rainfall zonation suggested in Fig. 3 (compare Fig. 4). The diminished mean precipitation proposed for the belt across the northern tier of states would result from the dry, cold, expanding air masses descending off the icecap as a result of the anticyclonic circulation.

This postulated cline of precipitation, declining from south to north—at least for the western states—might be substantiated from the ancient snow lines of some of the mountain peaks, if Antev's figures are accepted. In the studies previously mentioned, he suggests a displacement of 3000 feet downward for each decrease in mean temperature of 10°F. At Mount Rainier, Washington, where the mean temperature possibly decreased twice this amount, we would expect to find a lowering of the snow line of 6000 feet, 5500 feet being actual according to Flint (*8*). Hence, because of the proximity of this mountain to the coast, only a slight discrepancy is noted, and we might suggest only a small drop in mean annual rainfall, say from the present 100 inches to perhaps 80 or 90 inches. However, at Glacier National Park in Montana, the lowering of the snow line amounts to only 4500 feet despite the fact that the area must have suffered a temperature drop of close to 25°F at maximum glaciation. Here the discrepancy from the predicted amount is about 3000 feet, which might be explained by a decrease in annual precipitation to about one-half of its present 30-inch mean.

Development of the Ice Sheet and the Effect on the Biota

In order to describe the development of the continental ice sheet, we must first postulate an increase in precipitation, not over the whole of the earth, but at least in the region of Greenland and northeastern Canada to begin with. Because there is an abundant source of atmospheric moisture from the prevailing Iceland low pressure area, as well as from Hudson Bay during the warm months, it would not require too radical a meteorological change to increase the present mean annual rate (about 9 inches) to the minimum requirement of about 15 inches per year. Following this increase, in the second place, a gradually diminishing mean temperature in the more polar latitudes must be postulated. As the temperature fell and the glaciation increased in extent, the mean path of cyclones likewise was gradually moved southward, as was also the position of the Iceland low. Hence the greatest thickness of the glaciation would always be nearest the sources of moisture, with an attenuation in depth away from these areas. With these considerations in mind, it becomes possible to draw a series of maps, such as those in Figs. 5 to 9, to indicate the stages in the gradual development of the ice sheet.

As the glaciation increased in extent, the biota of the continent, naturally enough, was greatly influenced by the resulting changes. To understand better some of the details of these effects, as well as those of the glaciation and climatic changes that are not apparent from other sources, it may be well to examine some data from palynological and biogeographic sources.

Evidence from Northern States

Potter (*9*) analyzed the pollen content of 15 bogs in northern Ohio, all of which are postglacial, and found a sequence of dominant tree genera, from then to the present time, as follows: *Picea, Abies* and *Pinus, Betula, Quercus, Tsuga, Carya,* and *Fagus.*

At Cranberry Glades, W. Va., with an elevation close to 3400 feet, Darlington (*10*) made a study of the bog deposits. Since geologic evidence points to the formation of these bogs by the flooding caused by melting of the glacier, the lowest depths are actually slightly postmaximum. Nevertheless, pollen analysis of the lowermost levels (13 feet 6 inches) indicates more than 70 percent fir and spruce, more than 20 percent other cold-climate trees, and about 5 percent oak. Above the 11-foot depth, the profile shows a flora quite similar to that of the present time.

Deevey's studies in Connecticut (*11*) and in other localities in southern New England (*12*) show a parallel history, with spruce and fir strongly predominating at the lowest levels, followed by a gradual resumption of modern floral components. As would be expected, Fuller's (*13*) account of postglacial vegetation of the Lake Michigan region, Lane's (*14*) work on peats of Iowa, McCullough's (*15*) study of a locality in central New York, and Rosendahl's (*16*) description of the Pleistocene flora of Minnesota show a similar history for each region concerned. Numerous other studies (*17*) have been made, all of which tell almost exactly the same story.

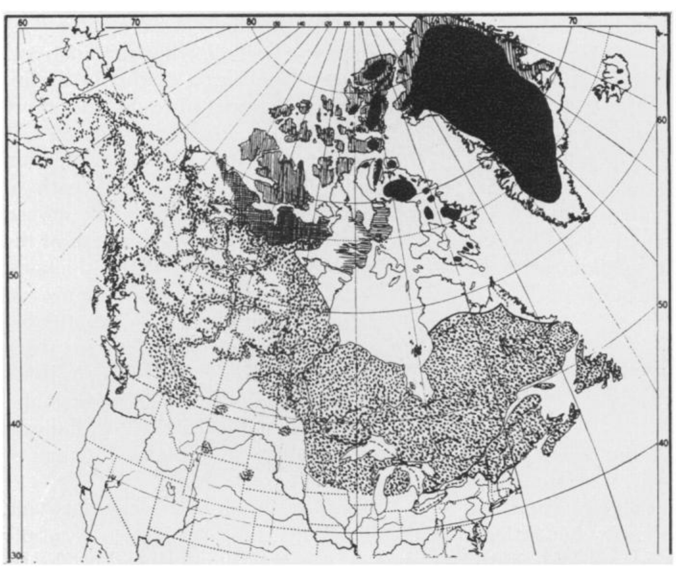
The net result of the afore-mentioned studies is the confirmation of the presence of a belt of fir and spruce across the northern section of the United States from New England into the Central States area, which followed the retreat of the glacier northward and was gradually replaced by more southerly types of vegetation until present-day conditions were attained. Furthermore, all the studies indicate that fir and spruce were strongly predominant at the time of their maxima—in combination, they formed 70 percent or more of the total tree pollen.

Evidence from Southern States

Pollen studies in southern localities reveal profiles that are somewhat different from those in the more northern states. These differences may be shown by the following citations.

North Carolina. Frey (*18*) presents a very detailed analysis of pollen taken from borings in the floor of Singletary Lake, which is located on the coastal plain of North Carolina. *Picea* appears at a depth of about 12 feet at most of his stations and is present from there to the final depth of 21 feet 7 inches, but in small quantities ranging from a fraction to 7.3 percent of the total tree pollens. *Pinus* and *Quercus* are present in abundance throughout all the borings, the former composing anywhere from 13.4 to 91.6 percent of the tree pollens at any given level, while the latter ranges from 1.7 to 63.5 percent. *Taxodium* is present in small amounts, with only minor gaps, down to a depth of 20 feet. At the uppermost and again at the lowermost deposits, *Tsuga* occurs in amounts not exceeding 2 percent. Hardwoods make up the remainder of the tree species. Grass pollens never exceed 20 percent and usually range less than 10 percent of the total tree pollens. No palm, mangrove, or other tropical pollen is reported. Maxima are poorly indicated, but there appears to be some correlation between upsurges in the amounts of *Picea* pollen and the *Sphagnum* present. A fairly marked one occurs at about 12½ feet and is probably Mankato, according to radiocarbon dating. Between 14 and 14½ feet is a very strong upsurge, possibly Cary; around 17 feet is a lesser one, possibly Tazewell, and, finally, between 18½ and 20 feet is another, possibly Iowan.

Since *Quercus,* an austral genus, and *Picea,* a boreal one, are present at even the coldest period in approximately equal numbers, we could assume a climate for this comparatively brief period that was similar to that of New York if it were not for the presence of *Taxodium.* The latter genus is apparently restricted, first by poor drainage and second by a January mean temperature of 35°F. Since this is the present-day January mean of the southern Appalachians, it seems not unlikely that the climate at its severest was similar to this but moister, which permitted *Picea* to survive. This



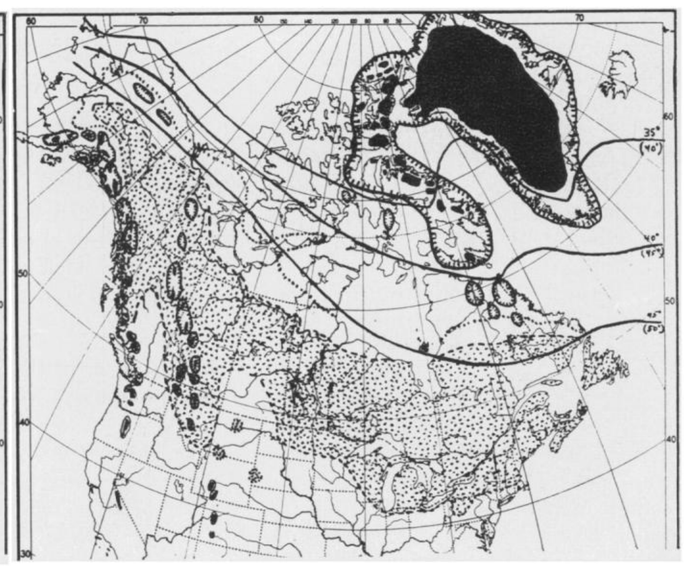


Fig. 5 (left). Present distribution of *Picea glauca* and musk ox in relation to extant arctic glaciation. Stippled area, range of *P. glauca*; crosshatching, range of *Ovibos moschatus moschatus*; horizontal lines, range of *O. m. niphoecus*; vertical lines, range of *O. m. wardi*; Black area, present arctic glaciation. Fig. 6 (right). Stage I in the development of the ice sheet, with a polar decrease in temperature of 5°F. Black areas, present glaciation; hachured lines, new limits of glaciation resulting from lowered temperature and increased precipitation in the region; stippled area, resulting new distribution of *Picea glauca,* the dotted line indicating its present actual limits. Isotherms are July means in degrees Fahrenheit; the new suggested values are above the isotherms, and the present actual values are in parentheses below the isotherms.

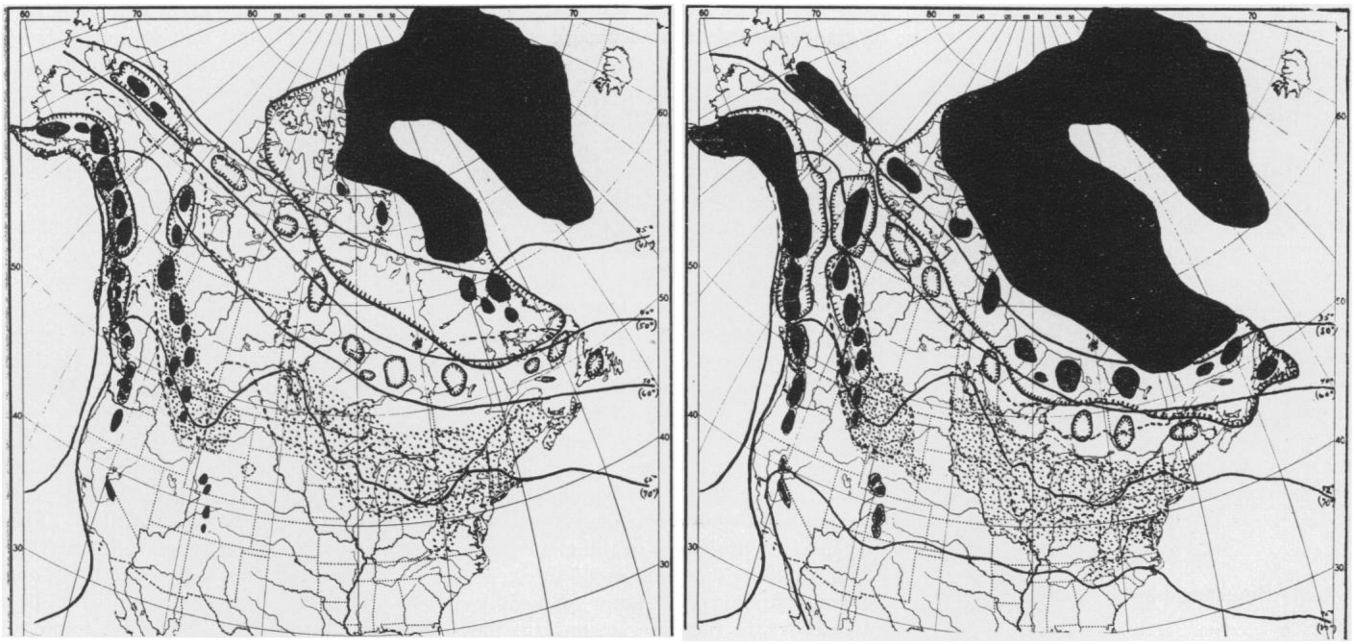


Fig. 7 (left). Stage II in the development of the ice sheet (total decrease in polar temperature 10°F). Black area, stage I glaciation; hachured lines, new limits of glaciation; stippled area, new distribution of *P. glauca*; dashed lines, limits of *P. glauca* in stage I. Isothermal legend same as that in Fig. 6. Fig. 8 (right). Stage III in the development of the ice sheet (total decrease in polar temperature 20°F). Legend same as that in Fig. 7.

maximum cold, which is equivalent to a decrease in winter temperature of 10°F and in the July mean of 5°F is indicated by the marked decrease in *Quercus* at the 13½- and 15½-ft levels. Perhaps, too, it would appear that the oak minimum marks the Mankato maximum more truly than do the spruce upsurges, for it is the only really sharply defined zone and includes at the same time maxima both for *Picea* and *Sphagnum*. The lowest depths would indicate a post-Cary origin of the lake and a continuing mild, moist climate during the interval.

Buell's (*19*) study of a North Carolina peat deposit, which is not so deep and appears to be more definitely placeable as Wisconsin in origin, is similar in detail. At the greatest depths, *Abies* pollen was found in amounts of 12 percent, along with *Pinus* and *Quercus* (38 percent each); *Carya, Betula,* and *Acer* make up the remainder.

Southern New Jersey. Potzger's (*20*) study of pollen spectra from bogs of the pine barrens of New Jersey reveals a profile not unlike that of Buell's study. The forests there during the Wisconsin glaciation contained northern elements but in rather limited percentages.

Florida peat-bogs. Unfortunately, Davis (*21*) in his excellent account of the peat bogs of Florida, fails to give a detailed, level by level analysis of the pollen that occurred in any peat deposit. Nevertheless, what records he does provide are of considerable interest. Near Tallahassee, at a depth of 90 to 96 feet (between 50 and 60 feet below present sea level) a peat deposit that contains spruce pollen has been found; this peat rests on upper Oligocene deposits and is covered by shale, clay, and sandstone with limestone streaks considered by Davis to be Pleistocene or postglacial. On the neck of the peninsula in core holes, peat deposits containing pollen of spruce and fir have also been found. One of these, containing only the spruce pollen, is at a depth 50 to 54 feet (27 to 31 feet below present sea level), while another, containing pollen of both species, is 19.5 to 22 feet below the surface (corresponding to a distance of 0.3 foot above to 2.2 feet below present sea level). Above both these deposits are marine deposits, and over these in turn are two further peat deposits that are of fresh-water origin. No cold-climate pollens have been encountered south of this region; all the peats of the southern half of Florida contain pollens of present-day flora only.

Louisiana. The fossil woods listed by Brown (*22*) indicate a similar mixed forestation for Louisiana. The deposits he studied, in the eastern part of the state, are covered by some 10 to 20 feet of loesslike soil and are assignd to the "Peorian" (Two Creeks?) interglacial period. Along with the boreal white spruce trunks and cones are found preserved woods of transitional species such as American elm as well as fossils of the oaks, magnolias, swamp tupelo, and cypress that are characteristic of the region today.

Eastern Texas. In recent years, pollen studies of three Texas bogs have been made by Potzger and Tharp (*23*). All three of these bogs show the presence of *Picea glauca, P. mariana,* and *Abies* at the lowest depths; the totals are 10 percent at the Gause bog in Milam County, 5 percent at the Paschke bog in Lee County, and about 1 percent at the Franklin bog in Robertson County. At these greatest depths, except at Paschke, where pines were dominant, grasses were present extensively and, in fact, made up close to 50 percent of the volume; they continue to dominate throughout most of the levels. *Quercus,* chestnut, alder, and pines are present, too, in small but significant volumes. At both the Paschke and the Franklin bogs, there is a scant reoccurrence of *Picea* at rather shallow levels—7 feet in the former, 5 feet in the latter. In no instance is there a report of the occurrence of tropical or semitropical pollens. The presence of only one other tree genus of possible importance—*Castanea*—is indicated; it is abundant at all three localities at levels corresponding to the reappearance of *Picea* and in those levels that are 1 and 2 feet above and below.

It is clear from these data that, throughout the southeastern United States, boreal tree species such as *Picea glauca, P. mariana,* and *Abies* sp. were at one time present, presumably at the time of the maximum of the last glacial epoch. However, it is likewise clear that, while these northern elements were present as far south as upper peninsular Florida, they never occurred in the belt from North Carolina (or even southern

New Jersey) to central Texas in amounts of more than 10 percent of the total tree population. Along with them persisted the tree species that are characteristic of the area today. While no studies are presently available for localities in the belt from Virginia to Kansas and Oklahoma we may presume that these areas were intermediate in climate and biotic types.

Before turning from palynological and fossil evidence to examine biogeographic data, I must point out one outstanding feature of the Texas bogs—the presence of an abundance of grass. Since eastern points lack this characteristic, it seems certain that this fact can have only one significance—that is, it indicates that the mean annual precipitation for the region was not greatly different from that of today.

Chiefly Biogeographic Evidence

Boreal forms. Today the musk ox, *Ovibos moschatus,* occurs, according to J. A. Allen (*24*), only in the tundra regions of the Arctic Archipelago and of the mainland west of the Hudson Bay, as is shown in Fig. 5. Three subspecies occur, *O. m. moschatus* on the mainland to the west, *O. m. niphoecus* along a small area of the Hudson Bay shore, and *O. m. wardi* throughout the Arctic Archipelago and along the coast of Greenland. According to G. M. Allen's account (*25*), these animals only rarely penetrate the low spruce forest that borders the tundra area. Hence, the musk ox is a fairly reliable indicator of tundra conditions. That such conditions prevailed just below the ice sheet is indicated by the finds of skulls of musk ox; Hay reports (*26*), however, only a very few specimens that are accurately assignable to the present species, as follows: (i) one specimen from Fayette County, Iowa, is dated as Kansan; (ii) a good hind part of a skull was found at a depth of 8 feet in Sioux County, Nebraska, and could be Wisconsin; (iii) the third and last well-preserved find is a small skull from Wabash County, Minnesota, which is dated as late Wisconsin. Although numerous other finds of fossil "musk ox" skulls have been made, all of these have been assigned to other genera such as *Symbos, Boötherium,* and *Gidleya.* Since these genera are entirely extinct, their habitat requirements are unknown, but because of their abundance throughout the grass belt of middle North America as far south as Texas, it seems that they were prairie, not tundra, animals. Hence, there is no good evidence that severe polar conditions existed within the United States except in close proximity to the glaciation.

The modern distribution of musk ox can indicate one other point of possible interest, but, in this case, it concerns the melting of the icecap. Since no ecological factor is known that would explain the absence of these creatures from the east side of Hudson Bay, it might be suggested that the central portion of the glaciation disappeared first, while much of the region to the south and east of the bay was still covered by ice. This would be quite in accord with the precipitation distribution postulated here, which would suggest that the area just east of the Rocky Mountains received rather scanty precipitation and a resulting thin ice covering, while the opposite conditions prevailed in the extreme west and east.

Another boreal form, of even more importance, possibly, than the musk ox, is the white spruce, *Picea glauca.* This species, the black spruce (*P. mariana*), the tamarack (*Larix laricina*), and balsam fir (*Abies balsamea*) are the characteristic trees, according to Harlow and Harrar (*27*), of the great belt of northern evergreen forest that stretches across the continent from Labrador to Alaska. Since these four have essentially the same ecological requirements, as is indicated by their constant close association, it will suffice to discuss only one of them, the white spruce, in detail.

The belt of white spruce is limited on its southern edge, in the region of 20 or more inches of annual rainfall, by the July isotherm of 70°F. Farther west, where the rainfall is scantier, its lower border is withdrawn to the north. In the western portion of its range into Alaska, the tree is found primarily along the banks of lakes, streams, and bogs. In Alaska, it is confined to the interior, never ascending the coastal mountains to heights of more than 2500 feet. The northern edge of its range is defined by the limit of the area of perpetually frozen soil. Grading into the species proper toward the north, there is found—throughout the Canadian Rocky Mountains, in isolated patches in Montana and Saskatchewan, and in the Black Hills of South Dakota— a subspecies by name of *P. glauca* var. *albertiana.* Neither the species nor the variety occurs in the mountains farther west or south of these points, as is shown in Fig. 5. The suggested distribution of the species during the steps in the development of the continental ice sheet that is shown in Figs. 6 to 9 attempts to explain the formation of the western subspecies by disjunction in its distribution at climax and also attempts to explain its present absence from the western coastal ranges, where ecological factors are apparently favorable for its existence, by the more rapid formation of glaciers in these highlands so that its southerly progress there was blocked. Furthermore, its present absence from peaks and high ranges of the Rocky Mountains south of Montana suggests that the intervening lowlands were much too dry to permit the further southerly extension of its range.

Since none of the other close associates of this species have a western subspecies, we might postulate less plasticity for the other three forms. Or, because all three are less tolerant than the white spruce, perhaps none were able to reach the favorable highlands and, hence, were confined to the eastern humid half of the country during maximum glaciation.

Tropical forms. At the other extreme of existence, we need to determine whether or not tropical plants were able to persist in southern Florida during the climax of the Wisconsin ice age. If a tropical belt had persisted for any considerable length of time, it would not be unreasonable to expect to find the existence of a considerable number of plant species, or at least subspecies, that are endemic to the region, since it is so isolated

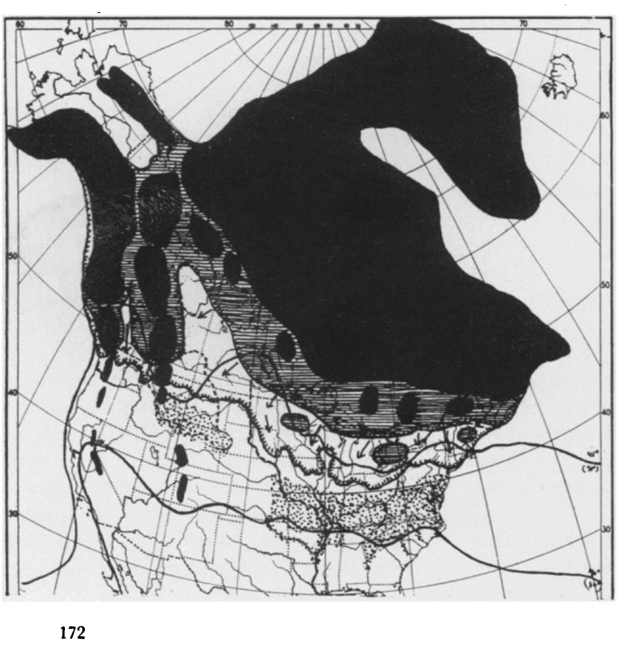


Fig. 9. Stages IV and IVa in the development of the Wisconsin ice sheet. Legend similar to that of Fig. 7; ruled area, new glaciation resulting from additional decrease in temperature of 5°F (a total of 25°); hachured lines, final extent of glaciation resulting from accumulative effects; arrows indicate direction of ice flow.

from other areas of similar climate. However, such is not the case. A study of typical tropical components such as the mangroves, palms, and cycads indicates that all have arrived either by water transport or by way of migrating birds or other animals, from the West Indies or Central America, for all, with minor exceptions, are very broadly distributed. For example, three species of mangroves (*Rhizophora mangle, Laguncularia racemosa,* and *Avicennia nitida*) occur along the coasts of southern Florida. These all have peculiar floating seeds that are highly resistant to salt water, and so their extensive range throughout the Caribbean Sea and Gulf of Mexico area is not surprising. Exclusive of *Sabal* species (palmettos), which are fairly cold-tolerant (as indicated by their presence throughout much of the southeast), of nine species of palms that occur in tropical Florida, six are found abundantly in the West Indies. Of the remainder, one (*Rhapidophyllum hystrix*) is found in shaded pine woods as far north as South Carolina and is, therefore, not a good indicator of tropical conditions, while the specific or even varietal status of a second form (*Thrinax keyensis*) is under question. The third species (*Coccothrinax garberi*) alone appears to be truly endemic. As far as the cycads are concerned, only one of the four (*Zamia silvicola*) is confined to the area concerned. Two of the others (*Z. integrifolia* and *Z. unbrosa*) occur in the northern portion of the state as well, while the fourth (*Z. angustifolia*) occurs in the West Indies and is not known to bloom in Florida. Hence, the low endemicity of the tropical flora seems to indicate the complete elimination of suitable climatic factors for its persistence during Wisconsin times.

Evidence from Mexico

In the highlands of the eastern portion of Mexico, extending from Nuevo Leon to Pueblo and into Oaxaca, there are a number of forests in which a species of *Liquidambar* that is indistinguishable from the eastern North American *L. styraciflua* occurs in numbers (see Miranda and Sharp, *28*; Hernandez *et al., 29*; Carlson, *30*; Leopold, *31*; and Sharp, *32*). Such forests occur, furthermore, in isolated patches throughout the state of Chiapas and in the neighboring area of Guatemala. In several instances, there are associated with the sweet gum other species of trees as well as herbs and ferns that likewise are known otherwise only in the eastern United States; they form up to 15 percent of the total plant species in some localities. Tree species that have been reported from these highlands, usually at elevations of about 5000 feet, are as follows: *Acer negundo* (box elder) at four Mexican and one Guatemalan localities; *Carpinus caroliniana* (hornbeam) and *Ostrya virginiana* (hop hornbeam) at nearly all stations; *Cercis canadensis* (redbud) at Tamaulipas and Hidalgo only; *Cornus florida* (dogwood) at Orizaba and Veracruz; *Nyssa sylvatica* (tupelo) at five stations in Mexico; *Prunus serotina* (black cherry) at four Mexican and one Guatemalan localities; *Rhus radicans* (poison ivy) at most stations; and *R. aromatica* (aromatic sumac) at Tamaulipas only. Thus it is evident that there is a strong relationship between the eastern Mexican highlands and the corresponding part of the United States, which indicates in a very definite manner the existence of an interconnection of the two regions at a former time. There remains, then, only the problem concerning when the interconnection existed.

If this interconnection were of comparatively recent date, one would expect to find some other of the more common species that predominate in the forests of the southern states. It seems highly significant that none of the species of *Quercus, Ulmas, Celtis, Magnolia,* and *Pinus* that occur in such abundance in east Texas are reported from these areas. While members of these genera are found in the regions under discussion, all are of species that are endemic to Mexico or Central America. Hence, it appears logical that the interconnection of the areas was at a rather remote date and that the eastern species still remaining in the Sierra Madre de Oriental are old, stable forms. That the latter assumption may be true is supported by the distribution of such forms as *Acer negundo* and the paleobotany of *Liquidambar* and *Nyssa,* which are reported from the Upper Cretaceous. *Acer negundo* is found throughout the Rocky Mountain states and along the Pacific Coast as well; here it occurs in a number of varieties, it is true, but all are considered to be conspecific with the eastern form. To me, the evidence appears to point to a time earlier than the Wisconsin during which there was greater rainfall in the eastern portions of northern Mexico and southern Texas, perhaps along with a depression of temperature, that permitted the forests of the southern United States to descend to the regions under discussion. Middle Pleistocene, perhaps the Kansan or Nebraskan period of glaciation, seems strongly indicated, or perhaps even the Pliocene.

In the western side of the country, pines are a characteristic feature of the higher elevations of the Sierra Madre de Occidental. As a whole, pines are incapable of growing in regions with an annual mean of rainfall of less than 20 inches, and the belt of these trees is abruptly interrupted to the north of Mexico by a band of arid land except at higher elevations (usually above 500 feet) where increased rainfall permits their survival. A study of the members of the genus *Pinus* of this area (see Loock, *33*; and Kearney *et al., 34*) shows that only six species are common to Mexico and the United States. Of these, *Pinus arizonica* (sometimes classified as a variety of *P. ponderosa*), *P. cembroides, P. flexilis,* and *P. reflexa* are common to the region of southern Arizona and southwest New Mexico and the western mountains of Mexico, but only as far south as Durango. One other species, *P. leiophylla* (*P. chihuahuana* of some writers), is distributed throughout the whole of western and southern Mexico but occurs also in the southwestern portion of the United States. The sixth form, *P. strobus* var. *chiapensis,* has a distribution that is so disjunctive that little doubt is left concerning the age of the former connection between the range of the species (which now is confined to the northeastern states and along the Allegheny mountains) and that of the variety (which is known only in southern Mexico). To me, all the other distributions seem to point to an increase of rainfall for the region of southern Arizona and southwest New Mexico into the western ranges of Mexico, but only as far south as southern Durango, at which time the first four species entered Mexico from the north, while *P. leiophylla* entered the United States from the south, probably at the maximum of the Wisconsin glaciation. To the north, the limitations on the distributions of all these species indicate unfavorable conditions for the region in between the mountain ranges of northern Arizona and those to the south; this is confirmed in part by the distribution of such northern elements as *Juniperus scopularum,* which is found at similar elevations as the pines listed in this paragraph but in the more northern portion of the Rocky Mountains.

In the great central region of northern Mexico, nothing could be found that indicates a moister climate than that which now prevails; this, considering the high mountain ranges that border it on almost all sides (which existed at least as far back as the Pliocene) is not surprising.

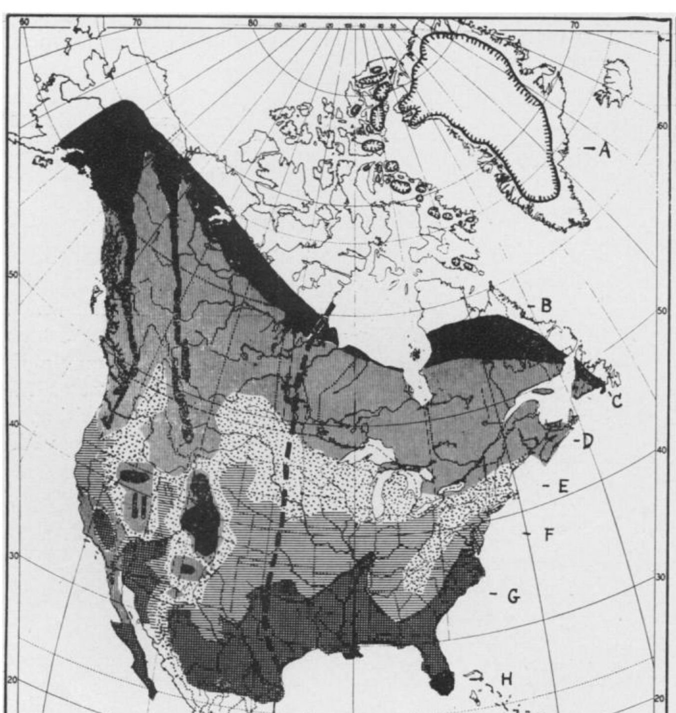
Hence, there appears to be no valid basis for any taxonomist or zoogeographer to assume, as has occasionally been the case in the past, that the biota of all of the continent was funneled, with the advance of the ice sheet, through Mexico into Central America, where hybridization would take place. Were this the case, there would certainly exist many more elements common to the east and west parts both of Mexico and of the United States as well as more elements common to these two nations. On the basis of the floral evidence examined here, it may be assumed only that the biota extended farther south only on the west coast, and there only to the lower border of Durango. In the east and central portions, no southerly extension of ranges occurred during the Wisconsin period.

Life Zones of the Wisconsin Era

If it is true today that the boundaries of the life zones and biotic provinces cannot be too sharply drawn, it would seem that this is doubly true for the last period of maximum glaciation. At least in the eastern half of the continent all available data point to a curious intermixing of boreal elements such as spruce with the present floral components, even in the southernmost parts of the United States, except southern Florida. However, we do not need to suppose that the presence of these northern types to the extent of 10 percent indicates that the whole region was transformed, say from the Lower Austral to the Hudsonian life zone. Since white spruce can be grown in cultivation many hundreds of miles south of its present range by supplying sufficient moisture, it might well be that it was enabled to extend its range into the southern area both by a somewhat lowered mean temperature and by an increase in rainfall. Furthermore, all the evidence for the presence of such cold-loving species in warmer regions is supplied by alluvial deposits and by fossil pollen derived from peat deposits, so that it could easily be assumed that these trees grew primarily along the banks of streams and in bogs (as they do today in the western part of their range, it will be remembered), leaving the uplands to the present vegetative types. Thus we may be fairly certain that there never existed great extensive evergreen forests in the eastern part of the country like those of northeastern Canada, at least not until after deglaciation had begun. Then—with the combination of general flooding, long-frozen soil, and poor deep drainage—white and black spruce, tamarack, and similar species, which are especially adapted for such conditions, were able to follow the retreating ice sheet more closely than were the broad-leaved trees. But that was postmaximum.

Beginning at the area adjacent to the ice sheet, we would find, because of the probably permanently frozen soil, a tundral zone, possibly replete with musk ox and reindeer, at least in the central stretches, bordered to the south at most by a very narrow border of spruce forests where frozen soil and poor drainage would not permit hardwoods to grow. Southward, then, in order, we could postulate Canadian, Transition, Upper Austral, and Lower Austral zones similar to those of today but necessarily narrower. In addition, in all probability they were more poorly defined, not only by the more southerly extension of northern forms, but possibly also by an extension to the north of some southern species made possible by the more abundant moisture. Because of the proximity of the ice sheet, severe cold waves were in all likelihood experienced father south than at present and at closer intervals, so that tropical forms could not exist except possibly where the Gulf Stream could provide a moderating influence as in the lower Keys, if they existed at that time. However, I do not know of any evidence for even this latter supposition; hence, a Tropical zone is not shown on the map.

In the western half of the continent, where high cold mountain peaks tower above hot arid or semiarid regions, the picture is highly complex. In the southern half of the area, the present life zones, as pointed out by Antevs, were depressed at least to a depth of one such zone by the decrease in mean temperature. Simultaneously, the increase of rainfall for this same region, indicated by that same worker but overlooked by him for life-zone consideration, would probably permit much the same sort of intermingling of biotic types as is found in the east, with such boreal forms as Douglas fir descending to low levels along streams and in the canyons and possibly forming a largely continuous network over much of the Rocky Mountain and north coastal area. However, as we have seen before, there likely existed a drier belt across central Arizona and on the basis of the distribution of the Rocky Mountain form



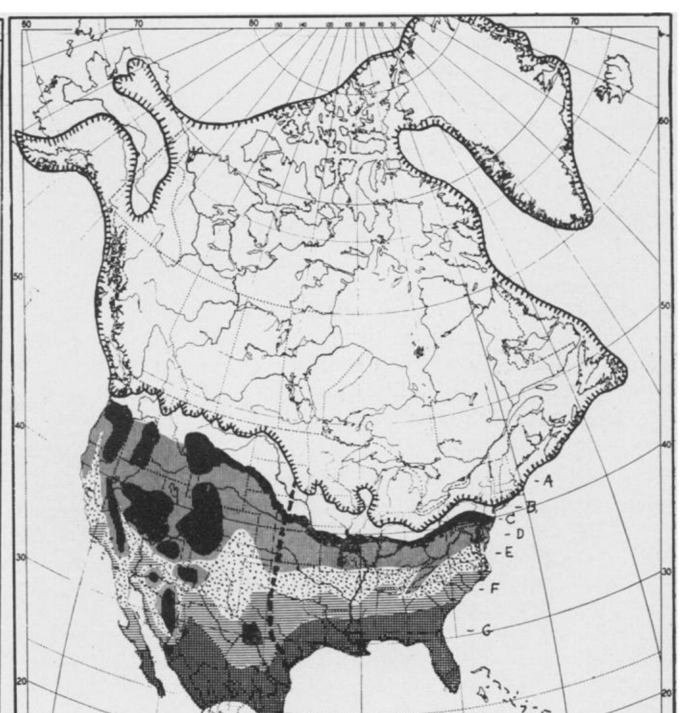


Fig. 10 (left). Present life zones (simplified from Merriam). (*A*) Arctic glaciation, (*B*) tundra, (*C*) Hudsonian, (*D*) Canadian, (*E*) Transitional, (*F*) Upper Austral, (*G*) Lower Austral, (*H*) Tropical. The heavy broken line marks the limit of 20-inch mean annual rainfall. Fig. 11 (right). Hypothetical life zones of the Wisconsin ice age. Legend same as that for Fig. 10.

Fig. 12 (left). Present distribution of the genus *Colaptes* in North America. Stippled area, range of *C. auratus*: (*A*) *C. a. borealis,* (*B*) *C. a. luteus,* (*C*) *C. a. auratus.* Black area, range of *C. cafer*: (1) *C. c. cafer,* (2) *C. c. collaris,* (3) *C. c. martirensis,* (4) *C. c. nanus,* (5) *C. c. mexicanus,* (6) *C. c. mexicanoides,* (7) *C. c. pinicolus.* White area (*Z*), zone of hybridization between *C. auratus* and *C. cafer.* Ruled area, *C. chrysoides*: (*a*) *C. c. mearnsi,* (*b*) *C. c. brunnescens,* (*c*) *C. c. chrysoides,* (*d*) *C. c. tenebrosus.* Fig. 13 (right). Hypothetical distribution of North American *Colaptes* during the Wisconsin maximum. Legend same as that in Fig. 12.

of the white spruce, a similar disruptive factor across central Wyoming. There is nothing to warrant an assumption that annual rainfall increased in the Basin and Range region to as much as 20 inches, so that the Sierra Nevada and southern coastal range belts were not interconnected with the Rocky Mountain biota.

Life zones, which ignore historical influences, are particularly unsatisfactory in the western states, but so are the biotic provinces of Dice, which exclude elevational ecological factors. Selection between these two possibilities then becomes a difficult matter, but because ecological considerations appear to be more important, I have attempted to reconstruct them, using all available data, for the glacial period under discussion (see Figs. 10 and 11).

Effects on Speciation

In general, it would seem, despite the extreme displacement of the range of many organisms, especially of those living in the more northerly reaches of the continent, that there was but slight effect on speciation among the North American biota as a result of the Wisconsin glaciation. It is especially apparent that eastern and western flora and fauna never became intermingled and that there was no funneling effect into Mexico and Central America. Possibly this continued isolation between the two sectors was brought about in part by the oblique position of the Canadian Rocky Mountains, which formed an effective barrier between southerly migrating species and the western United States. Probably equally effective also was the semiarid grassland area of the Central States. Nevertheless, several items of some general application to speciation problem may be indicated.

Of these, one, of interest chiefly because of its time implications, concerns the musk ox. As has been shown in a previous section, these animals are known to have lived in the tundra area just below the border of the ice sheet during Wisconsin times; they have assumed their present distribution in the 12,000 years since the melting of the glaciation. It seems extremely unlikely that the three subspecies now extant could have remained as isolated populations during their migration south and north as the glaciation advanced and finally receded, nor can any facts to found that support such isolation during the glacial maximum. Hence, it appears most likely that this subspeciation has occurred since the present ranges were assumed. On the one hand, this process of subspeciation has been speeded, in all likelihood, by the tendency of the animal to remain in herds and by the difficulty of the terrain in which it lives; on the other hand, it has been retarded by the relatively low biotic potential of the species.

As another example of subspeciation resulting from the last glacial period, the case of *Picea glauca* may be cited. The present distribution of its sole subspecies, *P. g. albertiana,* in the northern Rocky Mountains and in a few scattered situations as far east as the Black Hills, seems to point to isolation of an eastern and western population during the Wisconsin maximum. In this case, however, unlike the case of the musk ox, there can be shown no irrefutable evidence that this isolation did not occur during some previous period of glaciation. Nevertheless, in view of the slight differences between the two forms, there is no real reason not to believe that the isolation occurred as here indicated.

The case of *Colaptes* (*35*) in North America is even more subject to question, although it would appear that a zone of hybridization was present in the past as now. Hence, *C. auratus,* the yellow-shafted flicker, was confined to the eastern states during maximum development of the last ice age, with the ranges of its present three subspecies condensed (Figs. 12 and 13) in response to the narrowing of the life zones. Neither the supposed past nor the present actual distribution provides any basis for the placement of a date on the origin of the three forms. Nor does the presence of a fourth subspecies in Cuba and a fifth on Grand Cayman Island aid toward this end. All that can be gathered is that the subspeciation came about as a result of temperature differences in their respective areas. In the west, the subspecies of the red-shafted flicker, *C. cafer,* similarly provide little evidence of the effects of the last ice sheet on speciation. It may be proposed that the Pacific Coast form, *C. cafer cafer,* was forced southward, and that the widely distributed *C. c. collaris* was enabled to penetrate into northern Baja California and onto the adjacent coastal islands as a result of the increased rainfall suggested for the region. If such were actually the case, then it would follow that the subspecies *C. c. sedentarius,* which is found on Santa Cruz Island, the now extinct *C. c. rufipileus,* which was formerly resident on Guadelupe Island, and *C. c. martirensis,* which is still extant on the western slopes of the mountain ranges in northern Baja California, have arisen as a result of isolation since the glacier's retreat—that is, during the last 12,000 years. Now these three forms are very similar to *collaris,* whereas the southern race of the species, *C. c. mexicanoides,* is most closely allied to the nymotypical form of the northwest coast. This would suggest that the species originally was similar in body size and in coloration to *C. c. cafer,* and that *collaris, mexicanus,* and *mexicanoides* arose before Wisconsin times, perhaps during an interglacial period.

By following similar lines of reasoning, one could analyze speciation of all the innumerable members of the North American biota, but space will not permit further discussion here. In closing, I would like to repeat, however, that the effects of both the temperature change and the altered precipitation pattern must be borne in mind whenever such analyses are attempted.

References and Notes

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"*. . . Dr. Priestley you tell me continues his experiments with success. We make daily great improvements in* natural, *there is one I wish to see in* moral *philosophy; the discovery of a plan, that would induce & oblige nations to settle their disputes without first cutting one another's throats. When will human reason be sufficiently improv'd to see the advantage of this! When will we be convinc'd that even successful wars at length become misfortunes to those who unjustly commenced them, & who triumph'd blindly in their success, not seeing all its consequences.*"—Benjamin Franklin to Richard Price, Passy, 6 Feb. 1780.