

## Pleistocene Ecology and Biogeography of North America<sup>1</sup>

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During the past ten years, the related fields of Pleistocene chronology, biogeography, palynology, and prehistory have experienced vigorous growth. This growth may be attributed in part to methods of isotope dating, fresh interest in periglacial geomorphology, the application of pollen stratigraphy to archaeological and chronological problems, and increased appreciation of "vertebrate microfossils." Students of animal and plant distribution find themselves increasingly committed to archaeological and geological data. The information exchange is mutual and poses a challenge in interdisciplinary communication. For attempting to unify Pleistocene concepts within archaeological, biological, geological, and climatological specialties we are especially indebted to Braun (1955), Clark (1952), Devey (1949, 1953), Flint (1957), Frenzel and Troll (1952), and Moreau (1955). In North America Dillon's mapping of Pleistocene life zones (1956) has filled something of a vacuum in the area of biogeographic reconstruction.

My present purpose is to identify some of the problems that appear important in the terrestrial ecology and biogeography of North America during the late Pleistocene. This project follows the logical principle advocated by Devey (1949) that students of plant and animal distributions are obligated to consider the Pleistocene before working backward. To do so does not mean ignoring or neglecting the instructive record of Tertiary environment and life. The adopted course, however, is based on the belief that Pleistocene climatic change was not confined to the glacial period. Until proved otherwise, the more useful working hypothesis is that

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existing range lines and reflect populations date from the Glacial period. From the viewpoint of the biologist the foremost events in terrestrial ecology of North America during the Pleistocene appear to include the following: (1) the climatic sequence proper with its attendant displacement of biotic zones; (2) the arrival of prehistoric man; (3) the extinction of late Pleistocene vertebrates. To an unknown degree these events appear interrelated. The first part of my analysis is devoted to problems of climatic and environmental change, the second to extinction and the effect of man.

#### LATE PLEISTOCENE ENVIRONMENT

In view of the relatively poor pre-Wisconsin fossil and sedimentary record, it is expedient to concentrate on the last (Wisconsin) glacial sequence. Environmental change during the Wisconsin glaciation can be considered subequal to that which accompanied the earlier (Nebraskan, Kansan, Illinoian) glaciations. This assumption is based on the coincidence of the four glacial drift borders in eastern North America, the four equivalent periods of glacial temperature drop as recorded in oxygen-isotope analyses of marine foraminifera from the equatorial Atlantic (Emilian, 1955), and the apparent sequence of cool and warm mammalian faunas found in unglaciated North America (Hubbard, 1958).

Generally, biogeographers keep abreast of modern findings in glacial geology and are not deterred by such views as that of Scharff (1912, p. 156) that glacial drift was formed by marine deposition and that the climate of the Pleistocene was never colder than at present. Admittedly, there is lack of agreement concerning Pleistocene environment and life in the region where glacial geology provides least information, namely in the temperate and tropical zones south of the drift border. Braun (1951, p. 145) felt that "... the deciduous forest zone, although narrowed, maintained itself on the Appalachian Plateaus in southern Ohio and Kentucky while glaciers extended southward in Ohio." Thomas (1951, p. 166) followed suit: "The distribution and the ecology of many Ohio animals, I believe, raises strong presumption that they survived the Wisconsin, or perhaps the entire Pleistocene, close to the glacial border; some species in refugia within the limits of glaciated territory." Plants in question include buckeye (*Asclepias ostrya*), sweet gum (*Liquidambar*), *Agave*, and *Magnolia*. Animals with distributions that also

parallel the Wisconsin drift border in Ohio include the fence lizard (*Sceloporus undulatus*), copperhead (*Agkistrodon contortrix*), and upland chorus frog (*Pseudacris brachyphona*). To date there is no sound paleontological support for the postulated ice margin populations of temperate biotas.

On the contrary, evidence of Pleistocene spruce in southern Louisiana and spruce and fir pollen in northern Florida and eastern Texas seems impeccable (cf. Deevey, 1949; Braun, 1955). The interpretation of the evidence, however, is not immediately shown. Does it prove the existence of boreal forest at this latitude? Or does it reflect an azonal mixture of temperate and boreal floras throughout the unglaciated east as Braun (1955) and Drury (1956) maintained? Presently spruce grows near sea level in Connecticut and southern Michigan, 400 to 500 miles beyond the southern limit of spruce-fir-jack pine boreal forest. The Florida and Texas records of boreal elements may also represent marginal populations of species whose position of dominance lay farther north. We need not insist that fossil spruce meant boreal forest in Texas and Louisiana, but it may well represent population outliers of boreal forest occupying Kentucky and the Carolinas.

An area of intense frost action extending 50 to 100 miles south of the ice sheet is generally accepted by geologists (Fline, 1957), at least for eastern North America. Denny's studies (1951, 1956) of periglacial land forms in unglaciated Pennsylvania are relatively conservative. Peltier's (1949) more sweeping in their paleoclimatic conclusions. Quite recently a series of herb-dominated pollen zones have been reported from inorganic sediments in eastern North America (Andersen, 1954; Davis, 1957; Deevey, 1951; Leopold, 1956; Livingstone and Livingstone, 1958; Martin 1958a). I consider these findings as palynological confirmation of Full- and Late-glacial tundra zones.

At this point it may be helpful to insert a definition. Within the scope of the term tundra I would include the following: (1) treeless vegetation in the Arctic; (2) treeless Alpine zones on temperate and tropical mountains; (3) pollen zones in Pleistocene sediments featuring high percentages of herb pollen plus a small amount of spruce and other boreal tree pollen.

There is no question of floristic identity between these communities. As an example, *Aristida*, an element in the late-glacial pollen

zones of New England and Michigan, is not found in the Arctic. Both *Ambrosia* and *Ephedra*, another steppe species in the Late-glacial of Europe and America, present the problem of how we might distinguish cool prairie from tundra in a pollen diagram. Today these vegetation types are separated by a belt of woodland and forest. Is it possible that they were in contact during the glacial periods?

Perhaps the periglacial landscape was not entirely treeless. If scattered spruce, larch, or jack pine grew near the ice margin, they would have formed a taiga or boreal savanna. Presently the taiga lies between boreal forest and treeless tundra (Rousseau, 1952; Hare, 1954). Occasionally pieces of coniferous wood are found in glacial drift (Flint, 1957, p. 323). Rather than indicating that forest was overridden by ice, they may mean that the glacier swept through a taiga type woodland, a more plausible ice-margin environment. The relatively well-known and widely discussed Two Creeks "forest" bed, silted and covered by Valdres Ice (Wilson, 1932, 1936) is not an exception. In stump diameter, taper, and growth rate the Two Creeks trees resemble spruce woodland in central Ungava (see Hustich, 1954, for comparative data). In brief, fossil wood is not proof of forest!

We may expect that Full-glacial tundra, boreal forest, and deciduous forest formations were not identical in species composition or even in vegetational structure with their present bioclimatic analogues. Nevertheless, if there is an adaptive relationship between vegetation and climatic zones, it seems unreasonable to postulate an azonal system during the glacial period, as Drury has done (1956, pp. 80-90). The model proposed by Dansereau (1957), with narrow tundra bordering the ice at one point and maple or oak forest at others, also does not agree with either the concept of bioclimatic gradients or with Late-glacial pollen diagrams. In general the succession of pollen zones, tundra → boreal forest → deciduous forest in New England and boreal forest → mixed deciduous forest → oak-pine forest in North Carolina (Frey, 1953)<sup>1</sup> shows, I believe, the

<sup>1</sup> My interpretation of boreal forest in North Carolina is based on Frey's pollen zone 1C, in Singletary Lake and Jones Lake 1-1. This reveals dominance of pine, including many small grains, with up to 9% spruce, 7% oak, 1% birch, and 1% hickory. In fairness to Frey (1953, 1955) it should be noted that, although he regarded his results as evidence of climatic change, he does not advance the hypothesis of Boreal Forest in the Carolina. The case I would make for Boreal Forest rests chiefly on the small but crucial percentage of spruce and the scarcity or absence of broad-leaved species.

A writer authority on this region, D. R. Whitehead (personal correspondence) takes strong exception to such an interpretation of Frey's work, noting: (1) Size-frequency

historical integrity of generalized vegetation zones. On this conviction I have attempted to map late Pleistocene vegetation zones in two periods (Figs. 2 and 3). They are based on pollen stratigraphy, periglacial geomorphology and scattered plant and animal fossil records. Presumably, such a map will be of more value to the biogeographer than one based largely on biogeographic evidence that leads to a circular argument. If boreal forest replaced temperate deciduous forest in the Cumberland Plateau and southern Appalachians, it seems preferable to attempt to establish this fact in terms of pollen analysis, buried soils, and other fossil evidence.

#### Modern Vegetation Zones (Fig. 1)

Dansereau (1951) has stressed the importance of structure to the geographer and general ecologist, a viewpoint that I believe to be profitable also in paleoecology. Reconstruction of forest community composition from pollen data is beset with difficulties, for example in evaluating relative pollen rain among different wind-pollinated species and correcting for underrepresentation of insect-pollinated plants. However, it seems possible to determine structure of the simplest type, to distinguish forest, savanna, and grassland biocoenoses and, within the first, coniferous and deciduous formations (for definitions of these and other vegetational concepts, see Dansereau, 1957). The six major vegetation zones or formations in eastern North America include: (1) treeless tundra; (2) boreal woodland or taiga, a savanna formation of needle-leaved trees scattered in a shrub and lichen mat; (3) boreal forest with a continuous canopy dominated by needle-leaved evergreens; (4) temperate forest dominated by broad-leaved deciduous trees and shrubs; (5) temperate prairie and savanna; (6) subtropical savanna of evergreen sclerophylls and tall grasses. These six zones represent arbitrary divisions of an adaptive gradient controlled in general, if not always in detail, by climate. Is it unreasonable to assume that this gradient maintained its structural features and sequence during the glacial periods?

Features have not been worked out carefully for all the species of pine which are, or might be, expected in this area. Thus the allocation of small grains to the boreal species *P. banksiana* is premature. (2) Zone M2 from Frey's core LS-2 contains fairly high percentages of oak (about 15%) and birch (about 10%) as well as some pollen of *Taxodium*, *Myrica*, and other temperate elements. (3) The predominance of pine might be the result of "over-representation" of a species such as *P. serotena*, which surrounds large sites in the southeast today. In other words, oak, birch, and associated temperate plants occurred at sites some distance from the bay labels but were "swamped out" by the well-known heavy rain of pine pollen.

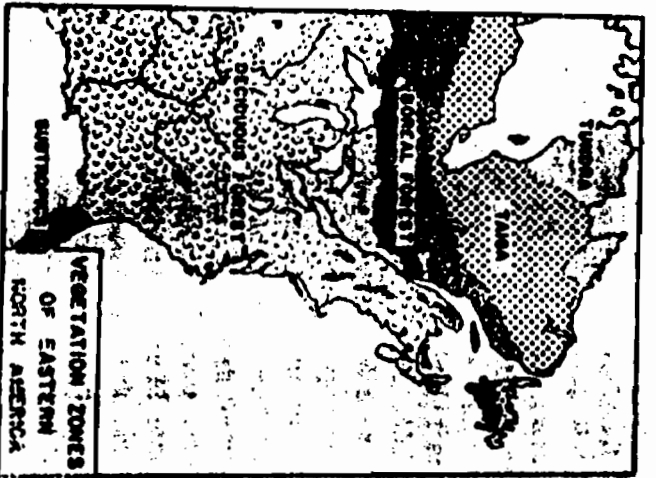


Fig. 1. Vegetation zones of eastern North America. Small, isolated mountain-top populations of boreal forest in parts of the Appalachians are not shown. The southeastern pine forests are considered part of the deciduous forest formation in a broad sense. Talign is assigned on the basis of its savanna-like structure; floristically it is not very different from boreal forest. P = prairie.

#### Full-Glacial (Fig. 2).

Of utmost importance to the student of animal and insect distributions is the extent of Full-glacial biotic displacement. Following Flint we may date this period as ending roughly 17,000 years ago. In New Mexico the San Augustin Plains, 7,000 feet in elevation, were occupied by forest with a spruce pollen frequency of 20% (Clisby and Sears, 1956). In Postglacial time the spruce has disappeared and non-arboreal species have become more important.

In eastern North America there are only two radiocarbon-dated pollen diagrams that may represent pollen sedimentation of the Full-glacial period. From a peatland in unglaciated Pennsylvania the peat in non-arboreal pollen lies 80 cm below a radiocarbon date of 13,500 B. P. (Martin, 1958a). Apparently the formation of

Pennsylvania predominant swale remains 50 miles beyond the ice margin dates from the Full-glacial period and coincides with a tundra-tunga vegetation of spruce, birch, other non-arboreal species, and scattered spruce and jack pine.

A longer late Pleistocene pollen sequence, perhaps extending back into the middle Pleistocene, has been found in the Carolina Bay lakes (Frey, 1951, 1953, 1955). Possibly retreating and truncation have occurred (Wells and Boyce, 1953; Frey, 1955). If the upper 10 feet of Frey's sequence is continuous, his zones M1, M2, and M3 should correspond to the Full-glacial period. In these pollen zones oak and other deciduous trees are scarce or absent; pine predominates with a high frequency of small-sized grains suggesting *Pinus banksiana*. There is a low but constant frequency of spruce. In terms of structure, the M zones indicate boreal, needle-leaved forest, with dominance of jack pine attributable to its well-known preference for sandy situations.

The local records of spruce pollen in Texas, Florida, and Louisiana are undated and, except for Potzger and Tharp's work (1947, 1954), unaccompanied by detailed stratigraphic study. If maximum displacement is represented, the difference between Full-glacial and present southern limits of marginal spruce populations would seem to be the same as the corresponding past and present southern limits of the boreal forest formation, that is, 800 miles.

Some type of mixed deciduous forest occupied the extreme south, with subtropical vegetation largely driven from Florida. Further discussion of Florida awaits expansion of the pollen studies begun by Wilson (Davis, 1946).

Certain periglacial land forms including boulder fields, colluvial soil mantles, and various types of patterned ground constitute reasonably secure evidence of climatic change. Others, such as loess, are apparently less reliable indicators of ice-margin conditions (Hack, 1953; Dylik, 1954). Uncritical identification of all "periglacial" features with a Full- or Late-glacial tundra climate is to be avoided. A few of these features can form at midlatitudes today. Yehle (1954) described soil tongues similar to periglacial frost cracks appearing in calcareous soils under the present climate. Goodlett (1954) reported patterned ground in miniature appearing on bare earth in central Pennsylvania. Recent colluvial creep and earthflows

in the unglaciated Appalachian Plateaus "... appear to be most common in pastures, but field and woodland areas are not entirely free from such movements" (Sharpe and Dorsch, 1942).

Wolfe's description (1953) of frost-thaw basins and related periglacial features in unglaciated New Jersey has been subjected to certain criticism. Yehle (1954) questioned the authenticity of the alleged frost cracks. Rasmussen (1953) and Devey (1957) noted that basins of rather similar appearance occur in the Carolinas and coastal Texas, beyond the limit of possible periglacial frost action. However, the involutions and ventifacts which Wolfe described would appear to remain sound evidence of a periglacial tundra climate.

Farther south, in the latitude of Washington, D.C., Hack (1955) and Nikiforoff (1955) found little geomorphological indication of a "periglacial climate," beyond stabilized dunes and a soil hardpan of uncertain origin. For this reason, I have included this area within the Boreal Forest (Fig. 3).

In the Appalachians the block fields or stone streams (Frost 1957) and glades including "bear wallows" may mark the lower limit of Full-glacial alpine tundra (Braun, 1955; Martin, 1958a). Cranberry Glades in West Virginia at 3,350 feet (Darlington, 1943) is perhaps the best known of the anomalous glade bogs; Core (1949) discussed others. In the Smoky Mountains inactive block fields covered with mosses and ferns and occasional yellow birch trees extend down to at least 4,500 feet. Braun (1955, p. 361) believed that they indicate a vertical tree line depression of 2,000 feet. It seems the present regional tree line does not lie at the top of the peaks as Braun implies. Spruce and fir grow as far as 6,500 feet, the top of the Smokies (Whittaker, 1956). I would allow an additional 2,000 feet for subalpine taiga and "Krumholz" and locate the theoretical present alpine zone at 8,500 feet. This would bring the relative depression of the Alpine Zone in eastern North America into line with that observed at the same latitude in the west, 4,000 to 4,500 feet (Antevy, 1954). In either case the distribution of glade bogs and inactive block fields reveals that a Full-glacial tundra zone extended down into the Great Smokies.

To the south of the region of a periglacial treeless zone we might expect buried organic soils, fossilized "straw bogs," or organic terraces of the type that typifies subarctic taiga and boreal forest (Drury,



1956). Drury (pp. 86-87) believed that fossil peat and muck deposits resembling those of Alaska are absent from the unglaciated east. It would appear, however, that serious search for ancient boreal forest landforms has not been made in the latitude formerly occupied by this vegetation type (Fig. 2). The famous buried soil of Spartanburg, South Carolina (Cain, 1944), might possibly represent such a

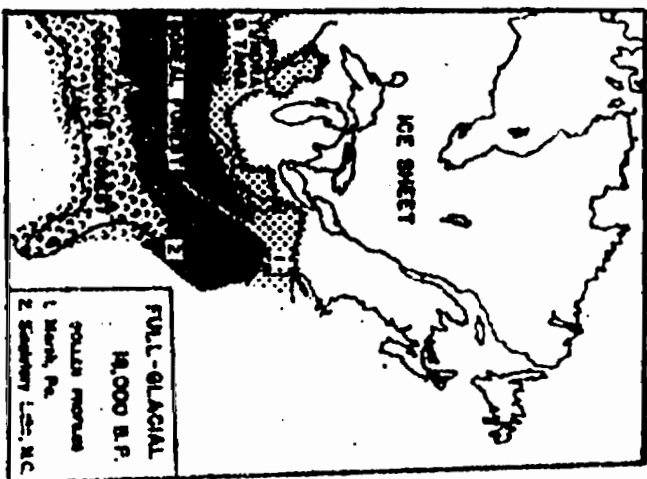


Fig. 2. Vegetation zones during the Full-glacial of the late Wisconsin. Tundra and taiga are mapped as a single zone with no attempt to distinguish them. Shelf exposure following sea level depression permitted some extension of vegetation beyond the present coast line.

feature, lying at the southern margin of the Full-glacial boreal forest. In addition to some hickory and oak these soils contain high percentage of spruce, jack pine, and fir pollen.<sup>1</sup>

Vertebrate fossils may provide some independent support to the existence of a narrow Full-glacial tundra zone. While uncritical acceptance of large mammals as climatic indicators is to be avoided,

<sup>1</sup> D. R. Whitford (personal communication) is greatly skeptical of pollen from these soils and thinks that they are more likely full-glacial than Full-glacial. He reports finding less spruce and fir than Cain (1944) encountered.

the fossil distribution of *Oribos* (see map of Kitts, 1953) fits the Full-glacial tundra zone fairly well. The barren ground caribou, *Rangifer arcticus*, is reported from late Pleistocene deposits and its Full-glacial range should be roughly similar to that of *Oribos*. Apparently the Postglacial distribution of these species has been so modified by both prehistoric and modern man that their value as tundra indicators is uncertain.

Rather than in eastern North America, the main Full-glacial refugia for tundra mammals and birds (Rand, 1948) lay in unglaciated Alaska. The tundra lemmings, *Dicrostonyx* and *Lemmus*, have not been found as fossils south of the ice sheet. The present range of the Peary Caribou, *Rangifer arcticus pearyi*, in northern Greenland and Ellesmere Land dramatizes the ability of caribou to survive at high latitudes under existing glacial conditions. It is barely possible that cycloaic nourishment of the Laurentian ice sheet in central Canada was accompanied by very low precipitation and sufficient ablation to expose the northern part of Greenland and the Arctic Islands. Mercer (1956) indicates ice of uncertain depth, but evidently not very thick, on Baffin Island in the glacial period. The evidence that Banks Island was largely unglaciated (Manning, 1952) adds support to the concept of local, restricted glacial activity in the Arctic during the Full-glacial of the Wisconsin, and of earlier periods.

The poverty of mammalian biotypes in the tundra of north-eastern Canada compared with northwestern Canada and Alaska is noteworthy. Tundra species of the northwest include *Sorex tundricus*, *Citellus undulatus dorreri*, *Clathromomys rutilus*, *Microtus oeconomus*, and *M. micrus*. These lack vicariants in eastern Canada. A faunal parallel to Hulten's *Beringia refugium* for the Arctic flora seems obvious.

### Late-Glacial (Fig. 3)

It is sobering to recall that pollen evidence of a North American tundra dates back no farther than Ixervey's study of Arrostock County in northern Maine (1951). Since then, Livingstone and Livingstone (1958) have confirmed Dewey's tentative recognition of an Allerød type sequence (not by a radiocarbon date of basal organic material), have shown that it was indeed contemporaneous with the Lower Dryas of the Upper period in Europe. The subsequent history of the known tundra, presumably involving

rapidly into central Canada during the Post-glacial period, remains a mystery.

Although they document changes in forest composition, Potzger and Courtemanche's Quebec profiles (1956) fail to throw much light on this problem. How was the glaciated portion of the Arctic re-

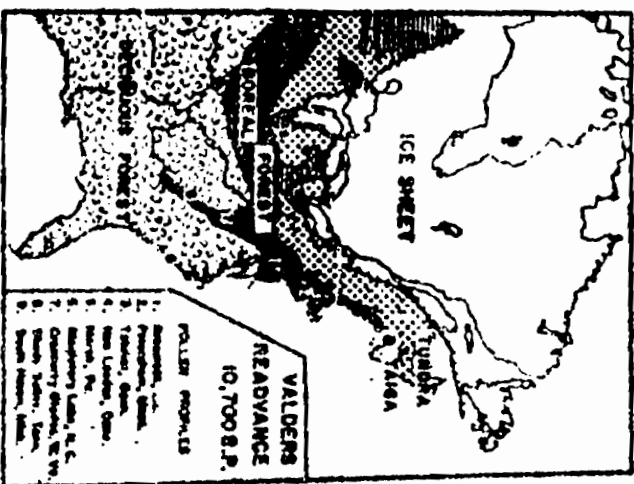


Fig. 3. Vegetation zones during the Valdian readvance. Tundra and taiga are not distinguished; the tundra may have been absent west of the Appalachians. Gills Lake, Nova Scotia, within the tundra-taiga zone at this time (Livingstone and Livingstone, 1958), is not shown. Horizontal ruling marks Lake Agassiz and the proglacial Great Lakes. East of Michigan the position of the Valdian drift border is uncertain. P = prairie.

populated? For the present it may be wise to avoid the issue, noting simply that it is unnecessary to assume a direct continuity of tundra from mid-latitudes to high latitudes. If the last ice to stagnate and melt was the Laurentian sheet, it may have "trapped" the retreating late-glacial tundra in southern Quebec during deglaciation of northern Quebec, and permitted tundra plants to invade north-eastern Ontario from the partly unglaciated North Appalachians. In western United States the late-glacial, from 17,000 to 10,200

B.P., represented a period of stagnation and retreat, with several climatic reversals and readvances of ice. Pollen records are still scattered, and dated diagrams are not as abundant as we might wish. However, they begin to approach in detail those available for Postglacial time. The stratigraphic break between the Postglacial and Late-glacial, which generally marks a rise in organic sedimentation, is a convenient level for a radiocarbon date. Partly for this reason, I have found it possible to assemble sufficient dated pollen horizons to attempt a vegetation map for the end of the Late-glacial during the Valdres readvance. Even though ice returned to central Michigan, considerable climatic improvement is indicated over the Full-glacial conditions. In northern New England Devey's discovery of Valdres tundra is confirmed by Livingstone (see Table I). C<sup>14</sup> dating of pollen zone A-4 in Connecticut indicates the presence of boreal forest rather than taiga or tundra. The Valdres readvance did not affect radically the forests of southern New England.

Mixed hardwoods and conifers, including spruce, occupied Glade Bog (2,700 feet) in Tennessee (Johnson, personal correspondence). Pine-spruce-birch-hemlock dominated the Cranberry Glades of West Virginia (3,400 feet). Alpine tundra had retreated or perhaps entirely disappeared from the southern Appalachians. Small ice fields, almost certainly surrounded by tundra, excavated circs in the Catskills, Adirondacks, and other high mountains of New England (Manley, 1955). Perhaps of greatest interest is the evidence from pollen studies that mixed deciduous forest had replaced the pine-spruce forest of the Carolina Coastal Plain (Frey, 1953). The Valdres forests of that area supported mesophytes such as beech and hemlock, temperate species no longer part of the regional pollen rain.

West of the Appalachians the situation is less clear. Andersen (1954) considered a typical Late-glacial profile from the George Reserve in southern Michigan to be of Younger Dryas age (Valders as currently understood in North America). However, if the C<sup>14</sup> dates from the George Reserve (M-223, M-224, each  $11,450 \pm 600$  B.P.) are from the same core as was used in Andersen's study, his NAP zone is older. Possibly it represents the Older Dryas (Port Huron) period. Andersen presented a thoughtful and skilled analysis of the problem of "rebedded" and "redeposited" pollen in Late-glacial sediments and made a strong case for allochthonous origin of such temperate genera as oak, sweet gum, and ash. The regional pollen

TABLE 1. Pollen Zones Apparently of Valdres Age

| <i>Locality and Core</i>               | <i>Pollen Zone and Depth</i> | <i>Pollen-Flora</i>         | <i>Radiocarbon Age</i>                  | <i>Reference</i>  |
|--|------------------------------|-----------------------------|---|---|
| 1. Aroostook Co., Me., Alder Lake      | L-3, 700-775 cm.             | Birch-pine-spruce-NAP       | None                                    | Deevey, 1951  |
| 1a. Richmond Co., N.S., Gillis Lake    | L-3, 475-500 cm.             | Birch-pine-alders-NAP       | 50 cm. below<br>10,340±220              | Livingstone and Livingstone, 1958                       |
| 2. Yeterham, Mass., Tom Swamp          | A-4, 850-990 cm.             | Spruce-pine-birch           | None                                    | Davis, 1957   |
| 3. Middletown, Conn., Durham Meadows   | A-4, 200-230 cm.             | Spruce-pine-fir             | ca. 30 cm. below<br>8,155±410           | Leopold, 1956; also Barendsen <i>et al.</i> , 1957      |
| 4. New London, Conn.                   | A-4                          | Upper part of Durham spruce | Y-447c, 10,480±140                      | Beetham in Barendsen <i>et al.</i> , 1957               |
| 5. Chester Co., Pa., Marsh 1           | B, 59-69 cm.                 | Pine                        | None                                    | Martin, 1958a   |
| 6. Singletary Lake, N.C., Si-25        | Ca, 12ft. 3 in.-13 ft. 3 in. | Oak-pine-hickory            | C-474, 10,224±510                       | Frey, 1951, 1953  |
| 7. Cranberry Glades, W. Va., 3,400 ft. | 13 ft. 6 in.                 | Fir-spruce-birch-hemlock    | 1 ft. below C-336,<br>9,434±840         | Darlington, 1943  |
| 8. Shady Valley, Tenn., 2,800 ft.      | B, 6¼ ft.                    | Pine-oak-spruce             | 1 ft. below Y-287,<br>9,500±150         | Barclay (pers. corres.), Barendsen <i>et al.</i> , 1957 |
| 9. South Haven, Mich.                  | 107 in.                      | Spruce                      | M-288a, 11,200±600<br>W-167, 10,860±350 | Zumberge and Potzger, 1956                              |

\* All localities except Gillis Lake, Nova Scotia, are shown on Fig. 3.

rain represented in the George Reserve clay is predominantly of spruce, various sedges, and grasses. With an NAP pollen sum not exceeding 40%, it appears that the vegetation may have been a taiga rather than a treeless tundra. For my immediate purpose, which is to map vegetation zones during the Valdres maximum, it seems best to withhold judgment on the age equivalent of Andersen's profile. It does tell us that there was a taiga-tundra period during deglaciation of Michigan.

Pollen studies of Potzger (Zumberge and Potzger, 1956) reveal Postglacial events in the Michigan basin and interrelate shifts in vegetation with changes in lake levels. Potzger failed to encounter any indication of tundra or taiga conditions during the period that he felt should have represented the Valdres readvance. In this regard his results agree with those of Davis, Leopold, and others in southern New England. Unfortunately, confidence in Potzger's sequence is considerably undermined by his consistent failure to recognize such pollen zones in any of his numerous studies throughout eastern North America. His rock-flour samples from the inorganic sediments underlying lake gyttja from Hartford Bog indicated no appreciable NAP pollen sum. Elsewhere in both Europe and America inorganic sediments of Late-glacial age generally mark zones of abundant herb pollen, such as Andersen encountered at the George Reserve. Unless Potzger's results are confirmed, I assume that the rock-flour levels in Hartford Bog record a tundra or taiga phase in the vegetational history of southern Michigan.

The inconclusive results of both Andersen and Potzger provide poor material for attempting to locate formation boundaries during the Valdres readvance. In extending the zone of taiga-tundra on Fig. 3 south through southern Michigan I have assumed that the proglacial Great Lakes reinforced the periglacial climatic influence of the Valdres ice sheet producing a poor environment for growth of forest. This judgment may be only slightly less arbitrary than my location of the boundaries of boreal forest and temperate deciduous forest in this region. West of the Appalachians there is no paleo-ecological record definitely of Valdres age to assist in locating these zones.

#### Postglacial

Beyond refinements in chronology and mounting evidence of a very close correspondence between climatic events in the New and

Old World (Deevey and Flint, 1957), little has been added to the Postglacial pollen sequence summarized by Deevey in 1949. The Hypsithermal, also known as Thermal Maximum, Xerothermic, Alithermal, etc., extended with intermittent pulsations from 9,500 to 2,000 years ago (Deevey and Flint, 1957). It is the most important climatic event of the period. Documentation of the classic Midwest Prairie Peninsula extension continues with Smith's recent valuable analysis of terrestrial vertebrates (1957). In addition to mapping relict outposts of prairie animals, Smith showed that it is possible to interpret anomalous and otherwise confusing splits in subspecific populations in terms of post-Xerothermic isolation. Instructive examples are found in *Aegistron concoloris* (copperhead), *Natrix erythrogaster* (copper-bellied water snake), *Diadophis punctatus*, and *Ophedrys vernalis*. In a bold and original interpretation Smith explained the history of the *Pseudacris nigrita* (chorus frog) complex in terms of invasion of *P. n. seriarum*, the eastern, forest-inhabiting race, by *P. n. triseriata*, a grasslands form from the west. Post-Xerothermic isolation left a segment of *P. n. triseriata*, recently described as *P. n. kalni*, in New Jersey and the Delmarva Peninsula. Thus on both sides of the Appalachians separate, isolated, populations of *triseriata* type chorus frogs integrate with *seriarum*.

Postglacial pollen diagrams indicate Thermal Maximum (C-2 pollen zone) shifts in species composition, with an increase in oak and hickory in southern New England and, locally, of hemlock in northern New England. In many diagrams a recovery of spruce follows in C-3. During the Thermal Maximum Whittaker (1956, p. 60) believed that spruce and fir were pinched off the tops of certain mountains in the Smokies. Displacement upward of 1,000 feet or more is indicated by absence of these trees in presumably suitable sites on peaks of less than 5,500 feet elevation.

Thermal Maximum changes, which command attention of the student of community composition, the evolutionist, and the biogeographer, were inappreciable in terms of the plant formations mapped in Fig. 1. They do not justify an attempt at a separate vegetation map.

#### Western United States, Mexico, and the Tropics

Exclusion from Figs. 1-3 does not imply that these areas escaped considerable late Pleistocene climatic and environmental change. For the present, however, it seems impossible to express this effect

tively on a Pleistocene vegetation map, unless one relies largely on biogeographic data as Dillon (1956) has done. Topographic complexity inevitably leads to considerable difficulties in large-scale mapping of vegetation. Twelve major units on Leopold's very useful vegetation map of Mexico (1950) suggest something of the problem.

Paleobotanical study of the Willow Creek flora of Santa Cruz Island, California, revealed a latitudinal shift in *Pseudotsuga*, *Cupressus*, and *Pinus* of perhaps 440 miles, less than the 800 miles of zonal displacement in eastern North America (Chaney and Mason, 1934). Studies of late Pleistocene fossil birds indicate an even less drastic shift. "The avifaunas of the Carpinteria asphalt and of some of the Pleistocene caves of northern and central California (Miller, 1937, 1939) indicate that the boreal avifauna extended 200 miles farther south along the coast, at least, and 1,000 feet lower on the interior mountains. Possibly even more extreme extensions occurred in other parts of the Pleistocene" (Miller, 1951, p. 610). The latter comment is crucial; either the Carpinteria and other Pleistocene cave faunas are not of Full-glacial age or the avifaunal displacement is discordant with that represented by the Willow-Creek flora. Actually, neither deposit may represent maximum displacement of the coldest period.

The same logic can be directed toward the RanchoLabrean biota of the famous tar pits. While the living representatives of this assemblage typify environments subequal to those found today in the Los Angeles basin (summary in Schultz, 1938), the spectacular finds of extinct animals stamp the assemblage as late Pleistocene. In the absence of C<sup>14</sup> dating or other absolute age estimate, it is futile to urge any bioclimatic theory relating the RanchoLabrean biota to Pleistocene chronology. However, one suspects that certain biogeographers have assumed that the fauna is of Full-glacial age and that it proves lack of climatic change at this latitude. Assumptions about the cause of large-mammal extinction in this biota, as in others, may be intertwined with climatic inference. In view of the results of isotope dating of similar late Pleistocene faunas, it seems we may anticipate an age postdating the Wisconsin maximum for the RanchoLabrean fauna.

Except for Clisby and Sears' work in New Mexico, late Pleistocene pollen studies have been confined to the Pacific Northwest and



Alaska (Hansen, 1947, 1953; Hesse, 1953, 1955). They have developed a sequence that parallels the Postglacial pollen zones of eastern North America. Hansen (1947) found a rise in grass-chenopod-composite pollen in south central Oregon in the Thermal Maximum. Apparently, grassland habitats replaced forest along the prairie-woodland border. Elsewhere in the west, archaeological cave sites and pluvial lake beds of the Great Basin promise much to the pollen analyst. Radiocarbon dating of lake sediments may be the most profitable means of correlating pluvial and glacial events, and radiocarbon dates of Searles Lake in southern California confirm a direct relationship between Great Basin pluvial lakes and the classic Wisconsin sequence (Flint, 1957, p. 232). To the ornithologist this should signify abundant and highly productive aquatic environments at a time when glacial ice covered most of the present breeding grounds of waterfowl and scolopacid shore birds.

An original analysis was made by Antevy (1954) of zonal displacement in New Mexico during the Wisconsin. Snowline depression, the hydrography of pluvial Lake Estancia, and the former distribution of *Myrmica* indicate a lowering of life zones in New Mexico on the order of 4,000 to 4,500 feet. The yellow-bellied marmot is reported from Basket-maker burials at 7,000 feet in northeastern Arizona (Lange, 1956). This, and its distribution in grassland of Utah at 4,500 feet, make it a less reliable Pleistocene thermometer than Antevy (1954), Stearns (1942), and Murray (1957) have assumed. Nevertheless, the vertical displacement of snowline and, apparently, of treeline (Martin, 1958b) seems to require a major shift in montane vegetation gradients.

Spruce (*Picea*) should be an ideal indicator of temperature change in the Southwest and should afford some biological control on the geological evidence of climatic change. Clisby and Sears' pollen study of the San Augustin plains (1956) indicated Full-glacial spread of spruce through central New Mexico at 7,000 feet, with a maximum frequency of 40%, sometime before 27,000 B.P. During the Pleistocene, almost certainly in the Wisconsin, spruce reached the Valley of Mexico (Sears *et al.*, 1955). To enter the Mexican Plateau, spruce, and any associated boreal animals and plants, had to descend to lower elevation. The lowest point on the Continental Divide between the Rockies and the Sierra Madre lies at about 4,500 feet in southern New Mexico. In the adjacent Chiricahua Mountains spruce

is found today in narrow, northerly ravines at 8,500 feet. These outposts are in extremely favorable microhabitats, and vertical displacement from a sheltered north slope at 8,500 feet to a level site at 4,500 feet would require climatic change of greater magnitude than the temperature depression encountered between these points (average lapse rate of 0.6° C per 100 meters or a total drop of 7.2° C.)

Myrtosiously, spruce disappeared south of Chihuahua, Mexico, in Postglacial time. Subalpine conifers immediately below treeline at 10,000 to 12,000 feet in the transverse volcanic belt of the Mexican Plateau include *Pinus hartwegii*, *Abies*, and *Cupressus*. Superficially, these boreal montane forests appear quite suitable for *Picea*, and more than one biologist has referred to them casually as "spruce-fir."

The best record on climatic change in Mexico comes from the sedimentary studies of Sears *et al.* (1955) and Hutchinson *et al.* (1956). They demonstrate important climatic fluctuations. However, the correlation of moist climatic intervals in Mexico with Cordilleran glacial advances (i.e., Flint, 1957, p. 233) is considerably less secure than Glacio-pluvial correlations in western North America. Biogeographical evidence and climatological theory raise the possibility that Postglacial pluvial periods in the Mexican Plateau are *negatively correlated* with minor glacial advances at high latitudes (Martin and Harrell, 1957). In the Thermal Maximum there is no sound evidence of drought in the Plateau.

The presence of Pleistocene spruce in the Valley of Mexico, the biogeography of relict montane plant formations such as Cloud Forest (see below), glacial cirque depression on Mexican volcanoes (White, 1956), Chirripo in Costa Rica (Weyl, 1955), and other tropical mountains above 13,000 feet makes it convenient to infer climatic cooling at low latitudes during the glacial period. The presence of an extensive North American ice sheet would, however, eliminate the present high-pressure system which brings summer cyclones to Mexico and the Southwest (J. E. McDonald, personal communication) and one wonders if winter Pacific storms would be shifted sufficiently to produce truly pluvial conditions in the Valley of Mexico in the Full-glacial period. Sears *et al.* (1955, p. 525) interpreted their Mexican diagrams as climatic oscillations of moist-warm and dry-uncertain, the latter representing the Wisconsin glaciation. Within Mexico and Central America some of the strongest indi-

cations of climatic change are found in plant-animal distribution in fragmented and isolated habitats such as the Cloud Forest. Griseom (1932, 1950) noted rather remarkable uniformity from northern South America to Mexico in bird life of the Subtropical Life Zone, which includes Cloud Forest. This habitat generally appears on windward slopes between 3,000 and 7,000 feet elevation. To account for the faunal uniformity Griseom (1932) postulated Pleistocene continuity of the Subtropical Zone, the result of its depression to sea level. It displaced the lowland tropical fauna which withdrew southward.

Stuart (1951, p. 32) noted that the present range of montane lizards and other temperate animals on either side of the Isthmus of Tehuantepec (e.g., *Basiliscus* and *Sceloporus malacothrix*) indicated a past cool corridor across the arid lowlands. But Stuart questioned the displacement of lowland Tropical Rainforest, which Griseom (1950, p. 358) located far south of its present limit in the period of extreme Pleistocene glaciation. "... a descent to sea level of a subtropical zone would have brought about either widespread extermination of the tropical fauna or acclimatization of that fauna to subtropical conditions. . . . The evidence, therefore, points to the presence of a [lowland] tropical environment in northern Central America even at the height of Pleistocene glaciation" (Stuart, 1951, p. 29). It seems we must have the argument both ways, altitudinal depression of subtropical conditions to achieve some continuity of Cloud Forest through Middle America from Mexico to Colombia, but with persistence as far north as Mexico of Arid-Tropical scrub and Tropical Rainforest. Actually, 3,000 feet may be too rigid a lower altitudinal limit for marginal populations of Cloud Forest species. Under extremely humid conditions subtropical animals may descend to 2,000 or 1,000 feet (Wetmore, 1943, p. 223).

The nature of Cloud Forest vegetation, avifauna, and biogeography in tropical America is under study by B. E. Harrell (1951). Marshall's exemplary analysis (1957) of Mexican oak-pine woodland also illustrates the biogeographic advantage of studying environmental rather than political units.

A brief summary of environmental changes in western North America and Central America during the late Pleistocene would include the following points: (1) direct correlation between glacial conditions in the Cordilleras and the growth of pluvial lakes in the

Great Basin; (2) coincidence of the Thermal Maximum in eastern and western North America; (3) very doubtful correlation of Glaciopluvial conditions in the subtropical latitudes and a negative correlation, controlled by summer cyclones, in Post-glacial time; (4) 4,000 to 4,500 feet displacement of biotic zones in the Southwest during the Full-glacial period; (5) displacement of tropical zones by perhaps 3,000 feet in the Pleistocene, exact time unknown, but possibly during the Glacial maximum.

#### EARLY MAN IN THE NEW WORLD

The foregoing cursory analysis of late Pleistocene environments is intended to clear the ground for a brief review of two events that stand foremost in Pleistocene ecology and paleontology. The importance of these events to students of modern biogeography is not immediately obvious and is often ignored. However, both the arrival of prehistoric man and the extinction of late Pleistocene animals pose major biogeographic, as well as paleontological, problems.

Man's arrival in the New World is a matter of continuing controversy. Fluted points, once associated mainly with early man in western North America, are appearing in many parts of the east. They confirm much older evidence of early man, evidence discounted during the Hrdlicka period of skepticism regarding Pleistocene man in the New World. The Schoop site in Pennsylvania (Wittke, 1952), the Quesd site in Alabama (Sodley, 1954), fluted points in Michigan (Quimby, 1958), in North Carolina, and an apparent late-glacial flint industry in the Manitoulin Islands (Lee, 1957), point to the presence of early man in Late-glacial as well as early Postglacial time in the eastern United States. Quimby (1958) related the geochronology of the Lake Michigan basin to archaeological discoveries and infers an association of spruce-fir forest, mastodons, and fluted points from about 10,000 to 7,500 B.C. Williams (1957) extended the latter to a more recent date, indicating no obligate relationship between mastodons and spruce-fir.

The biologist who may wish to review the impressive archaeological record of early man will profit by consulting Wornington's excellent book (1957) and Sellards' equally readable account (1952). Early man is not invariably associated with fluted points; the old desert cultures such as those at Danger Cave in Utah (Cummings, 1957) and at Frightful Cave in Coahuila (Taylor, 1956) represent

hunting-gathering people who did not prey on large animals. Fluted points may be an independent New World invention; they have not been found with paleolithic sites in Siberia (Wormington, 1957).

In South America early man had arrived at least by early Post-glacial time as is demonstrated by the well-known association of man and sloth at Pelli Aiki Cave, Chile. Cruent and Rouse (1956) and Rouse and Cruent (1957) report Paleo-Indian sites in northern Venezuela.

From the biological viewpoint it does not seem necessary to enter the Interglacial man controversy. If the Tule Spring site, Nevada, is correctly dated at older than 23,800 years, it clearly indicates that prehistoric man arrived before the Wisconsin maximum of 17,000 years ago. Presumably this would require arrival in Alaska, at least by early post-Sangamon time, of a people whose economy was specialized for hunting large animals in treeless tundra. It seems easier to establish a trans-Bering population in southern Alaska than to understand how, during the Wisconsin glacial period, such a population spread south through what is mapped as glaciated terrain.

For the ecologist and biogeographer one point remains clear. From the time of man's arrival we may assume a radical change in fire frequency. In the strict sense, theoretical climatic climax vegetation in savanna and grassland areas (Stewart, 1951, p. 319), and even in parts of the Eastern Deciduous Forest, cannot postdate man's arrival. In addition to savannas many areas of temperate forest may have been greatly modified and subclimax, consolidation, or even pioneer species favored at the expense of those typical only of climax positions in plant succession. The paleoecological dilemma posed by the B zone pine pollen period (Dansereau, 1953) may be resolved in terms of an *archaeological disclimax* controlled by early man. There is no longer much doubt about his presence in the East at that time.

#### LATE PLEISTOCENE EXTINCTION

In the words of Darwin: "It is impossible to reflect on the changed state of the American continent without the deepest astonishment. Formerly it must have swarmed with great monsters; now we find mere pygmies, compared with the antediluvian allied races." (*Voyage of the Beagle*, 1855, p. 222). In the hundred years since Darwin wrote

discoveries in both prehistory and paleontology have enriched considerably our knowledge of late Pleistocene fauna. Radiocarbon dates (Fig. 4, Table II) confirm the fact, evident to Darwin and Lyell, that extinction was mainly a Postglacial event. South of Alaska there is abundant proof that the time of maximum glaciation preceded most New World extinction.

Despite these refinements, the extinction of large mammals in continental North and South America and of small mammals in the West Indies has been a major unsolved problem, one certainly not inappropriate in a symposium dedicated to such matters. Until the cause or causes of extinction are understood, biogeographic and ecological interpretations based on the assumption that all fossil mammalian records are of paleoclimatic significance may be overly bold, if not entirely erroneous. Specifically, I would question paleoclimatic deductions based on fossil records of *Marmota* and *Cervus* in northeastern Mexico, *Erethizon* (porcupine) and *Hydrachobius* (capybara) in the Melbourne beds of Florida, "musk-ox-like" genera in New Mexico and Mexico, and *Tapirus* in Arizona (Haury *et al.*, 1950) and Pennsylvania. Strict application of the uniformitarian doctrine is to be avoided in each case; no responsible ecologist would insist that modern tapir habitat, Tropical Rainforest and Cloud Forest, extended into southern Arizona or eastern Pennsylvania in the late Pleistocene.

As Darwin stressed in *The Origin of Species*, extinction is the inevitable consequence of evolution and in itself will occasion no surprise. Through the Cenozoic equid genera disappear; *Hyracotherium* and others in the Eocene; *Mesohippus* in the Oligocene; *Miohippus*, *Parahippus*, and others in the Miocene; *Galhippus*, *Hippotion*, etc., in the Pliocene; and *Nannhippus* and *Pleistippus* in the early Pleistocene. They represent a record of replacement by morphologically modified and adaptively improved types of horses. In the late Pleistocene the extinction of North American *Egus* and South American *Egus* and *Hippidium* is not an equivalent event for it constitutes extinction without replacement. For perhaps 3,000 to 6,000 years in the Americas the horse was absent. Following post-Columbian reintroduction, feral horses recolonized grassland habitats with unsmearing haste. Darwin (1855, p. 299) reported that they spread from Buenos Aires to the Straits of Magellan, 1,300 miles, in 43 years.

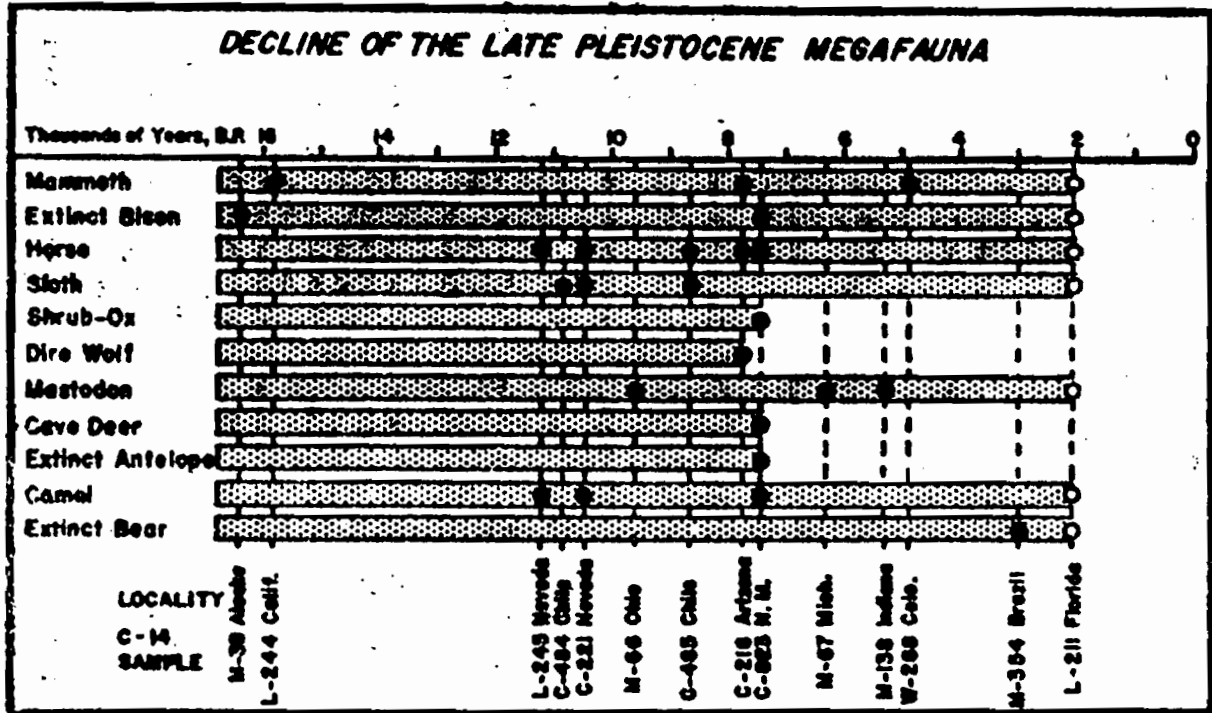


Fig. 4. Decline of the late Pleistocene megafauna in the New World. Age of last appearance for various large mammals is based on radiocarbon dating (see Table II). If the Florida date (L-211) is correct, it reveals survival of many mammals in the southeast beyond their time of extinction in western North America. Common names of the animals are not intended to be specific and more than one genus may be included.

TABLE II. Radiocarbon Dates Associated with the Extinct Late Pleistocene Fauna in America<sup>a</sup>

| Sample          | Location                  | Fauna                        | Comment   | Year, B.P.                                |
|-----------------|---------------------------|------------------------------|---|---|
| 1. L-300 R      | Santa Rosa Is., Calif.    | Dwarf mammoth                | Charred bone  | 29,700 ± 3000                             |
| 2. C-916        | Tule Springs, Nev.        | Bison skull, mammoth, carnel | Ancient occupation site, later flooded                          | > 23,800                                  |
| 3. M-38         | Fairbanks area, Alaska    | Bison cranial cavity         | Horn sheaths from gold-bearing gravels                          | 16,400 ± 2000                             |
| 4. L-244        | Santa Rosa Is., Calif.    | Dwarf mammoth                | Wood from base of mammoth-bearing alluvium                      | 15,820 ± 280                              |
| 5. C-301        | Fairbanks Creek, Alaska   | "Extinct mammal bones"       | Wood from 30- to 60-ft. depth                                   | 12,622 ± 750                              |
| 6. L-245        | Winnamucca Lake, Nev.     | Horse, carnel                | Lowest occupation in Flab-been Cave                             | 11,200 ± 250                              |
| 7. C-484        | Mythodan Cave, Ohio       | Myxodon                      | Dated shaft dung, no artifacts                                  | 10,800 ± 570                              |
| 8. C-221        | Grypana Cave, Nev.        | Neotrochilum albertense      | Dated shaft dung  | 10,864 ± 720<br>10,902 ± 440              |
| 9. L-231        | Suzette Co., N. J.        | Mastodon                     | Past associated with remains                                    | 10,075 ± 550<br>10,990 ± 200              |
| 10. L-197 G     | Severn-Pearlville, Alaska | —                            | Organic material  | 10,200 ± 800                              |
| 11. L-983       | Phulevian, Texas          | Bison, Panther               | Small shaft from bone bed with Panther                          | 9,400 ± 750<br>9,800 ± 500                |
| 12. W-223       | Picograph dale, S.D.      | Musk-ox (Ovibos)             | Dogon partly laminated with charcoal                            | 9,700 ± 600                               |
| 13. M-282       | Lemare Co., Mich.         | Mastodon                     | Wood laminated above a track                                    | 9,568 ± 1000                              |
| 14. A-9<br>A-10 | Nico, Corbale Co., Ariz.  | Meomastus columbi            | Charcoal in clay matrix around bones                            | 9,350 ± 300                               |
| 15. M-46        | Otteva Farms, Ohio        | Mastodon                     | Wood from laminae under skeleton; two dates are of black carbon | 3,470 ± 400<br>2,460 ± 400<br>9,600 ± 500 |
| 16. C-485       | 2311 Alton Cave, Ohio     | South horse, guanaco         | Buried bones with artifacts                                     | 8,000 ± 450                               |





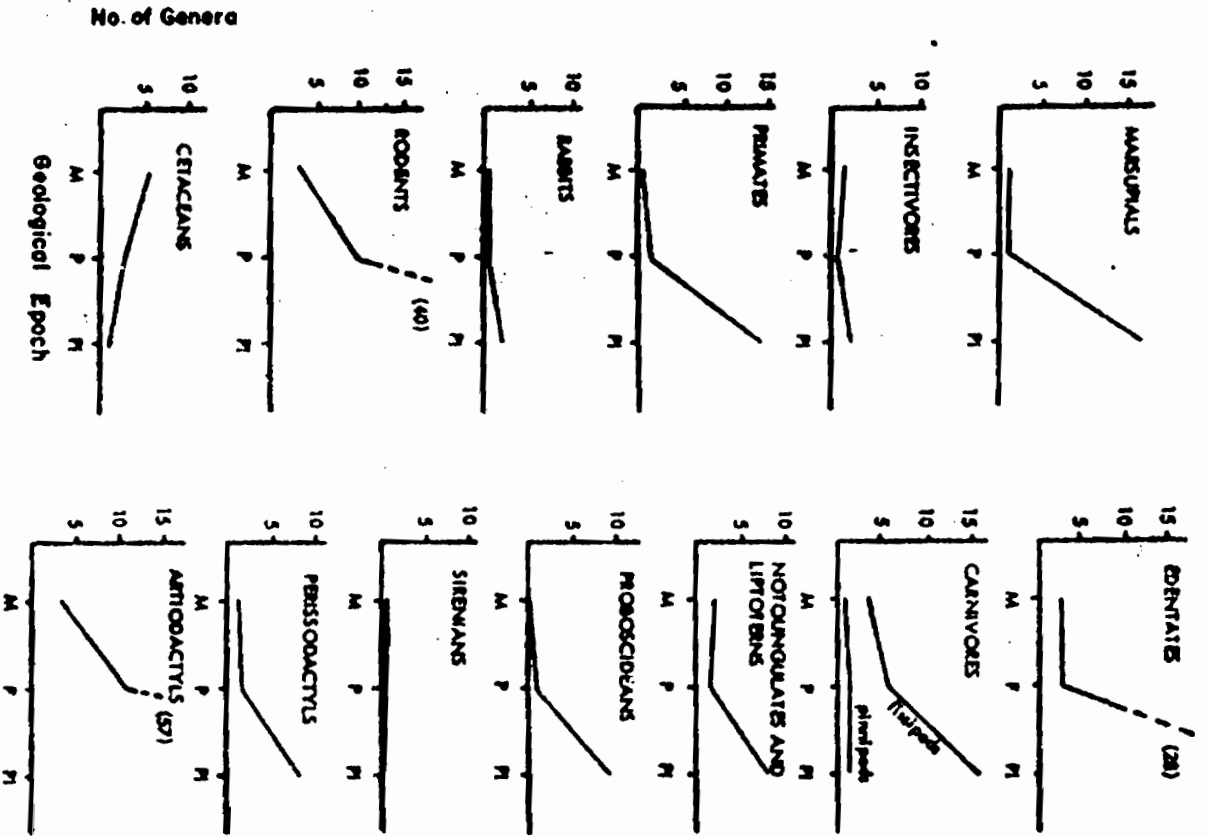


Fig. 5. Caption on facing page.

Before proceeding directly into a consideration of possible causes, it appears essential to examine the nature of late Pleistocene extinction more closely [cf. Simpson (1953) for a general treatment of phyletic extinction]. If it is no different from that of the early Pleistocene or Tertiary there is little point in proceeding farther.

#### Extinction without Replacement

In addition to *Equus*, cited above, the following North American genera, representing specific ecological life forms with respectable Tertiary lineages, disappeared in the late Pleistocene or sub-Recent time: the elephants and mastodons *Mammuthus* and *Mammot*, the camels *Tamias* and *Camelops*, the Old World antelope *Saiga*, the cervid deer *Sanguinaria*, and *Cervulus*, the shrub-oxen *Symbos*, *Euceratherium*, and *Prepioceros*, the pronghorns *Brametys* and *Steckoceros*, the giant beaver *Castoroides*, and others. They reflect abandonment of grazing and browsing habitats by roughly three-quarters of the mammalian herbivore fauna. In the West Indies four genera of ground sloths and sixteen of hystriocomorph rodents, also herbivores, disappeared in sub-Recent time.

The general rule that abandonment of life forms and the disappearance of genera or subfamilies without replacement occurred only in the late Pleistocene may have a single minor exception. *Borophagus*, a New World equivalent of the hyaenid life form, is unknown beyond the First Interglacial (Hibbard in Flint, 1957, p. 462). However, at no time since the extermination of the Upper Cretaceous duck-bills and other herbivorous dinosaurs has there been unbalanced extinction of equal magnitude.

Fig. 5. Generic extinction rate curves for various mammalian orders. The number of genera last recorded divided by estimated age for each epoch is shown for three Late Cenozoic epochs: M = Miocene, 17 million years; P = Pliocene, 11 million years; Pl = Pleistocene, one million years. Pleistocene extinction rates rose sharply in the primates, rodents, edentata, farnipeds, notoungulates, lipitoterns, proboscideans, perissodactyls, and artiodactyls. There was no comparable rise in extinction rates among the insectivores, rabbits, cetaceans, pinnipeds, and sirenians. Data on extinct genera were obtained from Simpson (1945); orders with poor late Cenozoic fossil records, as the bats, pangolins, and hyraxes, are not included.

#### Cenozoic Extinction Rates Rise in the Pleistocene

Extinction rates in number of genera per million years for several mammalian orders increased greatly at the end of the Cenozoic during the Pleistocene (Fig. 5). The data from Simpson (1945) represent last appearances of genera in each of twenty mammalian orders. To obtain extinction rates, one divides the number of genera last recorded in each period by the geological estimate of elapsed time, 17 million years for the Miocene, 11 for the Pliocene, and 1 for the Pleistocene.

It is obvious that only certain orders exhibit a strong Pleistocene effect. Those include the artiodactyls, proboscideans, marsupials, edentates, rodents, perissodactyls, fissipeds, and primates. Certain groups with moderately good late Cenozoic fossil records, as the cetaceans and pinnipeds, appear unaffected. The extinct Pleistocene genera of marsupials are all Australian and include large kangaroo and phalangerid herbivores. Within the primates, 8 of 14 extinct Pleistocene genera were lemur-like forms from Madagascar. Among the rodents, a rise in Pleistocene extinction rate can be attributed in part to the extinction of insular genera, 15 of them West Indian. Regarding the entire late Cenozoic record of mammals, extinction rates rise from 25 per million years in the Miocene, 40 in the Pliocene, to 203 in the Pleistocene. From this we may believe that Pleistocene extinction transcends that of the rest of the Cenozoic. Was it caused by climatic change of the Glacial periods?

#### Pleistocene Extinction Rates Rise in the Last Glacial Period

Hibbard's valuable list (1958; also in Flint, 1957) of Pleistocene mammals shows a considerable measure of extinction in the First Interglacial, the Aftonian. However, with the single exception of *Berypterus*, there is continual replacement of generic types until the Wisconsin.

Estimating the Glacial periods arbitrarily at 100,000 years each and the interglacials at 250,000 years we obtain for North America the following extinction rates, expressed as number of genera per 100,000 years: Nebraskan, 1.0; Aftonian, 6.0; Kansan, 5.0; Yarmouth, 1.2; Illinoian, 1.0; Sangamon, 0.0; Wisconsin, 31.0 (terminal records from Hibbard in Flint, 1957, with addition of Floridian Melbourne mammals). On this basis it is possible to conclude (1) that the extinction rate in the Wisconsin was considerably higher

than earlier in the Pleistocene and (2) that extinction is not related to the Glacial period or to the climatic change brought on by glaciation.

In part such figures may be an artifact of paleontological sampling. Late Pleistocene sediments, bogs, caves, and alluvium, are better preserved than older deposits exposed to a longer history of geological wear and tear. The late Pleistocene should be better known than a preceding fauna. Nevertheless, accepting the fossil record at face value, it seems that extinction was predominantly a Wisconsin phenomenon. The facts do not agree with the proposal that the rise in Pleistocene extinction rates is the result of climatic change.

#### Late Pleistocene Extinction Affected Only Large Animals

Obviously, this is not strictly true, as Eislely (1946) and Gil (1955) pointed out. On the one hand, cetaceans and pinnipeds were unaffected; on the other, small to medium-sized West Indian mammals, lizards, and birds disappeared. In tropical forests and savannas certain edentates survive, such as the anteaters and tree sloths. Their plains-dwelling relatives of subequal size, such as *Neotrotherium* and *Chalmersium*, disappeared. Moose, elk, white-tailed deer, and probably bison survived in temperate forests while, except for one species of pronghorn and the mule deer, the grasslands were stripped of large herbivores.

Nevertheless, the size relationship is crucially important. The vulnerability on most islands of relatively small animals (from the size of a Norway rat to that of a beaver) can be contrasted with that on continental areas where, aside from possible trimming of marginal populations, the extinction of such small animals did not occur at the end of the Pleistocene. I am indebted to K. C. Parkes for pointing out that, of the reasonably rich late Pleistocene passerine avifauna, there are recognized only two extinct genera, both in the family Icteridae and both cowbirds, *Pandanus* and *Pyelorkampelus* (Wetmore, 1956). It requires no great imagination to suggest that they shared a commensal table with the modern cowbird genera, *Molothrus* and *Tangaris*, and that extinction of the large herbivores reduced the variety of ecological niches for both scavenger and cowbird life forms. The extinct scavengers are more numerous and include the genera *Stragys*, *Taralornis*, *Cathartes*, *Neoglyphis*, and *Neophronopsis*.

**Extinction Marks the Boundary between the Pleistocene and Recent**

In the Rocky Mountain region Hunt (1953) reported that the disappearance of such large mammals as elephants, camels, and horses coincides with a widespread unconformity in the late Quaternary deposits. He correlated this break with the drought of the Altithermal and finds that extinction immediately predates it. While this relationship may be of geological utility in western North America, chronological detail does not bear out such a distinction between "Pleistocene" and "Recent" elsewhere on the continent. In Alaska thin gravels and clays containing remains of extinct mammals are at least of Late-glacial age or older. Organic material overlying the remains of elephant, horse, and extinct bison has been dated at  $10,200 \pm 800$  (L-137G) and  $9,400 \pm 750$  (L-137N) years B.P., (see discussion by Sigafos and Hopkins in Broecker *et al.*, 1956, pp. 156-157). Horn sheaths of *Bison crassicornis* were dated at  $16,400 \pm 2000$  (M-38).

In Mexico the Upper Becerra Peat, containing remains of the mammoth *M. imperator* is also considered as older than 10,000 B.P. (Wormington, 1957, pp. 91-99). Hibbard (1955) considered it early Wisconsin. MacNeish's important and, in large part, unpublished studies in southern Tamaulipas (1950, 1955), have revealed leaflike points associated elsewhere with the Becerra mammoths, but there is no evidence of extinct animals in his radiocarbon-dated middens, which cover the entire Post-glacial period (personal communication). Apparently extinction in both Mexico and Alaska preceded that in the Rocky Mountains.

In Florida and South America extinction postdated the Altithermal. Unquestionably this is the most controversial aspect of the extinction chronology, partly because it all but eliminates climatic change as an extinction cause. The vastly rich fauna of the Melbourne and Seminole beds of Florida was dated on archaeological and geochronological grounds by Rouse (1952) at 4,000 to 2,000 years ago. A radiocarbon date, L-2N,  $2,040 \pm 90$ , of charcoal from a newly exposed canal is "associated with extinct Seminole Field mammals, an 'archaic' spear point, flint chips, and burned bone . . . the date seems anomalously low in view of the extinct fauna" (field description; from unidentified collector in Broecker *et al.*, 1956, p. 161). The fauna of the Seminole Field includes the porcupine (spp.)

bara, dire wolf, short-faced bear, smilodon, ground sloth, glyptodonts, horses, a tapir, extinct peccaries, camels, mastodons, mammoths, and various small mammals conspecific with living species (Cooke, 1945, pp. 308-309). Forty years of scrutiny have not resolved the apparent contradiction that a rich and varied extinct savanna fauna survived here until a very late date, perhaps 4,000 to 2,000 years ago, contemporaneous with archaic man (Rouse, 1952; Heizer and Cook, 1952).

In South America an extinct mastodon, *Cuvieronius*, was found associated with pottery (Spillmann in Osborn, 1936, pp. 571-574). More recently a radiocarbon sample from Minas Gerais,  $3,000 \pm 300$  B.P. (M-354), "... should date the age of the extinct Giant Bear" (genus unspecified, collected by Evans and reported in Crane, 1956, p. 672). The recent review of mastodon remains and radiocarbon dates by Williams (1957) indicates that outside Florida the genus endured in eastern North America until at least 6,000 years ago and is associated with archaic artifacts.

One waits with keen anticipation additional study of these and other problem areas such as the West Indies. Tentative conclusions, based on the harvest of eight years of radiocarbon dates associated with extinct animals, follow: (1) Mexican and Alaskan large mammals were the first to be eliminated, this in Late-glacial time; (2) the Plains Megafauna disappeared in the early part of the Post-glacial period; (3) eastern temperate forest and tropical rainforests were the last continental refugia for large mammals; (4) the Floridian savanna, surrounded by forest, served as a refuge for plains herbivores after they had disappeared elsewhere in western North America.

#### A LATE PLEISTOCENE EXTINCTION MODEL

An idealized descriptive model designed to illustrate probability of extinction within the late Pleistocene terrestrial fauna would include many factors. Without doing violence to such a model we may be able to limit it to three: (1) body size, (2) habitat, and (3) total range of the species. Reasons for this choice and certain apparent exceptions to the model will become evident subsequently.

The probability of extinction in the late Pleistocene appears to have been maximized by large body size, usually accompanied by low values of  $r$  (intrinsic rate of increase), and  $T$  (mean generation

period): by open habitat, i.e., savanna, grassland, tundra, and desert, and by limited range, either insular or on such ecological islands as Alpine meadows surrounded by forest. Conversely, survival was enhanced by small size, forest habitat, and a large range for the species in question.

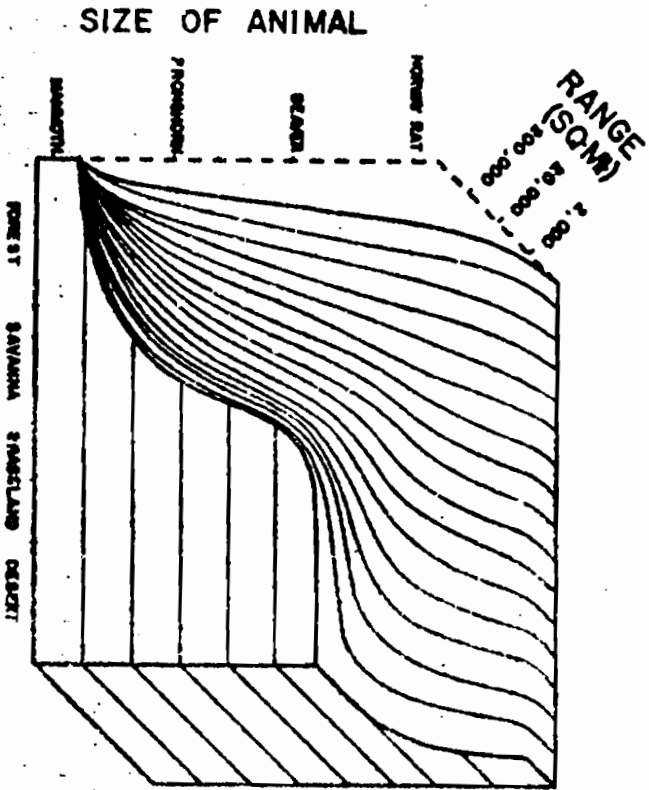


Fig. 6. A Late Pleistocene extinction model for New World mammals. This generalized model is intended to indicate the interaction of variables that appear to have been important in determining probability of extinction for any particular species or population. Points beneath the surface of the solid lie within the region of high extinction probability; those above the surface lie in the region of high probability of survival.

The primary question in late Pleistocene extinction revolves around the herbivores (trophic level A<sub>1</sub> in Lindeman's system). According to ecological and evolutionary theory it is axiomatic that a reduction in the number of species operating at one level will require reduction at higher trophic levels. Our present task is to



describe the pattern of herbivore extinctions, with the assumption that extinction of certain wolf, cat, cowbird, vulture, and vampire life forms followed inevitably.

Figure 6 is a diagrammatic attempt at such a descriptive model, showing high and low regions of extinction probability. The high regions lie within the shaded portion of the solid; the low regions lie above in the unshaded portion. Following Dansereau (1957), habitat can be divided conveniently into the four biomes: forest, savanna, grassland, and desert. All terrestrial communities from the equator to the Arctic fall within one of these units. Animal body size is divided into four classes, represented respectively by (1) Norway rat, (2) Norway rat to beaver, (3) beaver to pronghorn, (4) pronghorn to mammoth. Total range of the species in square miles is arbitrarily listed as very small (less than 2,000), small (2,000-20,000), medium (20,000-200,000), and large (200,000 and more). Three specific examples, which were used in constructing the model, illustrate its predictive function:

*Case A.* Upper-left-rear corner of the diagram. Small animals in a small area of forest, Puerto Rico.

Extinct. *Nesophonus*, an insectivore; *Acrotoceras*, a small ground sloth; and six genera of hystricomorph rodents: *Heptaxodon*, *Elasmodontomys*, *Isolobodon*, and *Proechimys* (surviving on mainland South America), *Heteropsomys*, and *Homopsomys*.

Surviving. Eleven genera of native bats; introduced *Rattus* and *Mus*.

Extinction intensity. Heavy.

*Case B.* Upper-left-front corner. Small animals in extensive forest, eastern North America.

Extinct. None known.

Range possibly reduced: *Neofiber*, round-tailed muskrat; *Erethizon*, porcupine; *Didelphis*, opossum.

Surviving. Twenty-one genera of native rodents, various other small terrestrial mammals and bats.

Extinction intensity. Very light.

*Case C.* Lower-center and right-front corner. Large animals in extensive desert, grassland, and savanna habitats, the Basin and Range province and western North America generally.

Extinct. *Mammuthus*, mammoths of two or three species; *Mam-*

mul, mastodon; *Paramysodon*, *Netherotherium*, and *Megalonyx*, ground sloths; *Glyptotherium*, glyptodont; *Polygonus*, peccary; *Tarupoiama*, long-legged llama; *Camelops*, camel; *Sangamonia*, extinct deer; *Brameryx*, tar-pit pronghorn; *Steckoceros*, pronghorn; *Eucerotherium* and *Prepioceros*, shrub-oxen; *Bootherium*, musk-ox; *Elymus*, horse and ass, various species.

Surviving: *Antilocapra*, pronghorn; *Odocoileus*, mule deer; *Bison*, buffalo, one species only.

#### Extinction intensity. Heavy.

In addition to these three cases it is obvious that other regional faunas fulfill the requirements. For example, the Greater Antilles experienced complete extinction of all beaver-sized and larger animals and partial survival only among the small mammals and reptiles. In Alaskan tundra and Mexican steppe there was a high extinction rate for large herbivores (pronghorn size and over), but not for small or medium-sized mammals. Applying the model to South America we would expect heavier extinction on the pampas and campo cerrado savannas than in the Amazonian rainforest.

Paleontology of the Pampean formation (Simpson, 1940) showed that a variety of ground sloths, glyptodonts, and other edentates, horses, certain camels, and the native ungulates, as the macraucheniids, toxodonts, mesotheres, and hegetotheres, disappeared from the plains areas. Some extinction of forest forms must have occurred, probably more than the scanty fossil record of mastodonts and beavers would indicate (tropical forest Pleistocene sediments are all but unknown). However, survival in the forest exceeds that on the plains. Peccaries, large edentates, monkeys, tapirs, capybaras, and various deer in the forest and forest margin contrast with the presence of only two large native herbivores in the pampas and in Patagonia, the guanaco or wild llama and the pampas deer.

If the model is adequate in these cases, it by no means explains lack of extinction under certain circumstances that call for it. The survival of four species of native camamelids in South America, at least two of them with relatively narrow ranges in the Andean Pura is mystifying, both in terms of the model and the extermination of the camamelids in North America. The survival of *Capromys ingrahami* on one of the smaller Bahaman Keys and of *Tesiodon*, the giant tortoise of the Galápagos, introduce an additional problem that appears worthy of special treatment.

**WEST INDIAN VERTEBRATES AND GALÁPAGOS TORTOISES**

Late Pleistocene and sub-Recent insular extinction throughout most of the world appears to have been intense. Certain oceanic islands exhibit the phenomenon of extermination without replacement noted in North and South America. Giant marsupials inhabited Australia (Gill, 1955), large flightless birds survived in New Zealand at least until 1300 A.D. (Deevey, 1955), and giant lemurs, tortoises, and large birds lived in Madagascar (Sibree, 1915). West Indian mammals, reptiles, and birds experienced extermination both of relatively medium-sized genera (tortoises and ground sloths) and of many smaller rodents. In this respect West Indian extinction differs from the continental record. Summary articles by Allen (1911) and Mathew (1919) have been superseded by Simpson's valuable zoogeographic synthesis (1956). Allen (1942) discussed most of the extinct mammals. Except for Cuban ground sloths (Allen, 1918; Aguayo, 1950) and Jamaican bats and rodents (Anthony, 1920; Koopman and Williams 1951; Williams, 1952b), the distribution of most of the extinct mammals is covered in Miller and Kellogg's *Checklist* (1955).

The extinction chronology is rather baffling and is not simplified by the possibility that certain forms such as *Nesophontes* may yet be found to survive in remote mountainous districts. I am indebted to K. F. Koopman for pointing out that more than 300 years elapsed between discovery of the islands by western man and the first serious scientific description of their fauna. Extermination in this interval, perhaps at the hands of superior competitors as *Rattus*, or as the result of clearing and cultivation, will be difficult to distinguish from prehistoric extermination. *Nesophontes*, for example, appears to have been contemporaneous with *Rattus*. In contrast *Tesimlo* and various ground sloths almost surely were not present at the time of the conquest. Ground sloths may have existed into the ceramic period (Aguayo, 1950), and the giant rodent *Quemisia* was apparently known to Orsted (Allen, 1942), but there is no certain evidence of other large hystriocompids (*Elasmisodonomys*, *Clidomys*, and *Amblyrhiza*) in post-Columbian middens and it is most unlikely that their presence would have gone unrecorded by early observers. Simpson listed twenty-two extinct genera of terrestrial mammals in the Greater Antilles. Even assuming some unnecessary splitting, the fossil fauna is quite impressive. By comparison, the present sur-

viving fauna of four genera is depauperate: *Solenodon* on Hispaniola and Cuba, *Oryzomys* (recently extinct?) on Jamaica, *Capromys* (here to include *Geocapromys*) on Cuba, the Plana Keys, Jamaica, and the Swan Islands, and the closely related *Plagiodontia* on Hispaniola.

Considering the poverty of chiropteran remains elsewhere, the fossil record of the West Indian bats is remarkably good. It has been used to identify relative faunal ages in Jamaica (Koopman and Williams, 1951; Williams 1952b). At first glance the presence of two genera of fossil bats now extinct in Jamaica seems to contradict the principle I have noted earlier that late Pleistocene extinction did not affect such animals. Other than commensals and parasites of large herbivores, such as the cowbirds and vampires, we would predict no elimination of life forms among the bats and birds. In theory climatic change during the Wisconsin and earlier Glacial advances altered the ecological opportunities for various genera and changed faunal composition at low latitudes. However, it is my present thesis that generic extinction did not accompany such events. Koopman and Williams' studies make it clear that the local extirpation of bats (*Tomalia* and *Brachyphylla*) in Jamaica was accompanied by replacement by related genera in the same subfamily. *Tomalia* and *Brachyphylla* survive in Central America and Hispaniola respectively. The Jamaican bat fauna remained rich and bears no resemblance to the annihilation experienced by the terrestrial herbivores. The shift in the species composition of bats may be attributed to climatic change.

On the other hand, the survival of a rodent, *Capromys* (*Geocapromys*) *ingrahami*, on the tiny Plana Keys and of *C. thomomys* on the Swan Islands, seems a serious violation of the general rule that the smaller the surface the greater the vulnerability to extinction (Fig. 6). The record of *Capromys* is instructive. *C. ingrahami* was described in 1891. Closely related fossil populations were subsequently found on the larger Bahaman Islands, Crooked, Eleuthera, Long, Great Exuma, Great and Little Abaco. In 1955 Rabb and Hayden (1957) revisited the Plana Keys, collected three specimens of the "rookie" and noted that the island had undergone little change since Ingraham's visit. East Plana Key is a small, rocky islet not more than 50 feet above the ocean, one-half mile wide, four to five miles long and "entirely" without fresh water except in the rainy season, when pools of fresh water may be found in holes in the rocks" (Allen, 1891). In the absence of fresh water it is doubtful that the

Carib Indians ever maintained permanent settlement on the island; Rabb and Hayden note that it is uninhabited at present. This feature may be crucial. We can attribute the remarkable survival of *Capromys* both on the Plana Keys and on the Little Swan Islands to lack of permanent prehistoric habitation. For the archaeologist this carries the corollary that the other Bahaman Islands were more intensively occupied.

The foregoing account emphasizes the mammalian fossil record. In addition, there were "giant" late Pleistocene lizards (Hecht, 1951, 1952) turtles (Williams, 1950, 1952a), and birds (Wetmore, 1937). The record of the tortoises, *Testudo*, is an important adjunct to the extinction of the large mammals. An interesting sidelight is their apparent extinction in the Greater Antilles before the main period of mammalian extinction (Williams, 1952a, p. 554). Elsewhere they evolved through the Tertiary and into the late Pleistocene. Species of relatively small size survive in northern South America. The New World giant tortoises remain only on the Galápagos. As in the case of *Geococcyx* on the Plana Keys, there is reason to believe that these islands escaped permanent occupation in prehistoric times. Heyerdahl and Skjelsvold (1956) reported no archaeological evidence of prehistoric occupancy of the Galápagos other than temporary or seasonal visits, and no preceramic contact. With a long reproductive time lag and no special defense against man, the giant tortoises must have been especially vulnerable to human predation. This may explain their early demise compared to the rest of the fauna in Cuba (Williams, 1952a). The Galápagos and Plana Key exceptions to the generalized extinction model (Fig. 6) indicate that it will apply only to regions permanently inhabited by prehistoric man.

#### CLIMATIC INDICATORS, EXTINCTION, AND MAN

"A hypothesis which implies that practically all the important fossil forms had existed until a comparatively Recent date and then became extinct in a geologically short period of time had seemed equally improbable to the writer; and yet it is to such a conclusion that a study of the evidence leads" (Romer, 1933). Flint (1957), Osborn (1936, pp. 1512-1513), and Sauer (1944) are also among those who indicate that prehistoric man was the principal agent of late Pleistocene extinction. If circumstantial evidence points to man, it does not reveal his methods. Sauer's fire drive hypothesis (1944)

may be important in understanding the possible hunting techniques of man against the large, gregarious plains herbivores. However, as Eislely (1946) noted, even the most ardent proponent of fire as an ecological force may hesitate to attribute the extinction of forest mastodons, the giant beaver (*Castoroides*), and the West Indian hystriomorphs to this technique. The mysterious survival of large African herbivores frustrates sweeping conclusions.

For paleoecological purposes it seems necessary to consider the significance of large vertebrates as climatic indicators. If prehistoric man is an extinction agent, how are we to interpret shifts in range in terms of paleoecological uniformitarianism? Tapirs and capybaras, today denizens of tropical forest, formerly ranged far to the north, respectively to Oregon and Pennsylvania and to Florida and Arizona. Are there compelling reasons to believe that, in the absence of man, these animals would not occupy the same range under the present climate?

The porcupine, opossum, and armadillo have notably extended their ranges within historic time. The opossum and armadillo moved northward (Guilday, 1958; Fitch *et al.*, 1952), the porcupine southward, into Sonora (Beason, 1953). These extensions can be attributed to climatic change. They can also reflect the reoccupation by these species of marginal positions in their former range, from which they had been eliminated in prehistoric time by human predation. The mountain top populations of *Marmota flaviventris* in southern Arizona, New Mexico, and northeastern Mexico were trimmed. Subalpine and boreal habitats, apparently suitable for marmots, persist in these areas today.

The giant tortoises, like the tapir and capybara, are another group in which a complacent assumption of tropicality is read into their ranges, for example, by Crook and Harris (1958, p. 241). Survival of tortoises only on remote oceanic islands seems to be attributable to the circumstance that they here escaped pre-Columbian extermination by man rather than to climatic change. Assumptions of climatic change based on the present distributions of relatives of the late Pleistocene fossil vertebrates are gratuitous as long as an alternate cause of extirpation is possible. In brief we may inquire whether tropical forests and narrow island refugia from climatic change or from the hunting practices of prehistoric man.

For extensive indicators of climate and past environments it may

be necessary to consider only plant distributions plus those small animals whose population density and reproductive capacity could keep pace with human predation.

Within our present knowledge there seems little agreement on the problem of extinction and man's role in it. Most authors who have reviewed the problem reduce it to the outcome of an interaction of all factors that can limit animal populations—predation, competition, parasitism, climatic change, evolutionary lag during environmental stress, and also the effect of man (Colbert, 1938; Gill, 1955; Hamilton, 1939; Osborn, 1906; Romer, 1945; Simpson, 1931, 1953). I believe this multiple hypothesis does injustice to the temporal and ecological record, i.e., (1) differential loss of large animals, (2) lack of evidence of major climatic change during the extinction period, (3) the narrow chronological range in which extinction occurred, and (4) the phenomenon of removal without replacement. It would appear that within the Cenozoic the late Pleistocene environment had some unique features. Man is the only one clearly identified.

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