

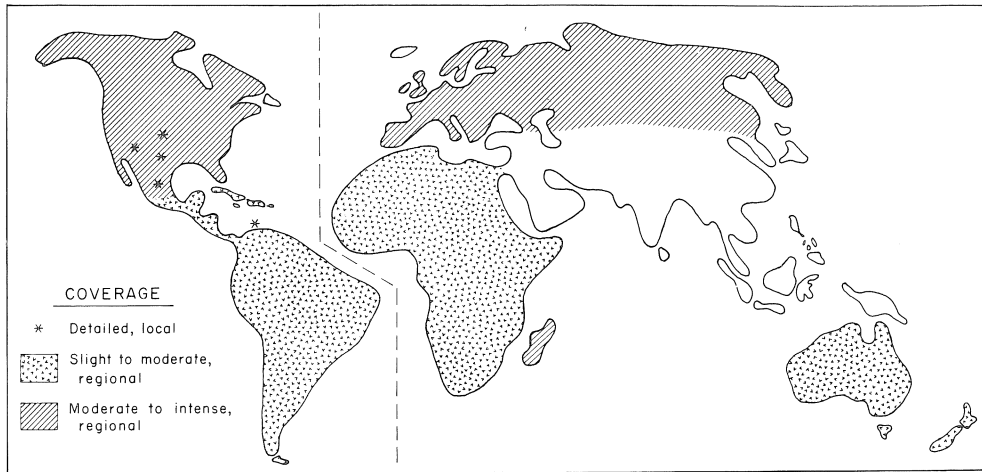
PLEISTOCENE EXTINCTIONS

The Search for a Cause

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World coverage of Pleistocene extinction as discussed by contributors to this volume.
Unshaded areas are not treated.

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PREHISTORIC OVERKILL¹

Abstract

A sudden wave of large-animal extinction, involving at least 200 genera, most of them lost without phyletic replacement, characterizes the late Pleistocene. Except on islands where smaller animals disappeared, extinction struck only the large terrestrial herbivores, their ecologically dependent carnivores, and their scavengers. Although it may have occurred during times of climatic change, the event is not clearly related to climatic change. One must seek another cause. Extinction closely follows the chronology of prehistoric man's spread and his development as a big-game hunter. No continents or islands are known in which accelerated extinction definitely predates man's arrival. The phenomenon of overkill alone explains the global extinction pattern. This interpretation of the cause of late-Pleistocene extinction was advanced by Wallace in the World of Life (1911). It finds chronological support in recent discoveries. It clarifies an otherwise incomprehensible part of the Pleistocene fossil record.

The end of the Ice Age saw the sudden decline of an extraordinary number of large vertebrates. Unlike the relatively gradual, essentially orderly replacement of new genera seen earlier in the Pleistocene and Tertiary, extinction rates suddenly skyrocketed. New genera did not appear. There was no generic replacement either by immigration or evolution (Martin, 1958, p. 400). As a result,

We live in a zoologically impoverished world, from which all the hugest, and fiercest, and strangest forms have recently disappeared . . . yet it is surely a marvelous fact, and one that has hardly been sufficiently dwelt upon, this sudden dying out of so many large Mammalia, not in one place only but over half the land surface of the globe [Wallace, 1876, p. 150].

At the time he wrote, Wallace regarded the cause of extinction as a direct outcome of the worldwide effects of Pleistocene glaciation.

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But in the voyage of the *Beagle*, Darwin had already shown that extinct Pleistocene fauna occurred in beds younger than the last glaciation. Wallace himself came to reject the effects of the glacial epoch as a sufficient explanation. In the *World of Life* (1911, p. 264), he wrote:

What we are seeking for is a cause which has been in action over the whole earth during the period in question, and which was adequate to produce the observed result. When the problem is stated in this way, the answer is very obvious. It is, moreover, a solution which has often been suggested, though generally to be rejected as inadequate. It has been so with myself, but why I can hardly say.

While crediting it to Lyell, Wallace reached the view that seems to me best supported by subsequent evidence, that no known environmental defects or crises, other than those brought by prehistoric man, can adequately account for the sequence of events. I would depart from Wallace's view in only one regard—he apparently also believed, following Lyell, in certain deep-seated general causes operating to exterminate large animals at the end of each geological era.

I do not consider the intriguing question of accelerated extinction at the end of the earlier geological eras (Bramlette, 1965; Newell, 1966) relevant to the matter at hand. In the late Pleistocene one has a far more detailed stratigraphy and chronology to work with. But the main point is that one finds a totally different pattern in the Pleistocene, one affecting mainly one class of organisms, the Mammalia. There is no upturn in extinction rate among marine organisms, such as typifies the close of Permian, Triassic, and Cretaceous. The phenomenon of accelerated extinction is unknown in the marine Pleistocene. If it had occurred, Lyell's method of dating marine Cenozoic beds would not have been so simple or successful.

THE PATTERN OF PLEISTOCENE EXTINCTION

I shall attempt to sketch salient features of late-Pleistocene generic extinction, with emphasis on North America, revising some interpretations presented in an earlier effort (Martin, 1958, p. 394–413). The reason for concentrating on genera is pragmatic. The generalized ecologic, chronologic, and phylogenetic interpretations for discussing an extinct genus are likely to be speculative enough without entering a taxonomic level in which more than a dozen valid specific names may be available in a group that could not possibly have evolved into as many good biological species. Are we to infer a dozen allopatric species in a genus that is seldom or never known to be represented by two

distinct morphological forms in a single fossil horizon? Even in the case of a thoroughly and very skillfully revised group, with much of its synonymy resolved, the critical identification of a species from a carefully dated outcrop of considerable archaeological or paleoecological significance may require presence of diagnostic parts such as horn cores or complete jaws. Ecologists, long subjected to various pressures to study modern communities at the species level whenever possible, may not fully anticipate or appreciate the hazards of trying to study Pleistocene mammals at the species level.

To turn now to the matter of Pleistocene chronology. Although many large extinct animals have yet to be dated by C^{14} and although the method itself continues to present discordant results, especially when applied incautiously, it seems possible to conclude on the basis of both relative and absolute dating that throughout the Americas, in Australia, and on the islands of Madagascar and New Zealand a major wave of generic extinction occurred once only, and at a time within the last 15,000 years. This was not the case in Africa and Southeast Asia, where most generic extinction occurred some tens of thousands of years earlier, essentially beyond the reach of the C^{14} dating method.

Apart from small oceanic islands, the animals lost were mainly "big-game" mammalian and avian herbivores of over 50 kg adult body weight (see Table 1). Doomed by the collapse of the herbivores was a retinue of ecologically dependent carnivores, scavengers, commensals, and, presumably, various unknown parasites. One need not assume any narrow predator-prey relationship. In fact, most mammalian predators seek a variety of prey species. One can assume that the loss of thirty-one genera of large herbivores at the end of the last glaciation of North America (Table 1) reduced the variety of carnivores. In other words, while one cannot say that saber-tooth cats disappeared *because* of the extinction of their supposed prey (such as mammoths), one can say that there had to be some feedback, some extinction of carnivores, when various herbivores disappeared. It happened that the saber-tooth was among those lost and the jaguar among those surviving. The fact that prehistoric man would not have hunted and killed saber-tooth cats or other large carnivores is not a valid criticism of the hypothesis of overkill. The question is whether or not he triggered extinction of the herbivores.

Generic extinction did not occur only at the end of the Pleistocene. *Nannippus*, *Plesippus*, *Stegomastodon*, *Titanotylopus*, *Canimartes*, *Trigonictis*, and other genera listed in Table 1 disappear from the United States at the end of the Blancan, over a million years ago. But the adaptive niches for horses, mastodons, camels, and large mustelids continued

to be occupied (see Hibbard et. al., 1965, p. 520). In contrast, in the late Pleistocene, the life forms lost were not replaced or maintained by related species. Possibly the browsing and grazing niches so suddenly abandoned by large animals in the late Pleistocene were partly refilled by an increase in biomass of small mammals and insects. But in the strict sense, the record is one of extinction without replacement.

Continental extinction of late-Pleistocene age also differs from that earlier in the Cenozoic in the lack of appreciable change among the small vertebrates. On the North American continent there is no terminal Pleistocene loss of small mammalian genera comparable to the loss of *Prodipodomys*, *Pliophenacomys*, *Pliopotamys*, *Pliolemmus*, and *Bensonomys* in the early-Pleistocene (Table 1). As in the case of the large herbivores mentioned above, most of the lost Blancan genera of small mammals have clear-cut phyletic replacements in the younger Pleistocene faunas. In contrast, there is very little difference between the Wisconsin glacial-age small vertebrates and the modern fauna, even at the species level. Of seventy small mammals—shrews, bats, and rodents—all but six are assigned to living species (Hibbard, 1958, with minor additions). Of sixty-nine amphibians and reptiles (excluding turtles and tortoises) of the same age, only three are considered extinct species (Gehlbach, 1965). Of seventy-three freshwater mollusks found in late-Pleistocene and Recent faunas of southwestern Kansas and northwestern Oklahoma in Jinglebob or younger faunas, only one is extinct (Hibbard and Taylor, 1960). Very few extinct species of mollusks are found in local faunas younger than the Sanders ("Aftonian"; see Taylor, 1965, p. 605).

Survival of the small includes survival of the pelagic. Unlike the Pliocene-Pleistocene boundary, which is marked in certain deep-sea cores by the loss of Discoasters, a reduction in variation of the *Globorotalia menardii* complex, disappearance of *Globigerinoides sacculifera fistulosa*, and appearance of *Globorotalia truncatulinoides* (Ericson et al., 1963), the Pleistocene-Recent boundary cannot be recognized by marine guide fossils. Around 11,000 years ago, the planktonic Foraminifera of the Atlantic changed as cool-water faunas gave way to warm. But the climatic shift was not accompanied by biotic extinction. At no time in the Pleistocene was there massive marine extinction comparable to the loss of belemnites, ammonites, and nanno-plankton that marks the Upper Maestrichtian-Danian boundary, commonly correlated with extinction of the dinosaurs (Bramlette, 1965). Nor were the largest mammals of the world, the cetaceans, affected by late-Pleistocene extinction.

Finally, late-Pleistocene extinction is not evident in the plant kingdom. While a major depression 20,000 years ago, with a worldwide drop in

vegetation zones of roughly 1,000 meters, is evident in pollen profiles of the time taken in unglaciated, mountainous areas of most continents, there are no extinct late-Pleistocene genera among the diatoms or vascular plants, two groups of organisms with extraordinarily rich fossil records. Only in the early Pleistocene, best known in western Europe, is the local extirpation of warm-temperate plants well known (Leopold, 1967). The lost European genera, such as *Liquidambar*, *Nyssa*, *Sequoia*, *Sciadopitys*, *Magnolia*, *Tsuga*, *Juglans*, *Eucommia*, and *Pterocarya*, survive in parts of eastern Asia or North America. It is notable, and I believe highly relevant to my interpretation, that despite all the theoretical reasons why glaciation should have made Western Europe a geographic trap for temperate biota, there is less, not more, evidence of generic extinction of mammals there than on other continents.

For these reasons, late-Pleistocene extinction must be regarded as imbalanced. It left empty niches in the terrestrial ecosystem, niches previously occupied by a succession of large herbivores through the Neogene. Only on oceanic islands were numerous small vertebrate genera obliterated. Among the animals lost were giant marsupials in Australia, moas in New Zealand, giant lemurs and struthious birds in Madagascar, about twenty-eight genera of mammals and one genus of tortoise in North America (Table 1), and a still poorly known but probably larger number of mammalian genera in South America. Late-Pleistocene generic extinction is less well marked in northern Eurasia. There *Mammuthus* (mammoth), *Coelodonta* (woolly rhino), and *Megaceros* (Irish elk) were the only common late-Pleistocene genera to disappear. Thanks to a refuge in the unglaciated eastern Canadian Arctic, *Ovibos* (musk-ox) survived in the New World. In both Africa and Southeast Asia, a major episode of Pleistocene extinction antedates the late Würm and apparently coincides with the end of the Acheulean cultural stage, ca. 40,000–50,000 B.P. Can the cause of this peculiar pattern be found in its chronology?

THE PLEISTOCENE OF O. P. HAY

With the recognition of multiple glaciation and the evidence from the mid-continent of four major drift deposits separated by well-developed soils, those in search of a climatic explanation for extinction recognized the logic of seeking some chronological order. If all of the four classic midcontinental glaciations—Nebraskan, Kansan, Illinoian, and Wisconsin—were of roughly equivalent magnitude, they should represent roughly equivalent climatic changes that would have imposed a roughly equivalent stress on the fauna. Extinction would be progressive, and its

chronology should show that animals climatically more sensitive were lost first. With this expectation, Hay proposed the following chronology in 1919 and again in 1923. I have attempted to indicate current correct generic names in certain cases.

A. Extinct by the end of the Kansan

<i>Megatherium</i> (= <i>Eremotherium</i>)	<i>Eschatius</i> (= <i>Camelops</i>)
<i>Glyptodon</i>	<i>Camelops</i>
<i>Stegomastodon</i>	<i>Camelus</i> ²
<i>Anancus</i> (= <i>Stegomastodon</i> or <i>Cuvieronius</i>)	<i>Hydrochoerus</i>
<i>Gomphotherium</i> (= <i>Stegomastodon</i> or <i>Cuvieronius</i>)	<i>Aftonius</i> (= <i>Euceratherium</i>)
<i>Elephas</i> (= <i>Mammuthus</i>) <i>imperator</i>	<i>Leptochoerus</i> ³
	<i>Trucifelis</i> (= <i>Smilodon</i>)

B. Extinct by the end of the Sangamon

<i>Myloodon</i> (= <i>Paramyloodon</i>)	<i>B. antiquus</i>
<i>Tapirus</i>	<i>Aenocyon</i> (= <i>Canis dirus</i>)
<i>Equus</i>	<i>Dinobastis</i>
<i>Taurotragus</i> ²	<i>Smilodon</i>
<i>Sangamona</i>	<i>Smilodontopsis</i> (= <i>Smilodon</i>)
<i>Bison latifrons</i>	

C. Extinct by the end of the Wisconsin

<i>Megalonyx</i>	<i>Bootherium</i>
<i>Elephas</i> (= <i>Mammuthus</i>)	<i>Mylohyus</i>
<i>Mammut</i>	<i>Platygonus</i>
<i>Cervalces</i>	<i>Bison occidentalis</i>
<i>Symbos</i>	<i>Castoroides</i>

Hay's chronology was soon challenged. Bryan and Gidley (1926) pointed out that bones of extinct camels, a group Hay considered extinct by mid-Pleistocene, were found in playa-lake deposits of unmistakably late-Pleistocene age. Stratigraphy and radiocarbon dates show decisively that extinct *Tapirus*, *Smilodon*, *Paramyloodon*, *Mammuthus imperator*, *Camelops*, and *Euceratherium* survived to, and through, the last glaciation. Thus most of the genera in list B plus some of those from list A must be added to list C. Others in list A are now regarded as having been

2. Old World genus, misidentified.
3. Extinct before the end of the Tertiary.

misidentified or as extinct before the end of the Tertiary. As Romer (1933), Colbert (1942), and others have noted, Hay's chronology for the large mammals is without substance. If Hay's Pleistocene extinction chronology survives, it is in the small mammal pattern (Table 1). Unlike the megafauna there is much more extinction in the early Pleistocene (Blancan) than later, as one might expect if climatic change initiated the main faunal changes. What about the megafauna?

Among large genera (50 kg or more in adult body weight), the recent list of Pleistocene distributions for the United States in Hibbard et al. (1965, p. 573, copied in Table 1), indicates four large mammals lost by the end of the Kansan, three at the end of the Yarmouth, none at the end of the Illinoian, and one at the end of the Sangamon. The spectacular upset comes at the end of the Wisconsin. By the end of the late-glacial, thirty-three genera are going or gone, far more than disappear in the rest of the Pleistocene put together (Table 1).

If the genera are arranged in the form of land-mammal ages, which avoids the assumption of correct glacial and interglacial age assignment, the results are similar. Extinction of eleven genera of large size occurs in the roughly two million years represented by the Blancan, six in the Irvingtonian, and thirty-five at the end of the Rancholabrean.

As matters stand, it is far easier to date post-Blancan Pleistocene local faunas by the arrival of new Eurasian large mammals than by the loss of old ones. It is unfortunate for Pleistocene geologists that the pattern of extinction is so disharmonic. If the extinct genera were more evenly spaced either in a random pattern or in one closely related to multiple glaciation as Hay proposed, relative faunal dating in the Pleistocene would not be so difficult.

For example, how can one tell a Sangamon interglacial fauna from a relatively warm interstadial fauna of the Wisconsin or even the Illinoian? Slaughter and Ritchie (1963) compared the Clear Creek fauna, from near Dallas, Texas, with the Jinglebob, Cragin Quarry, and Good Creek faunas, all referred to the Sangamon. The Clear Creek Formation includes *Geochelone* and probably *Bison latifrons*, both commonly considered pre-Wisconsin guide fossils. But a radiocarbon date of $28,840 \pm 4,740$ (SM 534) on shells from the Clear Creek Formation indicates interstadial age in the standard Wisconsin glacial chronologies of most geologists.

Unless the Clear Creek radiocarbon date is shown to be seriously in error or improperly associated with the fauna, it establishes *Geochelone* and *Bison latifrons* in a post-Sangamon horizon. For *Geochelone* there is no doubt; a small species, *G. wilsoni*, is reported from late-Wisconsin or post-Wisconsin deposits in Friesenhahn Cave and at Blackwater

TABLE 1. Pleistocene Extinct Mammals, Continental North America (Hibbard et al., 1965)

	Blancan			Irving-tonian		Ranchola-brean			Direct assn. with man	<15,000 B.P. by C ¹⁴	In beds <15,000 B.P.
	Pliocene	Nebraskan	Aftonian	Kansan	Yarmouth	Illinoian	Sangamon	Wisconsin			
LARGE (> 50 kg)											
<i>Machairodus</i> , saber-tooth cats											
<i>Ceratomeryx</i> , extinct pronghorn											
<i>Rhynchotherium</i> , mastodons											
<i>Pliauchenia</i> , extinct camels											
<i>Borophagus</i> , bone-eating dogs											
<i>Ischyrosmilus</i> , saber-tooth cat											
<i>Chasmaporthetes</i> , extinct hyena											
<i>Glyptotherium</i> , glyptodons											
<i>Nannippus</i> , three-toed horses											
<i>Plesippus</i> , zebrine horses											
<i>Stegomastodon</i> , mastodons											
<i>Titanotylopus</i> , giant camel											
<i>Hayoceros</i> , extinct pronghorn											
<i>Glyptodon</i> , glyptodons											
<i>Platycerabos</i> , extinct bovid											
<i>Stockoceros</i> , extinct pronghorns											
<i>Mammut</i> , American mastodons									x	x	x

TABLE 1.—continued

	Pliocene	Blancan		Irving-tonian		Ranchola-brean		Direct assn. with man	<15,000 B.P. by C ¹⁴	In beds <15,000 B.P.
		Nebraskan	Aftonian	Kansan	Yarmouth	Illinoian	Sangamon			
<i>Megalonyx</i> , ground sloths									?	x
<i>Tanupolama</i> , extinct llamas								x	?	x
<i>Cwieronius</i> , extinct mastodons								x		x
<i>Platygonus</i> , extinct peccaries									x	x
<i>Camelops</i> , extinct camels								x	x	x
* <i>Equus</i> , horses								x	x	x
<i>Paramylodon</i> , ground sloths									?	x
<i>Capromeryx</i> , extinct pronghorns								?		x
<i>Castoroides</i> , giant beavers									x	x
<i>Arctodus</i> , giant short-faced bears								?		x
<i>Nothrotherium</i> , small ground sloths								?	x	x
<i>Chlamytherium</i> , giant armadillos										x
<i>Dinobastis</i> , saber-tooth cat								?		x
<i>Smilodon</i> , saber-tooth cats									x	x
* <i>Hydrochoerus</i> , capybaras										x
<i>Mammuthus</i> , mammoths								x	x	x
<i>Mylohyus</i> , woodland peccaries									x	x
<i>Euceratherium</i> , shrub-oxen								x		x
<i>Preptoceras</i> , shrub-oxen								x		x

TABLE 1.—continued

	Blancan		Irvingtonian		Rancholabrean			Direct assn. with man <15,000 B.P. by C ¹⁴ In beds <15,000 B.P.
	Pliocene	Nebraskan	Aftonian	Kansan	Yarmouth	Illinoian	Sangamon	
<i>Hypolagus</i> , extinct rabbits								
<i>Parahodomys</i> , extinct woodrats								
<i>Simonycteris</i> , extinct bat								
<i>Etadonomys</i> , extinct kangaroo rat								
<i>Brachyprotoma</i> , extinct skunk								
<i>Plesiothomomys</i> , extinct gophers								
<i>Paradipoides</i> , extinct beaver								
* <i>Heterogeomys</i> , tropical gophers								

* Living in Asia or tropical America.

Draw (Slaughter, 1966). Thus the genus, if not the giant species, can be regarded as lasting to the end with the mammoth, horse, sloth, camel, and other typical members of the terminal Pleistocene megafauna. The point to stress again is the lack of a "logical" or progressive pattern of extinction in the Pleistocene of North America and the hazards of using extinct megafauna as guide fossils. Archaeologists especially need to guard against assigning a pre-Wisconsin age to artifacts associated with "interglacial" glyptodonts, extinct armadillos, or *Geochelone*.

Because virtually all the extinct Pleistocene megafauna of North America survived the stress of multiple glaciation, either some unique natural catastrophe must have precipitated extinction or else natural environmental changes had nothing to do with the event. The former interpretation is presented by Slaughter (1967). The environment in southwestern United States during the time of extinction is reviewed by Mehringer (1967). While the climate had been changing prior to the time of extinction, the fossil pollen record shows that conditions by

11,000 years ago were almost back to "normal"—back to the type of vegetation and climate supposedly typical of the earlier interglacials, an environment then congenial to mammoth, sloth, horse, and other extinct species. Why desert herbivores in particular, such as *Camelops* and *Nothrotherium*, should suddenly disappear at the moment of postglacial climatic recovery, with its expansion of arid habitats, is hard to explain. The ecology of extinction in the humid East is equally mysterious. Why should *Mammuth* and *Symbos*, which from their associated fossil pollen record inhabited a boreal environment of spruce during the late-Wisconsin (Semken et al., 1964; Ogden, 1965, p. 494–95), suddenly disappear just when the boreal vegetation zone was expanding into central Canada from its shrunken full-glacial position outside the Wisconsin ice margin?

The point is pithily put by Hibben (1946, p. 176):

Horses, camels, sloths, antelopes, all found slim pickings in their former habitat. But what was to prevent these animals from simply following the retreating ice to find just the type of vegetation and just the climate they desired? If Newport is cold in the winter, go to Florida. If Washington becomes too hot in the summer, go to Maine.

All extinction explanations must accord to the extinct fauna at least some reasonable biotic adaptability comparable to that of the living large mammals. In a year or two, any of the latter might migrate several times back and forth over the 1,000-km distance through which Wisconsin-age vegetation zones slowly moved.

RADIOCARBON CHRONOLOGIES

Although C¹⁴ dates more or less associated with extinct fauna promise a great deal of chronological refinement that should reveal much about the pattern and, it is hoped, the cause of extinction, certain hazards of "push-button" dating and even the overly enthusiastic extraction of poorly documented dates from date lists need be acknowledged. Before summarizing the more reliable radiocarbon dating results as they bear on Pleistocene extinction, I will cite some of the vexing cases. Hester (1960, p. 58) lists in detail the reasons why date and fauna may not go together; he also summarizes various questionable dates.

A good example of a misleading date on a very important extinct fauna is L-211, 2,040 ± 90, from St. Petersburg, Florida. Partly on the basis of L-211, I reached the conclusion (Martin, 1958), repeated in Pearson (1964), that the extinct megafauna of Florida survived long beyond the time of continental extinction elsewhere in North America.

The date was questioned by Hester (1960), and the dubious stratigraphic association is reviewed by Bullen (1964), who discounts the age on cultural grounds as well. Finally, one of the strongest points against late-postglacial survival of extinct fauna in Florida, as elsewhere, is failure to find such animal remains in postglacial archaeological sites. While late survival of extinct fauna in Florida remains a dim possibility, there is as yet no reliable evidence. At present it seems best to reject L-211.

Stratigraphic chaos, apparently the result of intense solifluction, has thus far defeated attempts at direct radiocarbon dating of the abundant remains of extinct horse, bison, and mammoth in Alaskan muck (W-891, W-1106, W-1108, W-1111, W-1113, W-937). The dates, on wood associated with the bones, appear much too young to represent the true age of the fauna and are thought to be intrusive. A more reliable and possibly terminal date is on hair and hide of *Bison (Superbison) crassicornis*, St-1663, 12,000 B.P. (in Péwé et al., 1965, p. 33). The muck deposits of unglaciated central Alaska are mainly of Wisconsin age.

In the case of Big Bone Lick, Kentucky, one of the richest late-Pleistocene deposits in eastern North America, two samples of wood initially thought to be associated with bones of extinct species proved modern (W-908, W-1357). W-1358, 10,600 ± 250, was recovered from wood associated with a proboscidean tusk and may be close to the terminal age of *Equus* cf. *complicatus*, *Myiodon*, *Mammut*, and *Mammuthus* in the area.

An anomalous set of dates, perhaps illustrating the hazards of attempting to use modern methods on a site repeatedly excavated in the past, is the Mother Grundy's Parlor series (Q-511, 552, 553/4). Charcoal of postglacial age definitely is not to be associated with late-glacial mammoth, hyena, and reindeer from this Upper Paleolithic cave (see Garrod, 1926, p. 135-45).

Dates on bone and teeth or tusk would seem to promise an easy solution to direct dating of the fauna. But even when inorganic carbon is removed and organic residues alone are dated, the results can be glaringly discordant with stratigraphic expectation. The noncarbonate fraction of bones of the first mammoth to be dated from Finland yielded an age of about 9,000 years (Tx-127), decidedly too young to represent the late-glacial pollen associated with the mammoth bones and several thousands of years younger than current geological estimates for mammoth extinction in Europe (Butzer, 1964, p. 410). A bone-collagen age of 8,000 B.P. (UCLA 705) from an ilium of dwarf mammoth from Santa Rosa Island is much younger than charcoal dates (of cultural origin?) associated with mammoth in the area. Even skeptics of the hypothesis making man the fundamental cause of extinction would probably agree

that the dwarf mammoth on this island could not have survived man's initial occupation by several thousand years. Either UCLA-705 must be too young or UCLA-106 and L-209-T (ca. 4,000 years older) must predate man's arrival (see also Meighan, 1965, p. 711). In the case of M-1516, a 4,000-year-old date was obtained on peccary (*Platygonus compressus*) bone from within a sand ridge of the shore of Glacial Lake Warren, which was drained and abandoned over 11,000 years ago. The absence of *Platygonus* from any postglacial Indian middens and from other postglacial vertebrate deposits is a further reason for regarding a 4,000-year record as quite improbable. Organic bone dates from Bonfire Cave, Texas, were several thousand years younger than the age of associated 10,000-year-old charcoal (Pearson et al., 1966).

NORTH AMERICAN EXTINCTION

Jelinek (1957) and Martin (1958) were among the first to propose radiocarbon chronologies for the late-Pleistocene megafauna of North America. The most thorough and most often cited effort was that of Hester (1960), in which dates associated with sixteen extinct genera were presented. Martin and Hester regarded 8,000 B.P. as the terminal date for many genera. Many issues of *Radiocarbon* have appeared since Hester's compilation; the new dates are listed in Table 2, and the more important ones are plotted in Figure 1. While they almost double the number of dated fossil records for the extinct fauna, they add only two genera, *Mylohyus* and *Tetrameryx*, to Hester's list. None of the new dates applies to the following sparsely and questionably dated genera: *Tanupolama*, *Smilodon*, *Sangamona*, *Arctodus*, *Euceratherium*, *Preptoceras*, and *Stockoceros*. The majority of the extinct late-Pleistocene genera and species have not been critically dated by radiocarbon (Table 1).

A much greater yield of radiocarbon dates of deposits apparently postdating the time of extinction is now at hand. Negative evidence is accumulating that makes questionable some of the younger dates on extinct fauna that Martin and Hester accepted. If native elephants, camels, horses, and sloths were still present in continental North America less than 10,000 years ago, their remains are unaccountably absent from a number of carefully excavated and carefully dated archaic and Paleo-Indian sites (Haynes, 1967). It is theoretically possible that the main wave of extinction, which now appears to have occurred around 11,000 B.P., left lingering enclaves of survivors that lasted well into the mid-postglacial. Such enclaves would be difficult to locate and even more difficult to date in the narrow stratigraphic units where they might

TABLE 2. North American Radiocarbon Dates Associated with Extinct Genera, Less than 20,000 B.P.

(Radiocarbon, Vols. 1-8)

Site	Extinct genus	Sample	Years B.P.	Comment
1. Aden Crater, N.M.	<i>Nothrotherium</i>	*Y-1163a Y-1163b	9,840 ± 160 11,080 ± 200	Body tissue affected by preservatives
2. Berrien Springs, Mich.	<i>Mammuthus jeffersoni</i>	*M-1400	8,260 ± 300	Tusk
3. Big Bone Lick, Ky.	<i>Equus</i> <i>Myiodon = Paramyiodon</i>	W-1358 *W-1357	10,600 ± 250 < 200	Wood with tusk Wood
4. Bonfire Shelter, Tex.	<i>Mammuthus</i> <i>Camelops</i> <i>Equus</i>	*W-908 Tx-153	< 250 10,230 ± 160	Wood Sample overlies extinct fauna, with extinct <i>Bison</i>
5. Byron, N.Y.	<i>Mammut</i>	W-1038	10,450 ± 400	Plant material beneath bone
6. Domebo, Okla.	<i>Mammuthus</i>	*TBN-311 SM-610 SM-695 SI-172 SI-175	4,952 ± 304 10,123 ± 280 11,045 ± 647 11,200 ± 500 11,200 ± 600	Untreated tusk Lignitic wood Wood Bone organics Humic acids
7. Ciudad de los Deportes, Mexico D.F., Mexico	<i>Equus, Mammuthus, other fauna of Upper Becerra Formation</i>	UCLA-111	18,700 ± 450	Wood from stump of <i>Cupressus</i>
8. Clovis, N.M.	<i>Mammuthus</i>	A-481	11,170 ± 360	Silty clay around skull
9. Elkhart, Ind.	<i>Mammut</i>	*M-694	9,320 ± 400	Bone
10. Fairbanks, Alaska	<i>Mammuthus</i>	*L-601	21,300 ± 1,300	Sample impregnated with preservatives
11. Gratiot County, Mich.	<i>Mammut</i>	*M-1254	10,700 ± 400	Molar; late-glacial pollen types
12. Gypsum Cave, Nev.	<i>Nothrotherium</i>	LJ-452	11,690 ± 250	Sloth dung
13. Jaguar Cave, Idaho	<i>Camelops</i> <i>Equus</i>	<i>Geochron. Lab.</i> <i>Isotopes Inc.</i>	11,580 ± 250 10,370 ± 350	Fauna associated with older date
14. Kalamazoo County, Mich.	<i>Symbos</i>	*M-639	13,200 ± 600	Bone
15. Kings Ferry, N.Y.	<i>Mammut</i>	Y-460	11,410 ± 410	Spruce wood from bone layer
16. Lehner Ranch, Ariz.	<i>Mammuthus</i> <i>Equus</i> <i>Tapirus</i>	M-811 K-554 A-42 A-378	11,290 ± 500 11,170 ± 140 11,240 ± 190 10,940 ± 100	Haynes gives average date for the bone bed and Clovis level as 11,260
17. Lindenmeier Site, Colo.	<i>Camelops</i> <i>Mammuthus</i>	I-141 *I-473 *I-632	10,780 ± 135 7,200 ± 200 11,200 ± 500	Folsom level Bone and tusk fragments Bone and tusk fragments
18. Lloyd Rock Hole, Pa.	<i>Mylohyus</i>	Y-727	11,300 ± 1,000	Fossil pollen record indicated mixing
19. Lubbock Reservoir, Tex.	<i>Equus</i> <i>Mammuthus</i> <i>Camelops</i>	I-246	12,650 ± 250	Shells
20. McCullum Ranch, N.M.	<i>Mammuthus</i> <i>Equus</i> <i>Camelops, sloth</i>	A-375	15,750 ± 760	No occupation
21. Monterey Bay, Calif.	<i>Hydrodamalis steller</i>	SI-115	18,940 ± 1,100	Historic distribution on Bering Island only
22. Murray Springs, Ariz.	<i>Mammuthus</i>	*A-69 bis.	8,270 ± 260	Overlies elephant bones
23. Northern Lights, Ohio	<i>Castoroides</i>	Y-526	11,480 ± 160	Wood associated with skull

P. S. MARTIN

PREHISTORIC OVERKILL

Table 2 (continued).

Site	Extinct genus	Sample	Years B.P.	Comment
24. Novelty Mastodon, Ohio	<i>Mammut</i>	OWU-126	10,654 ± 188	Wood, boreal pollen types
25. Pontiac, Mich.	<i>Mammut</i>	No lab. designation	11,900 ± 350	Organic material, spruce pollen
26. Powder Mill Cave, Mo.	<i>Aenocyon</i>	*GX-145	13,170 ± 600	Bone fragments
27. Rampart Cave, Ariz.	<i>Nothrotherium</i>	L-473A	9,900 ± 400	Sloth dung, surface
		L-473C	11,900 ± 500	Sloth dung, 18 inches
		L-473D	>38,300	Sloth dung, 54 inches
28. Rancho la Brea, Calif.	Extinct fauna in Pit 3	Y-354b	Range	Wood not necessarily
		Y-354a	between	associated with any extinct
		Y-355a	13,900	species
		Y-355b	and	
		Y-355A bis	15,400	
		LJ-55		
	Extinct fauna in Pit 9	UCLA-773D	13,300 ± 160	
29. Rawhide Butte, Wyo.	<i>Mammuthus</i>	*A-366	10,550 ± 350	Date younger than animal
30. Rochester, Ind.	<i>Mammut</i>	I-586	12,000 ± 450	Wood
31. Rodney, Ontario	<i>Mammut</i>	S-29	11,400 ± 450	Wood
		S-30	12,000 ± 500	Muck
32. Russell Farm, Mich.	<i>Mammut</i>	*M-347	5,950 ± 300	Tusk
33. San Bartolo Atepehuacan, Mexico	<i>Mammuthus</i> , plus Upper Becerra Formation	M-776	9,670 ± 400	Charcoal from lacustrine deposit; stone implements
34. Sandusky County, Ohio	<i>Platygonus</i>	*M-1516	4,290 ± 150	Bone; much too young to date Lake Warren beach containing bones
35. Santa Isabel Iztapan, Mexico	<i>Mammuthus</i> and Upper Becerra Formation	*M-774	2,640 ± 200	Bone; associated with stone implements; date much too young
36. Santa Rosa Island, Calif.	<i>Mammuthus exilis</i>	UCLA-106	11,800 ± 800	Charcoal
		UCLA-705	8,000 ± 250	Bone collagen; discrepancy with L-290-T, 12,500; charcoal
37. Scotts, Mich.	<i>Symbos</i>	*M-1402	11,100 ± 400	Bone
38. Seattle, Wash.	Fossil sloth	UW-8	12,300 ± 200	Peat, from pelvis
39. Sheridan, N.Y.	<i>Mammut</i>	*M-490	9,200 ± 500	Bone
40. Sullivan Creek, Alaska	<i>Mammuthus</i> <i>Equus</i> , other extinct species	*W-891	2,520 ± 200	Wood, muck, etc. should be reliable dates; association with extinct fauna questionable
		*W-937	200 ± 200	
		*W-1106	< 200	
		*W-1108	6,730 ± 260	
		*W-1111	< 200	
41. Sulphur River Formation, Tex.	<i>Mylohyus</i> <i>Equus</i>	SM-532	9,550 ± 375	<i>Mylohyus</i> slightly above younger date, <i>Amer. Antiq.</i> , v. 30, p. 351
		SM-533	11,135 ± 450	
42. Tule Springs, Nev.	<i>Teratornis</i> Sloth <i>Mammuthus</i> <i>Equus</i> <i>Camelops</i>	UCLA-503, 507, 512, 514, 518, 521, 522, 543, 604, 636, *549		Ten of eleven dates range between 11,500 and 14,000. UCLA-549 is slightly younger (9,520 ± 300) but not properly associated with fauna (C. V. Haynes, pers. corres.)
43. Tunica Bayou, La.	<i>Mammut</i>	W-944	12,740 ± 300	Wood, with bones
44. Tupperville, Ontario (Ferguson Farm)	<i>Mammut</i>	*S-16	6,250 ± 250	Gyttja immediately overlying skull; may be younger

P. S. MARTIN

PREHISTORIC OVERKILL

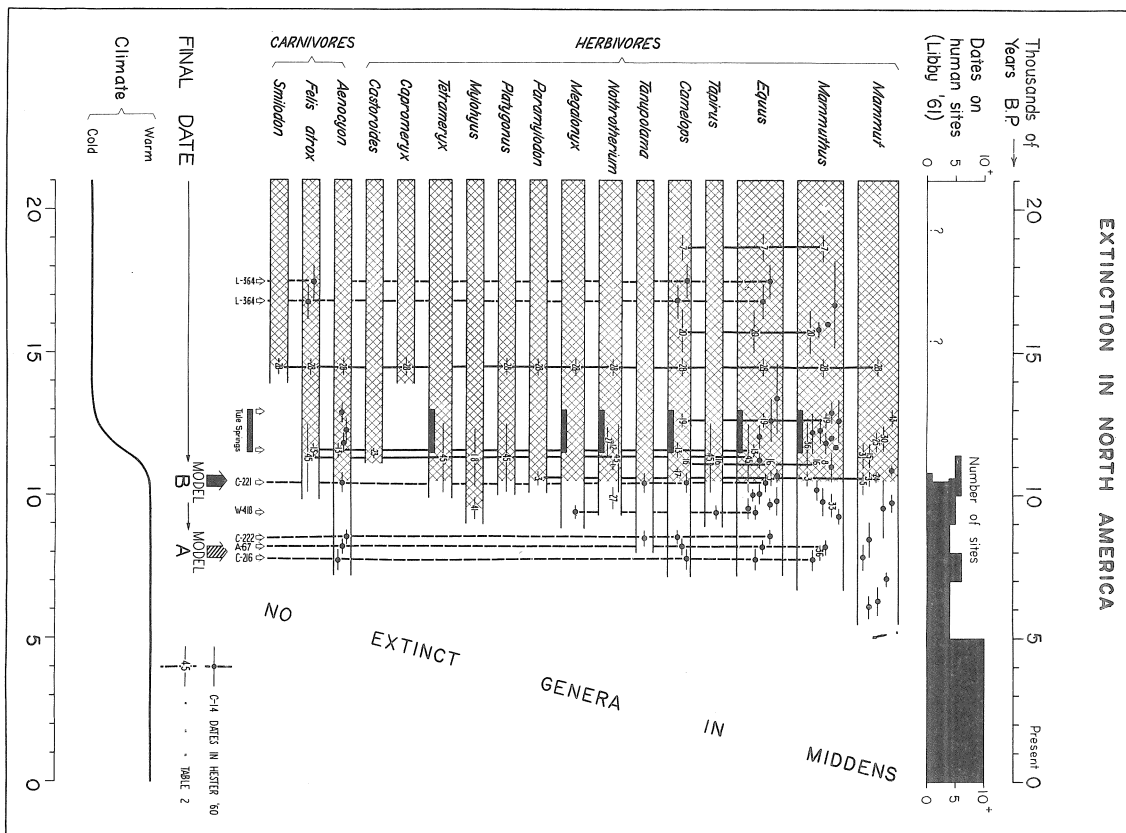
Table 2 (continued).

Site	Extinct genus	Sample	Years B.P.	Comment
45. Ventana Cave, Ariz.	<i>Nothrotherium</i> <i>Tetrameryx</i> , <i>Tapirus</i> , <i>Equus</i> , other species of the volcanic debris unit	A-203	11,300 ± 1,200	Charcoal
46. Genessee Co., Mich.	<i>Mammuthus</i>	M-1361	11,400 ± 400	Tusk, but agrees with pollen analysis of Oltz and Kapp
47. Kendall Co., Tex.	Extinct vertebrate fauna	Tx-250	> 10,600	Cave deposit, species not listed
48. Tupperville, Ontario (Perry Farm)	<i>Mammut</i>	GSC-211 S-172	11,860 ± 170 12,000 ± 200	Plant remains Plant remains
49. U.P. Mammoth, Wyo.	<i>Mammuthus</i>	I-449	*11,280 ± 350	Tusk, with associated artifacts
50. Wilson Butte Cave, Idaho	Horse, camel, sloth	M-1409 M-1410	14,500 ± 500 15,000 ± 800	Stratum C, with artifacts Stratum E, with artifacts

* Doubtful or unacceptable date, including dates on bone

P. S. MARTIN

Fig. 1. Carbon-14 dates and extinction of certain late-Pleistocene genera of North America.



PREHISTORIC OVERKILL

be sought. But even in the case of mastodon, to be discussed below, the claims for survival into the postglacial period (the last 10,000 years) can be questioned on grounds of ambiguous stratigraphic association, C^{14} age determination, or other uncertainty. In attempting to approach the terminal data for an extinct species, a certain number of "overshots" is to be expected. I am prepared to depart from my earlier view that a provocatively young date is likely to be accurate unless proved otherwise. The late- and postglacial sites in which dated beds of 10,000 to 8,000 B.P. fail to show a trace of extinct fauna include Frightful Cave; Coahuila (Taylor, 1956); cave deposits in the valley of Tehuacan, 9,000 years and younger in age (MacNeish, 1964); Danger Cave, Utah (Jennings, 1957, and Tx-85-89); Russell Cave, Alabama (M-766, M-590); Stanfield-Worley Bluff Shelter, Alabama (M-1152-3, M-1346-8); Kincaid Shelter, Texas (Tx-17-20); Eagle Cave, Texas (Tx-153); Raddatz Rockshelter, Wisconsin (Wittry, 1959, M-812, 813); and the pre-ceramic shell middens of Florida (Bullen, 1964) and California.

What do radiocarbon dates show concerning the extinct fauna itself? It is possible that extinct animals survived into the archaic of the early or mid-postglacial to coexist with human cultures that had abandoned their custom of hunting big game and were now hunting smaller prey and unknowingly making the first experiments with plant domestication? If all radiocarbon dates that Hester listed as questionable are discounted, the genera *Arctodus*, *Castoroides*, *Paramylodon*, *Platygonus*, *Smilodon*, and *Symbos* are associated with terminal dates of roughly 11,000 B.P. or older. None of the newer dates alters this interpretation (Table 2, Fig. 1). For the genera *Aenocyon* (*Canis dirus*), *Camelops*, *Equus*, *Mammut*, *Mammuthus*, *Megalonyx*, *Nothrotherium*, and *Tanupolama*, Hester lists terminal dates of roughly 8,000 B.P., with 6,000 B.P. for the mastodon. These form the basis of his conclusion that most of the fauna survived into the early postglacial.

For all genera except *Mammuthus* and *Mastodon* (to be considered below) there are only three sites, Gypsum Cave (C-222, 8,500 B.P.), Whitewater Draw (A-67, 8,200 B.P.; C-216, 7,800 B.P.), and Evansville, Indiana (W-418, 9,400 B.P.), on which the evidence for postglacial survival rests. One might expect, if they are valid terminal dates, to see them verified by newer records. But of the dates to appear since Hester's review (Table 2), only those that might easily have been contaminated, or those in uncertain stratigraphic association with the extinct fauna, are of postglacial age. Carefully controlled recent excavations at sites containing abundant bones of several genera of extinct animals in beds repeatedly and carefully dated, such as Tule Springs, Nevada, Blackwater Draw, New Mexico, and Lehner Ranch, Arizona, yielded no

evidence of generic survival beyond roughly 11,000 years ago. New dates on sloth (*Nothrotherium*) dung from Aden Crater (Y-1163b) and Gypsum Cave (LJ-452) are much closer to 11,000 than 8,000 years old. And despite its ideal nature from many standpoints, even sloth dung may not be totally free from contamination. A very small amount of younger wood or fiber, easily introduced into a cave by wood rats (*Neotoma*) could contaminate the sample, a possibility I would not discount for L-473A, 10,000 B.P., from Rampart Cave.

North American Mastodons and Mammoths

Haynes (1964) has reviewed the radiocarbon dates and cultural content of some of the best known Early Man-mammoth sites in North America. There is little doubt that Clovis fluted-point hunters pursued the mammoth for a very short period of time in western North America before being replaced after 11,000 B.P. by hunters who used Folsom points and killed *Bison*. Carefully dated extinct bison sites are well known in the postglacial period. There is no question of extinct *Bison* living thousands of years after 11,000 B.P. But what about the mammoth? Haynes (p. 1412) cautiously concludes that the change from Clovis to Folsom may be related to a decline in the mammoth populations. Not only are there no well documented cases of mammoth associated with man in postglacial deposits of the last 10,000 years, there are no well-documented cases of postglacial mammoth sites without him. Of the post-10,000-year dates on mammoth, M-744, W-288, JBN-311, and O-171 are questioned either by Hester or by authors of the date lists themselves. M-1400 is on tusk. C-216, A-67, and A-69 from Whitewater Draw and Murray Springs, Arizona, are not satisfactorily documented as far as the alleged association with mammoth is concerned. UCLA 705 was discussed above. The youngest securely dated records of mammoth are those of 11,000-year vintage from the Lehner Site, Tule Springs, Domebo (Leonhardy, 1966), and Clovis (Blackwater Draw). One possible exception is the Mexico City mammoth of San Bartolo Atepehuacan, found with an obsidian flake and no fewer than fifty-nine small chips of basalt and obsidian. A date on associated carbon fragments was 9,700 B.P. (M-776 Aveleyra, 1964, p. 404). Elsewhere there is every reason to assume that New World mammoths and their hunters had disappeared before 10,000 B.P.

There remains the matter of mastodon extinction, an event that most authors have regarded as postglacial, significantly later than the extinction of other Pleistocene genera and later than the early hunters. If it can be shown that mastodons were little affected by the intrusion of the

Clovis hunters and indeed survived them by 4,000 years, as Griffin claims (1965, p. 658), the case for prehistoric man as the major cause of extinction would certainly need to be seriously modified or abandoned. In addition to Griffin, Martin (1958), Hester (1960), Skeels (1962), and most recent authors except Quimby (1960) have accepted a terminal radiocarbon date at about 6,000 B.P. Commonly cited are dates on tusk from Lapeer County, Michigan, and on the Washtenaw County, Michigan, mastodon (M-347 and M-67 respectively), both around 6,000 B.P. In addition, there is an organic date of $6,250 \pm 250$ (S-16) on gyttja from Ferguson Farm, Tupperville, Ontario, immediately overlying bones of a mastodon. A collagen date on the bones themselves is significantly older (GSC 614, $8,910 \pm 150$). While even the latter is best regarded as a minimum date only, it is considered closer to the true age of the mastodon than the gyttja which is now thought to be intruded (A. Dreimanis, personal correspondence).

Is it possible that all postglacial dates on mastodons are overshots? No skeptical archaeologist would consider accepting a radiocarbon date of 6,000 to 8,000 years on an alleged Clovis site before subjecting it to the most minute excavation and examination, without demanding an effort at replication of the date on the critical beds, without considering carefully all the possibilities of intrusion, and without a field demonstration of the evidence to equally critical colleagues.

There are three reasons why cautious second thoughts may now be needed regarding widely accepted claims of postglacial mastodon survival. The first is the radiocarbon dates published in the last few years and listed in Table 2. Except for the Ferguson Farm date discussed above, all the new dates, which are on wood, gyttja, or material other than the bones themselves are of late-glacial age, ranging between 12,700 and 10,500 B.P. (W-1358, W-1038, Y-460, OWU-126, Pontiac, Michigan; I-586, S-29, S-30, and W-944). In contrast, of four mastodon dates on bone or tusk, three (M-694, M-347, and M-490) are younger than 9,500 B.P. The discrepancy between these and the organic dates may be attributed to inorganic carbonate replacement or to humic acid contamination rather than to a real difference in age of the fossils.

The second is the fact that palynological study of beds containing mastodon and mammoth bones in the northeast indicates an association with spruce-pine pollen zones (Ogden, 1965) and presumably spruce forests. This environment disappears from the Great Lakes with the retreat of Valdres ice about 10,500 years ago (Wright, 1964). Ogden quotes the 8,400-year radiocarbon date, supposedly associated with the Orleton Farms mastodon (M-66), but he does not mention that the pine-spruce pollen counts from near the mastodon bones must predate

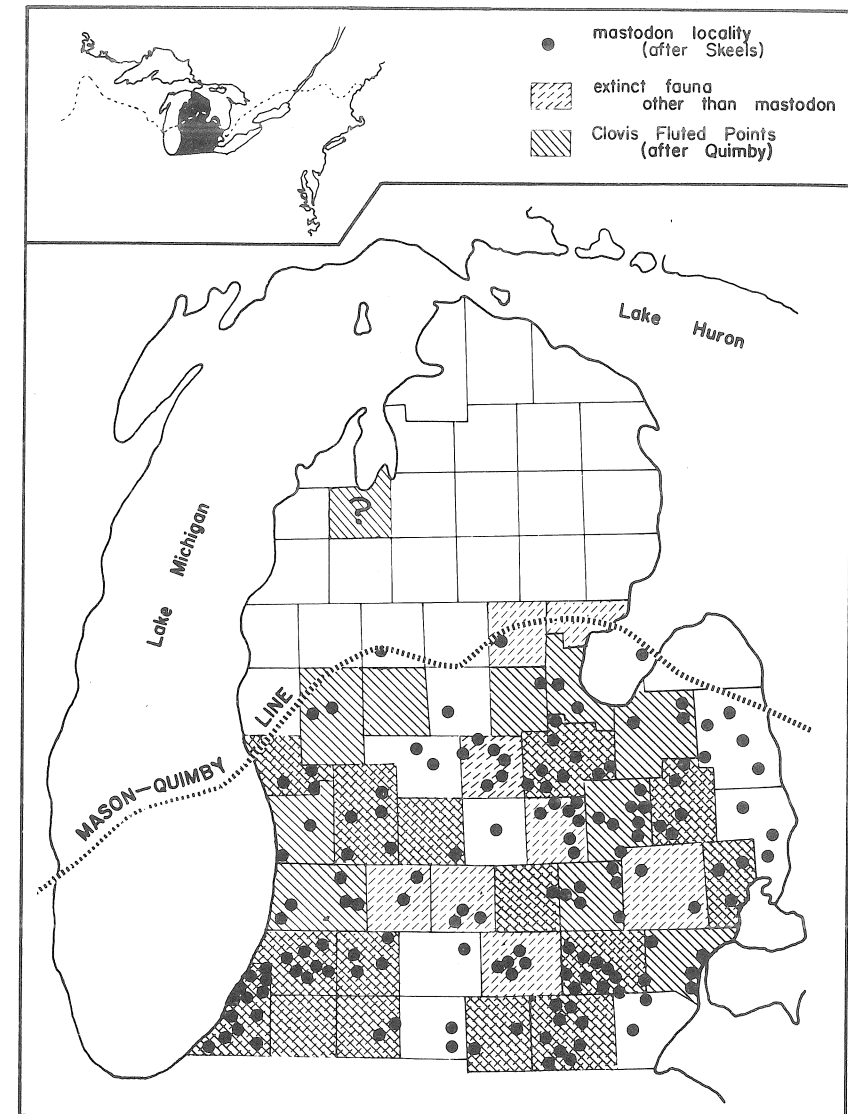


FIG. 2. Distribution of Michigan mastodons (after Skeels, 1962), other extinct Pleistocene genera, and fluted points (after Quimby, 1960).

this interval. Griffin (1965, p. 656) has rejected as not in direct association the Archaic projectile points found near the Orleton and other mastodons. The radiocarbon date (M-66) may be no more reliable.

The third difficulty in accepting a 6,000-year extinction date for mastodon emerges from study of its fossil distribution (Fig. 2). This proboscidean is the most common Pleistocene fossil in northeastern United States, so it may have once been as important in vertebrate biomass of the region as *Loxodonta* is in the game parks of central Africa. Skeels (1962) reports 163 records from Michigan alone. She proposes that its extinction there was hastened by its failure to follow the boreal forest environment across the Great Lakes into Canada after deglaciation. But the northern limit of the mastodons in Michigan is not the Straits of Mackinac, as one might imagine if the elephants were trapped in a cul-de-sac south of the Great Lakes. The distribution of the 163 fossils is remarkable (Fig. 2). Although both mastodons and mammoths succeeded in crossing the Grand River outlet of Lake Warren, they did not range beyond Osceola and Gladwin counties at the latitude of Saginaw Bay (44° N). Equally remarkable is the distribution of fluted points from surface sites in Michigan. As Quimby (1958, 1960) noted, they are found only in the same part of the state as fossil mastodons—but south of what I have drawn as the “Mason–Quimby Line.” One doubtful record, possibly an import, is that of a fluted point in Grand Traverse County (J. B. Griffin, personal correspondence).

The fluted-point hunters are regarded as occupying the lower peninsula of Michigan between the time of deglaciation and before the abandonment of the Main Algonquin Lake level, which was 24 ft above present Lake Huron (Griffin, 1965, p. 659). In the chronology of the Great Lakes post-Algonquin beaches were forming 10,500 to 10,000 years ago. From Skeel's map, it seems possible that a few mastodons saw the initial fall of Lake Algonquin; there are three fossil records in the Saginaw Bay region that appear to lie below Algonquin beach levels.

The mystery of why fauna and fluted points apparently terminated at the Mason–Quimby Line (Fig. 2), rather than reaching the Valdres ice margin, remains unexplained. But it is a minor matter compared with that of explaining why, if the species survived until 6,000 years ago, mastodons failed to spread throughout the state, and from the beachhead in southern Ontario on into central Canada. Beyond possible interglacial records there are no bones of mastodon north of the fluted-point line of Mason (1962) copied on the inset of Figure 2. A more than coincidental association between fluted points and mastodons in the Southeast is mapped by Williams and Stoltman (1965, p. 677).

Griffin (1965) protests the lack of stratigraphic association between

fluted points and extinct fauna in the East. But there are very few stratified fluted-point sites anywhere in mastodon country east of the Mississippi, and fewer in which suitable conditions for bone preservation exist. Unless more substantial documentation is forthcoming, present claims of postglacial mastodon survival based on radiocarbon evidence alone are insufficient. Meanwhile, the Mason–Quimby Line is evidence of the sort to be expected if overkill were the cause of mastodon extinction.

This hypothesis also makes credible some of the peculiar cultural attributes of the Paleo-Indians. Mason (1962, p. 242) concluded:

It seems more than coincidental that the end of the Paleo-Indian cultural dominance, as measured by radiocarbon and other dating techniques, agrees closely with the demise of the fossil Pleistocene big-game animals; or to put it another way, that it was during the period characterized archaeologically by such artifact types as Folsom and Clovis that the great Pleistocene extinctions were taking place. It would push the limits of credibility to view as likewise coincidental the fact of the emergence of the generalized subsistence basis of the Archaic cultures during the disappearance of the Pleistocene fauna and fluted points. In other words, there is expressed a functional relationship between these culture types and the total ecology of which they are parts.

I have purposely avoided the question of a “pre-projectile-point stage.” Bryan (1965) develops the hypothesis of a generalized leaf-shaped, percussion-flaked, stone-point tradition innovated in North America fairly early in the Wisconsin glacial stage. Müller-Beck (1966) states that “The first invasion of man in the New World for which a reliable archaeological reconstruction seems possible—there could have been earlier invasions—took place about 28,000 to 26,000 years ago.” Both authors advance their conclusions on typological and paleontological grounds, recognizing that there is no indisputable radiocarbon-dated evidence for man in the New World older than that associated with the fluted-point hunters of around 12,000 years ago. If C^{14} dates from Wilson Butte Cave, Idaho, can be replicated, it may extend man's New World chronology.

The possibility that *Homo sapiens* spread into the Americas long before the late-glacial by no means eliminates the hypothesis of overkill. One may assert that the postulated users of core tools, choppers, and perhaps even bone tools were not specialized for killing big game, and thus had little effect on the megafauna, unlike the Clovis hunters of elephants or the Folsom hunters of extinct *Bison*. Possibly the easily hunted giant species of *Geochelone*, as yet unknown in beds of late-

glacial age of the American continent, owe their extinction to a pre-projectile-point culture. What would upset the hypothesis of overkill would be clear-cut cases on the continent of many of the extinct animals surviving beyond the time of the big-game hunters, or clear-cut cases of massive unbalanced Pleistocene extinction anywhere before man.

NEW ZEALAND

That extinction of a variety of medium to large-sized herbivores can occur within a few hundred years after prehistoric man's initial appearance is shown by the extinction chronology of New Zealand (Fleming, 1962). New Zealand occupies 103,000 square miles, slightly smaller than the State of Colorado. There were no native terrestrial mammals, but twenty-seven species of extinct moas, including a 10-ft-tall *Dinornis maximus*, have been discovered in astonishing numbers in postglacial deposits, 800 to the acre in Pyramid Valley and that many in a pocket (30 × 20 × 10 ft deep) at Kapua (Duff, 1952). These giant flightless birds can be traced to the late-Miocene (*Anomalapteryx*). Regarding extinction, the orthodox theory was that many were extinct before man arrived, thus most had died out naturally (Duff, 1963a, p. 6). Partly on the basis of radiocarbon dates of moa bones, stomach contents, associated charcoal, and tussock bedding and partly on recent archaeological findings, Fleming (1962) has concluded that such was not the case. Twenty-two of the extinct moa species have now been found in association with prehistoric man (Fig. 3, Table 3). Sixteen moas have been dated by radiocarbon analysis of the bone itself, although some of the bone may have been contaminated by younger humates. In addition to the moas, a number of other birds became extinct in the same general period; half of these have been found in cultural association. Reviewing the last ten years of New Zealand archaeology, Golson and Gathercole (1962) conclude: "Nevertheless one definite result has emerged from this aspect of the decade's work. Possible climatic and genetic factors notwithstanding, man as the moa's first mammalian predator was a prime instrument in its extinction."

Duff (1963a, p. 6) has abandoned his hypothesis that moa extinction must have been due largely to natural causes, although he is still concerned with the absence of the giant moa *Dinornis maximus* in most of the moa-hunter camps; he still suggests a considerable reduction in moa numbers before man's arrival.

Fleming (1962) reports little evidence of early and mid-Holocene moa extinction, an extremely important fact in comparing the New Zealand pattern with that of Australia and the Americas. Despite

TABLE 3. New Zealand Dates and Extinct Fauna

Locality	Fauna	Sample	Date A.D.	Comment
1. Blenheim	(Moa hunter site)	NZ-50	1100	Charcoal
2. Paptowai, Otago	(Moa hunter site)	NZ-134	1185	Charcoal
3. Hina Hina	(Moa hunter site)	NZ-53	1210	Charcoal
4. Tahakopa River Mouth, Otago	<i>Dinornis maximus</i> <i>Euryapteryx gravis</i>	NZ-136	1320	Charcoal
		NZ-137	1490	Bone of <i>Euryapteryx</i>
		NZ-138	1490	Bone of <i>Dinornis</i>
		NZ-139	1640	Bone of <i>Euryapteryx</i>
		NZ-140	1560	<i>Moa</i> sp. All bone dates may be too young.
5. Hawksburn Valley, Otago	Moa bones	NZ-62	1350	Charcoal
		NZ-61	1360	Charred wood with <i>Moa</i> bone fragments
6. Tautuku, Otago	<i>Dinornis torosus</i>	NZ-60	1500	Femur of <i>Euryapteryx</i>
		NZ-59	1550	Burned <i>Moa</i> bone
		NZ-146	1670	In occupation deposit

piedmont glaciation and widespread periglacial phenomena on South Island and despite volcanism with the extensive blanketing of North Island by nutrient-poor pumice and ash, no species of the giant birds are definitely known to have disappeared before man's arrival.

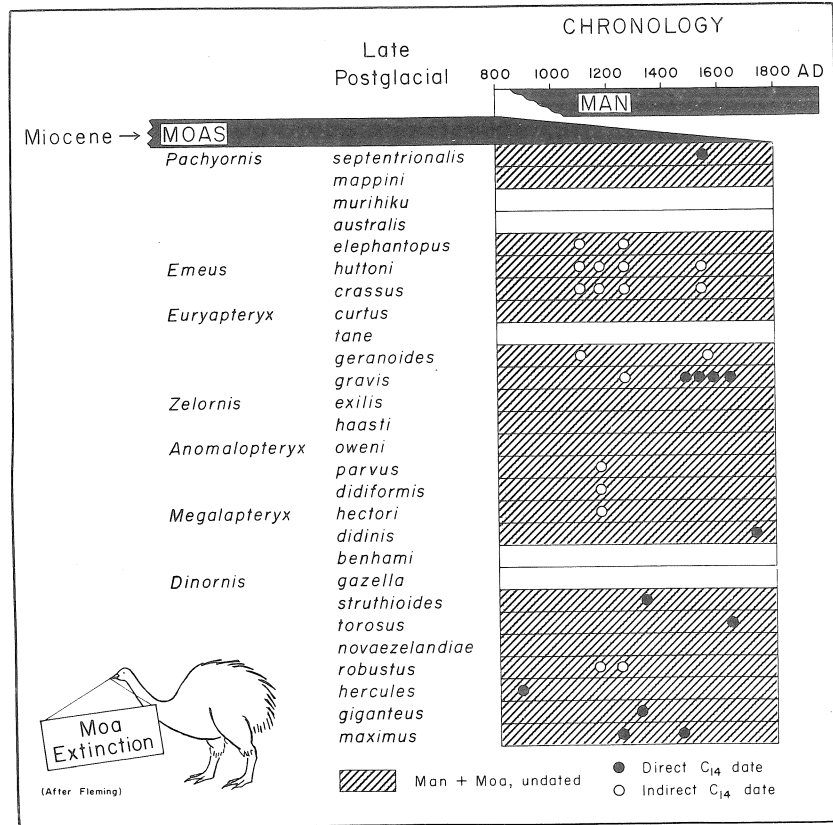


FIG. 3. Carbon-14 dates and extinction of moas in New Zealand (after Fleming, 1962).

Duff (1963b) notes that the moa hunters must have independently developed techniques for seeking their prey; they were of East Polynesian origin and, unlike the Upper Paleolithic cultures, had no tradition of big-game hunting. They developed new techniques fairly rapidly. A simple one was fire, widely used in South Island, to judge by charcoal horizons in the soil. Golson and Gathercole claim that the moa hunters retained their tools even after the birds were largely extinct and marine resources were their main source of food. Retention of hunting tools

and persistence of a hunting tradition through the time of minimum numbers of his prey would establish man's role as a superpredator, still selecting big game whenever possible, even after his main food supply came from other sources.

Ultimately, when the Maori arrived in A.D. 1350, most of the giant birds were gone, so when first questioned on the subject a hundred years ago the Maori could provide no convincing accounts of the birds. Less explicable was the initial refusal of New Zealand scientists to regard prehistoric man as the cause for moa extinction. Fleming (1962, p. 116) remarks:

It seems we are reluctant to blame our fellow men for a pre-historic offense against modern conservation ideals and would rather blame climate or the animals themselves. The simplest explanation is to attribute all late Holocene extinction to the profound ecological changes brought about by the arrival of man with fire, rats, and dogs.

AUSTRALIA

Crop contents of the extinct giant marsupial (*Diprotodon*) were dated at over 40,000 B.P. (NZ-205); dentine from a lower jaw of *Diprotodon* was 6,700 B.P. (NZ-206), apparently too young to represent the true age of the fossil (Table 4). At Lake Menindee a rich assemblage of extinct marsupials can be associated with GaK-335 (19,000 B.P.) and LJ-204 (26,000 B.P.). Although Gill (1963) concludes that aboriginal entry began at least 20,000 years ago, the evidence of man at the time has been questioned by Mulvaney (1964). More convincing dates on prehistoric man are GaK-334 (11,600 B.P.) from Nools, where Tindale recovered a flake assemblage below a microlith assemblage, and those at Kenniff Cave, where Mulvaney (1964) obtained samples dated at 13,000 and 16,000 years (NPL 33 and 68) and associated with a "Tasmanoid" industry.

Younger dates from Lake Menindee, NZ-66 and W-169 of 6,000 and 8,600, respectively, are now thought to be associated with essentially modern faunas (Hubbs et al., 1962). A terminal date for *Nototherium* (not to be confused with the southwestern United States sloth *Nothrotherium*) may be Gx-105, 14,000 B.P., on bone fragments of a jaw. Although all bone carbonate dates are suspect, the age agreed with the collectors' estimate and is also equivalent with Y-170, 13,700 B.P., according to Hubbs et al. (1962), the youngest dating definitely applicable to a varied assemblage of giant marsupials. This is in accord with absence of extinct fauna from Nansump Cave in beds dated at 12,000 B.P. (Lundelius, 1960.)

TABLE 4. Australian Dates and Extinct Fauna

Locality	Fauna	Sample	Date	Comment
1. Lake Menindee, N.S.W.	<i>Macropus</i> <i>Terragus</i> (giant kangaroo) Extinct animals	LJ-204	26,300 ± 150	Charcoal from hearth
2. Boolounda Creek, S. Australia	<i>Nototherium</i>	GaK-335 GX-105	18,800 ± 800 14,000 ± 250	Charcoal from hearth Bone fragments from jaw
3. Orroroo, S. Australia	<i>Diprotodon</i>	NZ-381	11,100 ± 130	Molar
4. Lake Callabona, S. Australia	<i>Diprotodon</i>	NZ-206	6,700 ± 250	Dentine from lower jaw, supposedly same animal as WZ-205, > 40,000 (crop contents)
5. Lake Menindee, S. Australia	Extinct genera	NZ-66	6,570 ± 100	Shells associated with Tartangan artifacts

Thus it appears that both prehistoric hunters and the main wave of extinction swept through Australia slightly before these events occurred in North America. Many additional geochronological data are needed before intercontinental cultural, climatic, and extinction chronologies can be compared more critically. But there is no longer doubt that man and the extinct Australian marsupials coexisted (Gill, 1963).

TROPICAL AMERICA

Although the extinct late-Pleistocene fauna from Central and South America is less well known than that of the United States, it is obvious that the inventory of extinct genera and species exceeds that of higher latitudes. In a preliminary account of a single fauna in Bolivia, Hofstetter (1963) recovered the following extinct genera, far more than are known from any single fossil locality in North America: *Nothropus*, *Megatherium*, *Glossotherium*, *Lestodon*, *Scelidotherium*, *Glyptodon*, *Chlamydothorium*, *Neothoracophorus*, *Hoplophorus*, *Panochthus*, *Neochoerus*, *Theriodictis*, *Arctotherium*, *Smilodon*, *Macrauchenia*, *Toxodon*, *Cuvieronius*, *Notiomastodon*, *Hippidion*, *Onhippidium*, *Palaeolama*, and *Charitoceros*. It is apparent that the Pleistocene game range of South America was especially well stocked, as one would expect in a tropical ecosystem. Extinction impoverished the tropical American fauna to a greater degree than that of the temperate regions. Did it occur before, after, or coincidental with extinction in temperate North America?

In South America, sloth dung, one of the best materials for critical radiocarbon dating, indicates survival to just over 10,000 years ago of ground sloth associated with extinct horse at Mylodon Cave and Fells Cave (Sa-49, W-915, C-484) (Table 5). If C-485 (8,639 B.P.) on burned bone from Palli Aike Cave, Chile, and Sa-47 (6,500 B.P.), Ponsomby, Patagonia, are also correctly associated with sloth and horse, a remarkably late survival could be claimed. However, no extinct animal remains were found in somewhat older rock shelters from Minas Gerais, Brazil (P-521, P-519), excavated by W. B. Hurt. For this reason the use of Palli Aike, Ponsomby, and certainly the 3,000-year age on "extinct giant bear" from Minas Gerais (M-354) may be questioned as valid terminal dates for the fauna. If the date of 14,000 B.P. (M-1068) from Falcon, Venezuela, associated with extinct giant sloths, horse, and mastodon, is also associated correctly with big-game hunters in South America, it would, of course, obliterate the concept of their relatively late (12,000 B.P.) arrival in the New World. Apparently, more dates support the view that extinction in South America coincided with or slightly postdated that in North America, but those who believe in a slow,

TABLE 5. South American Dates Associated with Extinct Fauna

Locality (Radiocarbon, Vols. 1-7)	Fauna	Sample	Date	Comment
1. Muaco Site, Falcon, Venezuela	Mastodon <i>Megatherium</i> , <i>Equus</i>	M-1068	14,300 ± 500	Association with Early Man needs verification
2. Fell's Cave, Chile	Giant sloth, horse	W-915 Sa-49	10,720 ± 30 10,200 ± 400	Charcoal from firepit Sloth dung, C-484, in same layer as 10,832 ± 400
3. Ponsomby, Patagonia	Extinct horse	Sa-47	6,500 ± 400	Date on peat deposit associated with the oldest archaeological level

steady reduction of the late-Pleistocene fauna over tens or hundreds of thousands of years have yet to be confronted with the sort of dating evidence that invalidates this interpretation elsewhere.

In the West Indies, extinct vertebrates were of too small a size to have suffered extermination on the mainland (Martin, 1958, p. 409). Rouse (1964) attributes the extinction of at least some of the twenty-two genera of mammals found in prehistoric middens and cave earth to the arrival of man two to four thousand years ago. Subfossil "giant" species of small or medium-sized terrestrial vertebrates are still being discovered (cf. Ethridge, 1964), and a giant land snail, presumably also extinct, is known from Hispaniola (Clench, 1962). Whereas some of the native West Indian fauna may have disappeared as a result of catastrophic post-Columbian ecologic changes, brought by the introduction of *Rattus*, it appears that more disappeared before the fifteenth century. Here, as elsewhere, the main circumstance pointing toward prehistoric man's role in extinction, without shedding light on details of the process, is the matter of chronology. The fauna survives until man arrives.

On the continent, there is some archaeofaunal evidence of local extirpation of medium-sized animals in certain intensely occupied areas like the Valley of Mexico, where Vaillant (1944) reported deer (*Odocoileus*) to be virtually exterminated two thousand years ago. The postglacial withdrawal of mule deer and antelope from southern parts of the Mexican Plateau has been attributed to vegetation change (Alvarez, 1964; Flannery, 1966), but overkill by expanding prehistoric populations seems at least equally probable. Peccary, marmot, and porcupine bones are notably scarce or absent in refuse from the more densely inhabited parts of the prehistoric Southwest. Local hunting may have wiped out these mammals during the late Pueblo period. In the Antilles, late prehistoric extinction of the larger lizards, rodents, and sloths probably occurred as a result of intense seasonal search for animal protein, when the relatively numerous prehistoric tribes were not cultivating manioc and maize, their mainstay. A comparable region in which the effect of prehistoric man on extinction of medium- to small-sized animals remains to be determined is the islands of the Mediterranean. The disappearance of *Myotragus* in Minorca seems much more closely timed to the earliest record of human occupation of the island than was once realized (Waldren, personal correspondence).

AFRICA

The "rose-colored glasses" view of prehistoric man in Africa is well put by Harper (1945, p. 15): "As long as the African Continent was occupied by primitive savages, without modern weapons, animal life was, in a

large sense, in a virtual state of equilibrium." I shall take this opportunity to point out a grave error in the assumptions of various scientists writing on the question of big game and the Pleistocene (e.g. Eiseley, 1943; Mason, 1962, p. 243; Leopold in Talbot and Talbot, 1963, p. 5; and, alas, Martin, 1958, p. 412). These authors failed to realize that Africa, no less than the other continents, suffered its episode of accelerated megafaunal extinction. Perhaps some of them were thinking of the last twenty thousand years, when it is true that practically no extinction occurred (Flint, 1957, p. 277; Butzer, 1964, p. 400). Perhaps others were misled by Theodore Roosevelt's chapter (1910), "A Railroad Through the Pleistocene," where he compares the game of the East African plains with the American Pleistocene fauna. Whatever the reason, they have assumed that the African megafauna survived the Pleistocene unscathed, and Eiseley in particular has used this point as an argument against the hypothesis of New World overkill.

Although its fossil fauna is far from adequately known, roughly fifty genera disappeared during the Pleistocene (see Hopwood and Hollyfield, 1954; Cooke, 1963). Furthermore, in Africa, as in America, most of the surviving large animals are also known as Pleistocene contemporaries of the extinct genera. The living genera of African big game represent only 70 per cent of the middle-Pleistocene complement (Martin, 1966). Thus despite its extraordinary diversity, the living African fauna must be regarded as depauperate, albeit much less so than that of America or Australia.

The time of "middle"-Pleistocene extinction was barely within the range of reliable dating by radiocarbon—i.e. over just forty thousand years ago. Fortunately, the rich archaeological content of many fossil beds aids in age interpretation. Toward the end of the Acheulian, and often associated with the stone bifaces and other tools of these big-game hunters in sites such as Olduvai (Bed IV) in Tanzania, Olorgesailie and Kariandusi in Kenya, and Hopefield and the Vaal River gravels in South Africa, the following large mammals are last recorded: *Mesochoerus*, *Tapinochoerus*, *Stylochoerus*, *Libytherium*, *Simopithecus*, *Archidiskodon* (*Elephas*), and *Stylohipparion*. Eight additional extinct genera of the period are known only from middle, or occasionally late, Pleistocene sites in South Africa (Cooke, 1963, p. 98–101). All are absent from Middle Stone Age sites, and thus were extinct *before* the major depression of African montane vegetation zones of full- and late-glacial age recently reported by pollen stratigraphers (Coetzee, 1964; Livingstone, 1962; Morrison, 1961; Van Zinderen Bakker, 1962).

On stratigraphic and faunal evidence, Leakey (1965) attributes extinction of the Olduvai Gorge genera to drought. Clark (1962) places the

evolved Acheulian at about 57,000 B.P., and, on the basis of intercontinental correlation with the Brørup Interstadial, he considers the First Intermediate Period (after the Acheulian) of 40,000 B.P. to have been dry.

If drought decimated the African mainland fauna at the end of the Middle Pleistocene, it managed to leave unscathed the endemic and ecologically vulnerable insular fauna of Madagascar. Seven genera of extinct lemurs, the pigmy hippopotamus, two species of giant tortoise, and two genera of struthious birds occur in very late Pleistocene beds. No earlier episode of extinction is known there. All the animals were contemporaries of prehistoric man, who did not reach the island until remarkably late in the postglacial. One date on charcoal associated with pottery and iron hooks is also a time when the roc, *Aepyornis maximus*, was abundant (GaK-276, A.D. 1100). Unless substantial paleobotanical evidence for a unique drought can be found in the "First Intermediate Period" in Africa, or evidence for a major decline of the Malagasy fauna prior to man's arrival, the evidence for a climatic cause of extinction in Africa suffers from the same ad hoc appeal that has made it an unacceptable explanation for the pattern elsewhere.

Late-Pleistocene extinction in Africa long precedes that in the Americas and Australia, as would be expected in view of man's gradual evolution in Africa. A major point for paleontologists to recognize is that the question "Why no extinction in Africa despite man's antiquity?" is misleading. There was a major wave of generic extinction in Africa although not so intense as in South America. Extinction in Africa seems to coincide with the maximum development of the most advanced early Stone Age hunting cultures, the evolved Acheulian of abundant, continent-wide distribution. The case of Africa neither refutes the hypothesis of overkill nor supports the hypothesis of worldwide climatic change as a cause of extinction (Martin, 1966).

CONCLUSION

In continental North America, the only major episode of generic extinction in the Pleistocene occurred close to eleven thousand years ago (Fig. 1). Provisional ages for the start of major extinction episodes elsewhere are: South America, 10,000 B.P.; West Indies, mid-postglacial; Australia, 13,000 B.P.; New Zealand, 900 B.P. (Fig. 3); Madagascar, very late postglacial (800 B.P.); northern Eurasia (four genera only), 13,000 to 11,000 B.P. (Table 6); Africa and probably Southeast Asia, before 40,000 to 50,000 B.P. Radiocarbon dates, pollen profiles associated with extinct animal remains, and new stratigraphic and

TABLE 6. Eurasian Dates and Extinct Fauna

Locality	Fauna	Sample	Date	Comment
1. Lena River, Siberia	<i>Mammuthus</i>	Y-633	30,000	Skin
2. Lake Nojiri, Japan	<i>Megaceros</i>	GaK-269	31,000 ± 2,500	Wood, 97 cm
	<i>Elephas</i> sp.	GaK-268	21,600 ± 900	Wood, 61 cm
		GaK-267	16,150 ± 550	Wood, 40 cm
3. Yokoyama, Japan	<i>Elephas</i> , horse	GaK-312	28,400 ± 1,800	Charred wood
	<i>Megaceros</i>			
4. North London, England	Mammoth, reindeer	Q-25	28,000 ± 1,500	Plant debris
5. Chekolsouka, Siberia	<i>Mammuthus</i>	MO-215	26,000 ± 1,600	Mammoth hair
6. Cambridge, England	Reindeer, <i>Mammuthus</i>	Q-590	19,500 ± 650	Plant detritus
7. Lascaux Cave, France	(Magdalenian paintings)	GrN-1632	17,190 ± 140	Charcoal
8. Lascaux Cave, France		Sa-102	16,100 ± 500	Charcoal
9. Hanaizumi Formation, Japan	<i>Palaeoloxodon tokunagai</i> <i>Megaceros</i> , <i>Loxodonta</i>	Y-594	15,850 ± 360	Wood with worked (?) bones
		N-132, N-133 N-141-3	14,900 to > 36,800	Relationship to fossils not given in date list
10. Naguno, Japan	<i>Megaceros</i>	GaK-161	15,750 ± 390	Wood with giant elk bones
11. Pont du Chateau, France	Elephant, rhino, horse, cave bear, etc.	Sa-103	13,500 ± 450	Peat, beneath the fauna
12. Peggau, Austria	Cave bear	GrN-2036	13,370 ± 150	Charred wood
13. Vailly-sur-Aisne, France	Mammoth	Sa-53	11,550 ± 450	Tooth
14. Taimyr Peninsula, Taimyr Lake, Siberia	Woolly mammoth	T-297	11,450 ± 250	Sinews
	Woolly mammoth	Mo-3	11,700 ± 300	<i>Salix</i> wood from mammoth horizon
15. Bernese Overland, Switzerland	Cave bear	B-152	10,150 ± 200	Bones
		B-153	9,500 ± 150	Bones
16. Calabria, Italy	"Pleistocene fauna with extinct species"	R-186	10,030 ± 90	Charred bones, Upper Paleolithic industry
17. Kunda, Estonian SSR	Mammoth	TA-12	9,780 ± 260	Tusk, does not belong to Mesolithic campsite
18. Couternon, France	<i>Elephas primigenius</i>	Gif-341	9,440 ± 350	<i>Pinus sylvestris</i> fragment; mammoth found at same level
19. Helsinki, Finland	Mammoth	Tx-127	9,030 ± 105	Bone, too young to agree with pollen content
20. Derbyshire, England	Mammoth, hyena, horse, etc.	Q-551	8,800 ± 300	Charcoal, unaccountably young ages
		Q-552	7,662 ± 140	
		Q-553/4	6,915 ± 140	
			6,705 ± 140	
21. La Manche, France	Mammoth tooth	Gif-342	8,720 ± 300	Total carbonate sample

archaeofaunal evidence show that, depending on the region involved, late-Pleistocene extinction occurred either after, during, or somewhat before worldwide climatic cooling of the last maximum of Würm-Weichsel-Wisconsin glaciation (Fig. 4).

While it occurred at a time of climatic change, the pattern appears to be independent of a climatic cause. Outside continental Africa and Southeast Asia, massive extinction is unknown before the earliest known arrival of prehistoric man. In the case of Africa, massive extinction coincides with the final development of Acheulean hunting cultures, which are widespread throughout the continent.

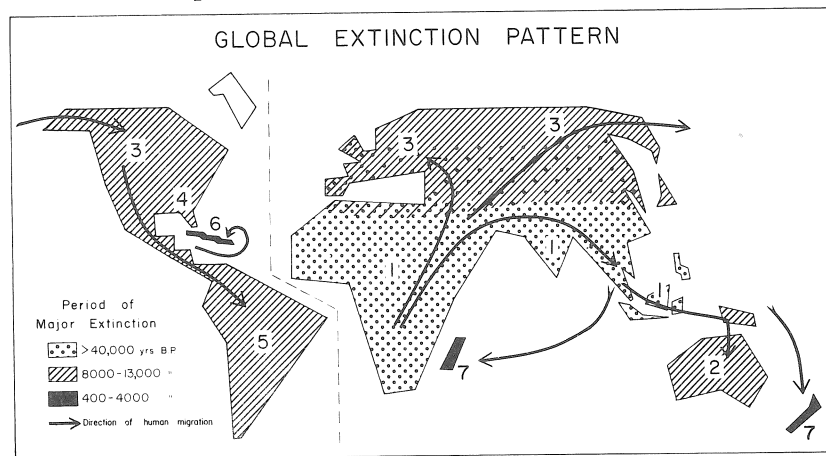


FIG. 4. The global pattern of late-Pleistocene extinction in sequence: 1, Africa and southern Eurasia; 2, New Guinea and Australia; 3, Northern Eurasia and northern North America; 4, southeastern United States; 5, South America; 6, West Indies; 7, Madagascar and New Zealand. In each case, the major wave of late-Pleistocene extinction does not occur until prehistoric hunters arrive.

Yet the notion of prehistoric overkill is commonly dismissed out of hand. In his book on extinct and vanishing birds of the last few hundred years Greenway (1958, p. 29) suggests that prehistoric men and birds "arranged a means of living together to the end that no birds were extirpated." At least one very perceptive neo-Darwinian evolutionist and humanist probably speaks for many in regarding it as "almost inconceivable that Indians alone put an end to the whole vast horse population of the late Pleistocene over so enormous an area." After considering and discounting all other possible explanations of horse extinction at the end of the Pleistocene, Simpson (1961, p. 200) held:

This seems at present one of the situations in which we must be humble and honest and admit that we simply do not know the answer. It must be remembered too that extinction of the horses in the New World is only part of a larger problem. Many other animals became extinct here at about the same time. The general cause of extinction then or at earlier times must have been the occurrence of changes to which the animal populations could not adapt themselves. But what precisely were those changes?

Indeed, it is not when horses alone but when the full complement of extinct Pleistocene animals are considered, when all major land masses are included in the analysis, and especially when the chronology of extinction is critically set against the chronology of human migrations and cultural development (as in Fig. 4) that man's arrival emerges as the only reasonable answer to Simpson's question. To be sure there is much ignorance left to admit. We must beg the question of just how and why prehistoric man obliterated his prey. We may speculate but we cannot determine how moose, elk, and caribou managed to survive while horse, ground sloth, and mastodon did not. One must acknowledge that within historic time the Bushmen and other primitive hunters at a Paleolithic level of technology have not exterminated their game resources, certainly not in any way comparable to the devastation of the late-Pleistocene. These and other valid objections to the hypothesis of overkill remain. But thus far the hypothesis has survived every critical chronological test. On a world scale the pattern of Pleistocene extinction makes no sense in terms of climatic or environmental change. During the Pleistocene, accelerated extinction occurs only on land and only after man invades or develops specialized big-game hunting weapons.

It seems to me that the chronologic evidence strongly supports the conclusion of an earlier Darwinian who took pains not to dismiss the phenomenon as trivial and who ended a lifetime of study by concluding, in a generally overlooked part of his work, that man must in some way be the destructive agent (Wallace, 1911, p. 261-67).

The thought that prehistoric hunters ten to fifteen thousand years ago, (and in Africa over forty thousand years ago) exterminated far more large animals than has modern man with modern weapons and advanced technology is certainly provocative and perhaps even deeply disturbing. With a certain inadmissible pride we may prefer to regard ourselves, not our remote predecessors, as holding uncontested claim to being the arch destroyers of native fauna. But this seems not to be the case. Have we dismissed too casually the possibility of prehistoric overkill? The late-Pleistocene extinction pattern leaves little room for any other explanation.

I have sought and received stimulating conversation and correspondence on this problem from colleagues, teachers, and students. Without attempting to evaluate the magnitude of their help, or to imply their endorsement of my use of it, my grateful thanks at least are due the following: J. B. Griffin, J. E. Mosiman, L. S. B. Leakey, D. Livingstone, J. G. Clarke, C. V. Haynes, V. M. Bryant, P. J. Mehringer, J. Schoenwetter, M. S. Stevens, J. Elson, C. W. Hibbard, Roger Duff, R. J. Mason, Ruth Gruhn, D. S. Byers, C. Ray, K. P. Koopman, A. Dreimanis, M. K. Hecht, and C. A. Reed. It goes without saying that each contributor to the chapters in this book has greatly added to my efforts at understanding the extinction problem. A final acknowledgment remains, above all, to Marian.

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DIFFERENTIAL EXTINCTION DURING LATE-PLEISTOCENE AND RECENT TIMES

Abstract

In any deteriorating ecosystem, large herbivores are more drastically affected than are small herbivores, by virtue of their greater demands upon the system for space, food, and cover. This produces a situation of differential extinction; the large "big-game" forms are eliminated. This is a natural consequence of interspecific ecological competition operative throughout the history of terrestrial vertebrate evolution.

Our inability to account for individual extinctions, such as that of the ground sloths, and for continental extinction patterns is not due to lack of adequate reasons but merely to lack of grounds for singling out one or several of a great variety of possible causes. The great prime mover was the unprecedented (at least in mammalian history) harshening of the environment during the Pleistocene, with sudden and great changes in the distribution of temperature and moisture throughout the world. To single out a particular predator or a set of circumstances is fun but futile.

Attempts to sharpen the focus of the extinction picture by singling out possible causes may not be possible. It is inconceivable that the same extinction pattern prevailed throughout the globe without being affected by local conditions—accidents of geography, local climates, different faunal and floral associations. The fact that these late-Pleistocene extinctions were so widespread and geographically almost simultaneous does call for a major overlying cause, however. I suggest that the prime mover was post-Pleistocene desiccation. Evidence for such an episode is present on all continents, and its effects would have been both swift and lethal. It may have been the spur to turn man from hunting to a life centered around animal husbandry and agriculture.

For at least a century naturalists have noted and speculated upon the cause of worldwide extinction of many large terrestrial mammals in the