

**PLEISTOCENE EXTINCTIONS
IN THE CONTEXT OF
ORIGINATION-EXTINCTION EQUILIBRIA
IN CENOZOIC MAMMALS**

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Pleistocene Extinctions in the Context of Origination-Extinction Equilibria in Cenozoic Mammals

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SOME OF THE MOST INTERESTING MAMMALS of the Pleistocene are now extinct. The rhino-sized marsupial *Diprotodon* of Australia, the large koala-like primate *Megaladapis* of Madagascar, the antlered giraffe *Sivatherium* and robust hominid *Australopithecus* of Africa, the woolly rhinoceros *Coelodonta* of Eurasia, the camel-like litoptern *Macrauchenia* of South America, and the giant beaver *Castoroides*, Jefferson's ground sloth *Megalonyx*, and mastodon *Mammot* of North America are representative of animals no longer with us. The Pleistocene sabertooth cats, *Smilodon*, *Dinobastis*, and *Homotherium*, are among the most conspicuous of extinct carnivores.

Viewed in the context of the entire Cenozoic era, are Pleistocene extinctions unusual? Thinking more broadly, how are the disappearances of old taxa (extinction) related to the evolutionary first appearances of new taxa (origination)? How is our understanding of both of these processes colored by problems of perception in comparing relatively recent events with older ones receding and fading into the geological past?

Patterns of Origination and Extinction in Cenozoic Mammals

Simpson (1953) summarized the history of diversification of carnivore genera in a matrix reproduced here as Table 10.1, based on his 1945 classification of mammals. Simpson's matrix shows the number of genera that first appeared in each subdivision of the Cenozoic (rows), and when each of these genera disappeared (columns). Simpson's data are now somewhat out of date (many of the Paleocene and Eocene genera he included in Carnivora have since been transferred to other orders) and the geological time scale has been revised; but his matrix shows several surprising things relating to the origination and extinction of Cenozoic mammals.

Simpson assigned durations to each subdivision of the geological time scale, and used the distribution of data in Table 10.1 to derive the survivorship curve shown in Figure 10.1. Survivorship was then used to predict the number of genera originating in the Pleistocene that should survive to the Recent (Table 10.2). Of thirty-four genera originating in the Pleistocene, Simpson predicted that thirty-three should survive until the Recent. Only nineteen did so, leading Simpson (1953) to offer an explanation involving unusually high mortality in the Pleistocene:

Table 10.1. Distribution of Genera of Carnivora (Except Pinnipedia)

(Figures are numbers of known genera)
Last Known Appearance

		Paleocene			Eocene			Oligocene			Miocene			Pliocene			Pleistocene	Recent	Total First Known Appearance
		L	M	U	L	M	U	L	M	U	L	M	U	L	M	U			
			L	5	0	0	1			
Paleocene	M	..	12	0	1	13	
	U	5	3	8	
	L	8	5	3	16	
Eocene	M	7	4	11	
	U	13	6	1	0	0	2	22	
	L	9	1	4	5	2	0	1	22	
Oligocene	M	3	3	
	U	0	3	1	4	
	L	20	0	3	2	25	
Miocene	M	9	3	7	1	1	1	..	22	
	U	8	8	1	0	0	2	19	
	L	23	5	4	1	7	40	
Pliocene	M	4	2	0	2	8	
	U	4	2	3	9	
	L	15	19	34	
Pleistocene	15	19	34	
Total last known appearances		5	12	5	13	12	20	15	5	4	28	14	14	41	11	11	19	33	262

SOURCE: Simpson (1953: Table 11)

Among the carnivores, survival to Recent agrees sufficiently with expectation for genera that appeared before late Pliocene, but it is much lower than expectation for late Pliocene and Pleistocene genera. The discrepancy was largely, perhaps wholly, caused by the unusually high mortality of the Pleistocene.

Another interpretation is possible. The average number of genera appearing in each of six subdivisions of the Miocene and Pliocene was 20.5 (Table 10.2). If only 20.5 genera had made first appearances in the Pleistocene, 98 percent survivorship would yield twenty expected survivals, almost equal to the nineteen actual survivals observed. Viewed from this perspective, the striking feature of Simpson's tables is not the number of last appearances in the Pleistocene but rather the great number of first known appearances in the Pleistocene. In the Miocene and Pliocene, Simpson's subdivisions average 19.8 last known appearances of carnivore genera (compared with nineteen observed in the Pleistocene) and 20.5 first known appearances (compared with a surprising thirty-four in the Pleistocene).

Pleistocene Originations and Extinctions

The three orders of mammals that include the most genera with a good fossil record are Rodentia (about 560 genera), Artiodactyla (about 500 genera), and Carnivora (about 260 fissioned genera). Romer (1966) most completely summarizes available data on the stratigraphic ranges of genera. His data can be used to calculate rates of origination and extinction for genera of each of the three orders through the course of the Cenozoic. Rodents, artiodactyls, and carnivores span a full range of ecological types, they are essentially worldwide in distribution, and they have a good fossil record. Hence, patterns of origination and extinction in these three orders should accurately

Table 10.2. Expected and Actual Generic Survivorship to the Recent

Time	Genera Appearing	Percentage of Approximate Expectation of Survival to Recent	Expected Survivals	Actual Survivals
CARNIVORA				
Early Miocene	25	0	0	0
Middle Miocene	22	2	0	0
Late Miocene	19	15	3	2
Early Pliocene	40	23	9	7
Middle Pliocene	8	37	3	2
Late Pliocene	9	90	8	3
Pleistocene	34	98	33	19

SOURCE: Simpson (1953: Table 12)

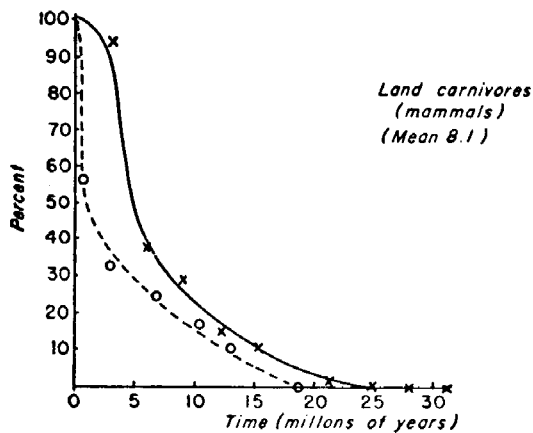


Figure 10.1. Survivorship curve for genera of carnivorous mammals showing the percentage of all genera (ordinate) surviving to a given age (abscissa). Solid line is based on genera now extinct. Dashed line is based on surviving genera. (From Simpson 1953, Figure 5)

represent the general Cenozoic mammalian pattern. Changes and additions to Romer's data published since 1966 alter some details, but the large sample size available for each of the three orders makes it unlikely that general patterns would be altered significantly. Pseudo-origination and pseudo-extinction, by evolution of one genus directly into another, cannot be estimated accurately, but these should inflate both origination and extinction curves by a constant proportion.

Analysis of Romer's data for fissiped Carnivora using Simpson's method (1953, see Table 10.1) shows that 55 genera originated and 12 genera became extinct in the early Pleistocene. According to Romer, no genera made evolutionary first appearances in the late Pleistocene, but 24 genera became extinct. In other words, as Simpson's data and discussion imply, the number of originations of carnivore genera in the early Pleistocene was approximately twice the number of extinctions in the late Pleistocene. Similar analysis of Artiodactyla shows that 145 genera originated in the early Pleistocene and 72 genera became extinct in the late Pleistocene. Analysis of Rodentia yields 176

early Pleistocene originations and 67 late Pleistocene extinctions. In both large mammals and small, carnivores and herbivores, it appears that Pleistocene originations exceeded Pleistocene extinctions by a wide margin (Gingerich 1977).

Cenozoic Rates of Origination and Extinction

The standard method of calculating rates requires that the number of originations or extinctions in any geological interval be divided by the estimated length of the interval in millions of years (cf. Simpson 1953). Rates of origination and extinction for rodents, artiodactyls, and fissiped carnivores combined are listed in Table 10.3. All three orders were represented in the fossil record by early Eocene time and, as shown by the great increase in total genera (Table 10.3), all three underwent a great diversification subsequent to their origin. Results of calculating rates of origination and extinction in this way are illustrated graphically in Figure 10.2A. Assuming the duration of both early and late Pleistocene (in Romer's sense) to be about 1 my, the rate of extinction seen in the late Pleistocene is 163 genera per million years. More striking, however, is the much higher rate of origination in the early Pleistocene, when new genera of rodents, artiodactyls, and carnivores appeared at a rate of 376 genera/million years. The high rate of generic origination in the early Pleistocene greatly exceeds the rate of late Pleistocene extinction. Comparisons with rates of origination and extinction earlier in the Cenozoic show that late Pleistocene rates of extinction for these three groups exceeded

Table 10.3. Rates of Origination and Extinction in Cenozoic Genera of Rodentia, Artiodactyla, and Fissiped Carnivora

Rates are calculated as total number of originations or extinctions in an interval divided by the duration of the interval or by the total number of genera known from the interval. Data on generic ranges are from Romer (1966). Temporal durations are estimated from Berggren (1972) consistent with Romer's subdivision of epochs. The time scale, especially placement of the Miocene-Pliocene boundary, has been revised subsequent to Romer's work, but this should not affect general patterns evident in his data.

Epochs		Approximate Duration (my)	Total Genera	Originations		Extinctions			
				Total Number	Rate Per Million Years	Rate Per Total Genera	Total Number	Rate Per Million Years	Rate Per Total Genera
Paleocene	Early	3	0	0	0.0	0.00	0	0.0	0.00
	Middle	3	3	3	1.0	1.00	1	0.3	0.33
	Late	6	4	2	0.3	0.50	1	0.2	0.25
Eocene	Early	5	27	24	4.8	0.89	12	2.4	0.44
	Middle	3	47	33	11.0	0.70	19	6.3	0.40
	Late	8	118	89	11.1	0.75	76	9.5	0.64
Oligocene	Early	6	132	90	15.0	0.68	63	10.5	0.48
	Middle	2	111	42	21.0	0.38	42	21.0	0.38
	Late	6	115	46	7.7	0.40	46	7.7	0.40
Miocene	Early	6	238	169	28.2	0.71	155	25.8	0.65
	Middle	2	146	63	31.5	0.43	45	22.5	0.31
	Late	3	168	67	22.3	0.40	57	19.0	0.34
Pliocene	Early	6	334	223	37.2	0.67	178	29.7	0.53
	Late	4	256	100	25.0	0.39	110	27.5	0.43
Pleistocene	Early	1	522	376	376.0	0.72	85	85.0	0.16
	Late	1	439	2	2.0	0.00	163	163.0	0.37

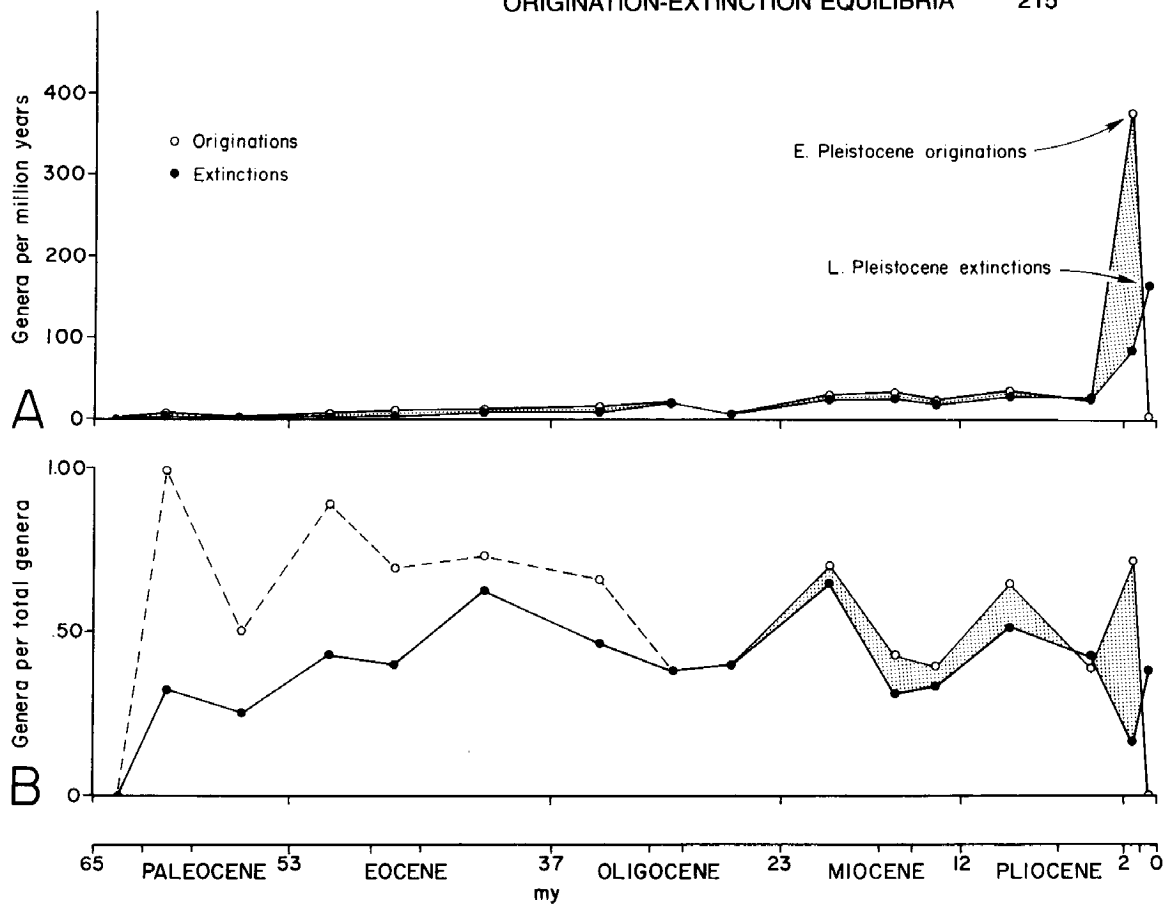


Figure 10.2. Patterns of change in the origination and extinction of genera of Rodentia, Artiodactyla, and fissiped Carnivora, expressed in (A) terms of genera per million years or (B) genera per total genera for each subdivision of the Cenozoic time scale. Note the close correlation of origination and extinction throughout most of the Cenozoic. Note also the unusually high rate of early Pleistocene originations preceding late Pleistocene extinctions, regardless of whether this is expressed in terms of rate per million years or percentage of the total fauna. Based on data from Romer (1966) (see Table 10.3, this chapter). Early Pliocene of Romer is now regarded as late Miocene by most authors, i.e., the Miocene-Pliocene boundary is now placed at 5 mya.

early and late Pliocene rates by a factor of four or five. Early Pleistocene originations of these groups exceeded Pliocene rates by a factor of more than ten, and earlier Cenozoic rates by an even wider margin.

Given the great overall increase in total number of rodent, artiodactyl, and carnivore genera during the Cenozoic, it is possible that high rates of Pleistocene originations and extinctions are an artifact of increasing diversity, or of an increasingly well-sampled fossil record, or both. This bias can be corrected by calculating rates of generic origination and extinction as proportions of the total number of genera under study in any given time period. Standardized rates, in genera per total genera, are also listed in Table 10.3. These standardized rates are plotted in Figure 10.2B. As before, origination rates appear to exceed extinction rates in the early Cenozoic during the explosive initial radiation of the three orders studied, but during most of the later Cenozoic origination and extinction proceeded at about the same rate. When corrected for total known

diversity in each subdivision of the time scale, the late Pleistocene extinction rate is slightly below average for the whole of the Cenozoic. The standardized early Pleistocene rate of originations, on the other hand, is exceeded only by abnormally high middle Paleocene and early Eocene origination rates. Both Pleistocene rates would increase by a factor ranging from two to eight relative to other subdivisions of the time scale if the durations of subdivisions were also taken into account.

Origination-Extinction Equilibria and Pleistocene Extinctions

One notable feature of the origination and extinction curves shown in Figure 10.2 is the way origination and extinction follow each other. When origination rate is high, extinction rate tends to be high as well. Paleocene and Eocene local faunas have diversity values characteristic of extant mammalian faunas (Rose 1982), suggesting that there is little reason to expect steep secular trends in overall Cenozoic mammalian diversity. High rates of origination are thus necessarily accompanied by high rates of extinction, and vice versa, because these two processes are in dynamic equilibrium (MacArthur and Wilson 1963, 1967; Webb 1969). The actual level of the equilibrium, in a sense the diversity capacity (MacArthur and Wilson's *saturation*), at any time is determined by the environment. As long as saturation levels remain constant, faunas can experience unlimited substitution of one genus or species for another, i.e. turnover may be high or low, but net diversity can only fluctuate within narrow limits.

The relative height of any origination/extinction pair of points in Figure 10.2 is a measure of the amount of faunal turnover in a given time interval. Assuming that origination and extinction are in dynamic equilibrium constrained by environmental diversity capacity, the difference in height between origination and extinction in any origination/extinction pair is a measure of change in the level of environmental saturation. Where origination rate greatly exceeds extinction rate we can infer an increase in saturation, and where extinction exceeds origination we can infer a decrease in this quantity. Thus the early Miocene and the early Pliocene (*vide* Romer 1966, "early Pliocene" of Romer is now regarded as late Miocene by Berggren 1972 and most authors) appear to have been intervals of high mammalian faunal turnover compared to the late Oligocene or middle and late Miocene (middle Miocene).

The fact that origination and extinction track each other so closely suggests little change in saturation through the Miocene and Pliocene. However, as we have seen, during the early Pleistocene mammalian originations greatly exceeded extinctions, suggesting a marked increase in saturation level or diversity capacity. Given that the extinction rate remains in close equilibrium with origination rate, the high rate of late Pleistocene extinctions can be viewed as a natural equilibration ending a one- to two-million-year interval of high saturation that followed an unusually high rate of early Pleistocene originations. In this context, what requires explanation is not late Pleistocene extinctions but the very high rate of early Pleistocene originations.

Coincidence of an unusually high origination rate with a low early Pleistocene extinction rate (fig. 10.2) produced a Pleistocene fauna of exceptionally high diversity. Diversity usually has a positive correlation with temperature, productivity, and stability (Klopfer 1959, Fischer 1960, Pianka 1966), but the Pleistocene was a time of climatic cooling and instability (Flint 1971). Hence these factors cannot explain the increased diversity. An explanation is possibly to be found in the fragmentation and diversification of habitats accompanying successive Pleistocene glaciations. Spatial heterogeneity has a positive effect on faunal diversity within communities (MacArthur and MacArthur 1961) and between communities (Kurtén 1969, Valentine and Moores 1970, Flessa 1975), and this appears to be a plausible explanation for abnormally high origination rates and low extinction rates in the early Pleistocene.

In North America, Pleistocene glaciations apparently compressed latitude-parallel life zones (Dillon 1956, Delcourt and Delcourt 1981), which were fragmented longitudinally by large rivers fed by glacial meltwater. One would expect greater endemism and at the same time predict higher rates of species differentiation in such a complex environmental mosaic. Fluctuating climates facilitate dispersal, and immigration undoubtedly complemented speciation in augmenting origination rates and diversity. Both voles and shrews exhibited higher species densities during the Wisconsinan glaciation than is evident at the same localities today (Graham 1976). This trend toward greater diversification of shrews and voles in local faunas can presumably be extrapolated to other mammalian groups as well.

A large proportion of late Pleistocene extinctions could represent the natural result of faunal equilibration associated with return to nonglacial geographic and climatic conditions toward the end of the Pleistocene. Retreat of continental ice sheets would reduce environmental heterogeneity, and former high levels of Pleistocene mammalian diversity might no longer be supportable.

Origination-Extinction Equilibria Within the Pleistocene— A Test of the Environmental Heterogeneity Hypothesis

High rates of origination at the beginning of the Pleistocene and high rates of extinction at the end of the Pleistocene may reflect increased diversity capacity during this epoch caused by increased environmental heterogeneity associated with continental glaciation. This hypothesis predicts that *within* the Pleistocene, glacial intervals should have more diverse faunas than interglacials. Or, stated in terms of origination (or appearance in a restricted geographic area) and extinction (disappearance), rates of origination should exceed extinction by a significant amount during glacial intervals and extinctions should approach or exceed originations during interglacials.

Origination and Extinction Within the Pleistocene

Kurtén and Anderson (1980) provide the most extensive compilation available of temporal ranges for North American Plio-Pleistocene mammals. The Blancan Land Mammal Age is divided into four successive intervals, and the Irvingtonian and Rancholabrean are divided into three each. Irvingtonian-1 coincides with the Nebraskan glacial interval, Irvingtonian-2 corresponds to the Aftonian interglacial, and Irvingtonian-3 includes both Kansan glacial and Yarmouthian interglacial intervals. Rancholabrean-1 corresponds to the complex Illinoian glacial interval, Rancholabrean-2 represents the Sangamonian interglacial, and Rancholabrean-3 corresponds to Wisconsinan glaciation (Kurtén and Anderson 1980).

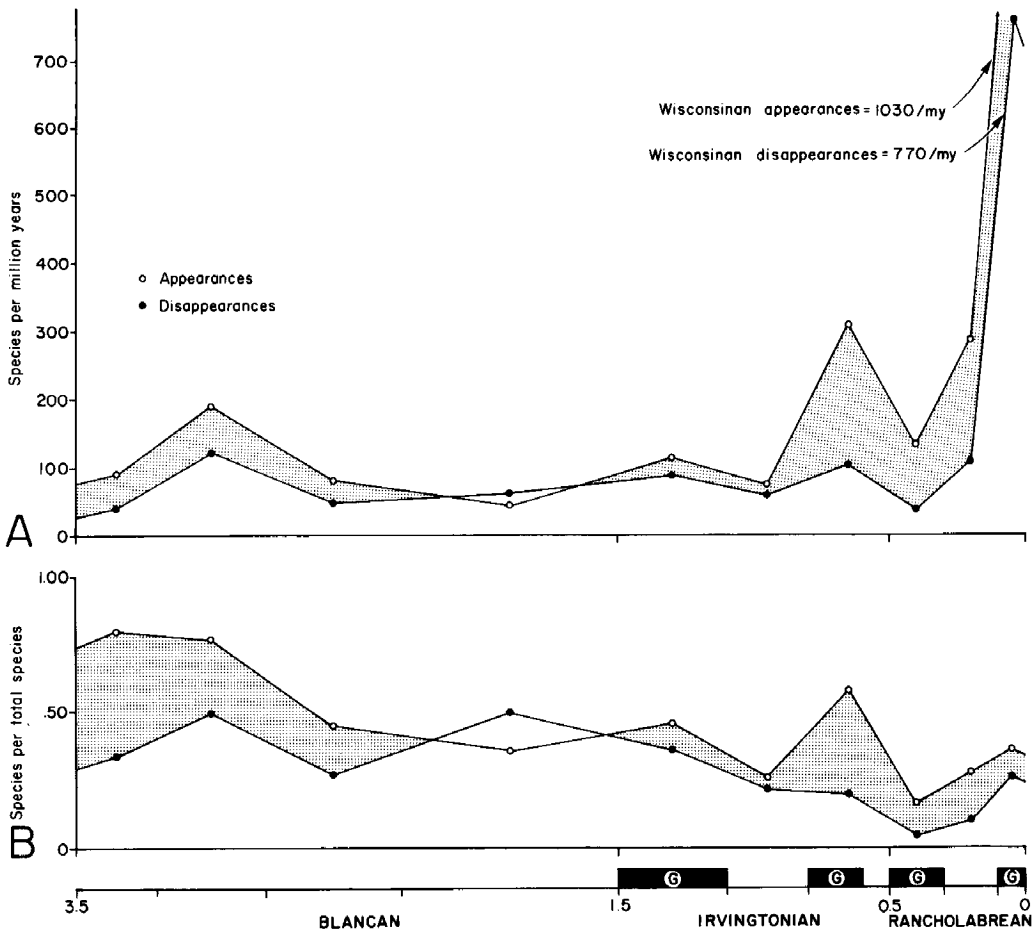
Rates of appearance and disappearance for all North American species of Plio-Pleistocene mammals are summarized in Table 10.4, and these data are shown graphically in Figure 10.3. As noted for Cenozoic mammals in general, rates of appearance and disappearance track each other closely and appear to be in dynamic equilibrium. Appearances almost always exceed disappearances by a small margin. Whether calculated in terms of species per million years or species per total species, there are three peaks indicating a high rate of appearance of new species. These peaks correspond to glacial intervals in Irvingtonian-1, Irvingtonian-3, and Rancholabrean-3, respectively. The rate of disappearance of species in glacial intervals, which should be low, appears to have remained near the average for Plio-Pleistocene mammals when considered in terms of species per total species.

Table 10.4. Rates of Appearance and Disappearance in North American Species of Plio-Pleistocene Mammals

Rates are calculated as total number of appearances or disappearances in an interval divided by the duration of the interval or by the total number of species known from the interval.

Land-Mammal Age	Glacial (G) or Interglacial (I)	Approximate Duration (my)	Total Species	Appearances		Disappearances		Rate Per Total Species	
				Total Number	Rate Per Million Years	Total Number	Rate Per Million Years		
Blancan-1	Preglaciacion	0.3	35	28	93.3	0.80	12	40.0	0.34
Blancan-2	Preglaciacion	0.4	100	77	192.5	0.77	50	125.0	0.50
Blancan-3	G (Montane)	0.5	91	41	82.0	0.45	25	50.0	0.27
Blancan-4	I (Plio-Pleistocene)	0.8	103	37	46.3	0.36	49	61.3	0.48
Irvingtonian-1	G (Nebraskan)	0.4	100	46	115.0	0.46	36	90.0	0.36
Irvingtonian-2	I (Aftonian)	0.3	87	23	76.7	0.26	18	60.0	0.21
Irvingtonian-3	G/I (Kansan/Yarmouthian)	0.3	163	94	313.3	0.58	32	106.7	0.20
Rancholabrean-1	G (Illinoian)	0.2	158	27	135.0	0.17	8	40.0	0.05
Rancholabrean-2	I (Sangamonian)	0.2	208	58	290.0	0.28	22	110.0	0.11
Rancholabrean-3	G (Wisconsinan)	0.1	289	103	1030.0	0.36	77	770.0	0.27

SOURCE: Kurtén and Anderson (1980) for species ranges, temporal framework, and glacial/interglacial sequence



One glacial interval, Rancholabrean-1, is characterized by unusually low appearance and disappearance rates, and in this sense it does not conform to expectation. There are several possible reasons for this. Rancholabrean-1 represents the interval of Illinoian glaciation, which is itself complex, including at least one major interstadial (Frye et al. 1965, Schultz and Martin 1970). The first appearance of the taxon defining the beginning of the Rancholabrean, *Bison*, is not well dated, and it may have immigrated into North America sometime during the Illinoian rather than at the beginning of this glacial interval (Kurtén and Anderson 1980, p. 5). Finally, the distinction between Irvingtonian and Rancholabrean faunas now appears less sharp than it was originally assumed to be (Kurtén and Anderson 1980, p. 37).

Correspondence of three out of four Pleistocene peaks of high appearance rate with glaciation provides some corroboration of the environmental heterogeneity hypothesis outlined above to explain high rates of Pleistocene origination of new taxa, but the evidence available from mammal distributions within the Pleistocene is still inadequate for a definitive test. Finer subdivisions of the Pleistocene mammalian record and better correlation with complex glacial cycles will be required before a definitive test of the environmental heterogeneity hypothesis can be attempted.

Extinction of Large Mammals

It is worth noting that the equilibrium between origination and extinction in large mammals follows a pattern similar to that of mammals in general through most of the Pleistocene (Table 10.5). However, as Martin (1967), Van Valen (1970), Webb (this volume), and others have noted, extinction affected large mammals very differently at the end of the Pleistocene. The rate of disappearance of large mammals in Rancholabrean-3 greatly exceeded their rate of appearance (fig. 10.4). Large mammals (Artiodactyla, Perissodactyla, and Proboscidea) disappeared in Rancholabrean-3 at a rate of 290 species/million years more rapidly than new species appeared in this interval. Stated in terms of species per total species, 56 percent of large mammalian species disappeared in Rancholabrean-3 and were not replaced by new large mammals. Viewed in the context of origination-extinction equilibria in Cenozoic mammals (fig. 10.2), or viewed in the context of appearance-disappearance equilibria for Pleistocene mammals in general (fig. 10.3), the disappearance of 56 percent of the large mammal fauna without replacement is unusual. This aspect of Pleistocene extinctions cannot reflect simple equilibration to previously existing levels of environmental saturation. It could represent a temporary lag in replacement (we are, after all, only 10,000 years removed from Wisconsinan glaciation), or it could possibly be a consequence of increasing human predation decimating large mammal populations that will never be replaced.

Conclusions

Pleistocene extinctions are real and significant, but they should not be viewed in isolation from the other half of the dynamic equilibrium that controlled Pleistocene faunal diversity: originations. Mammalian generic origination rates throughout most of the

Figure 10.3. Patterns of change in the appearance and disappearance of all species of North American Plio-Pleistocene mammals, expressed in (A) terms of species per million years or (B) species per total species. Note the general correlation of rates of first appearance with rates of disappearance. Wisconsinan first appearances ("originations") exceeded Wisconsinan disappearances ("extinctions") by 360 species per million years or, expressed as genera per total genera, by 9 percent. (Based on data in Kurtén and Anderson 1980) (see Table 10.4 this chapter.)

Table 10.5. Rates of Appearance and Disappearance in North American Species of Large Plio-Pleistocene Mammals (Artiodactyla, Perissodactyla, Proboscidea)

Rates calculated as in Table 10.4.

Land-Mammal Age	Glacial (G) or Interglacial (I)	Approximate Duration (my)	Total Species	Appearances			Disappearances		
				Total Number	Rate Per Million Years	Rate Per Total Species	Total Number	Rate Per Million Years	Rate Per Total Species
Blancan-1	Preglaciation	0.3	2	2	6.7	1.00	0	0.0	0.00
Blancan-2	Preglaciation	0.4	16	14	35.0	0.88	5	12.5	0.31
Blancan-3	G (Montane)	0.5	15	4	8.0	0.27	0	0.0	0.00
Blancan-4	I (Plio-Pleistocene)	0.8	19	4	5.0	0.26	7	8.8	0.37
Irvingtonian-1	G (Nebraskan)	0.4	23	11	27.5	0.48	5	12.5	0.22
Irvingtonian-2	I (Aftonian)	0.3	27	9	30.0	0.33	6	20.0	0.22
Irvingtonian-3	G/I (Kansan/Yarmouthian)	0.3	33	12	40.0	0.36	3	10.0	0.09
Rancholabrean-1	G (Illinoian)	0.2	40	10	50.0	0.25	3	15.0	0.08
Rancholabrean-2	I (Sangamonian)	0.2	52	15	75.0	0.29	11	55.0	0.21
Rancholabrean-3	G (Wisconsinan)	0.1	52	11	110.0	0.21	40	400.0	0.77

SOURCE: Kurtén and Anderson (1980)

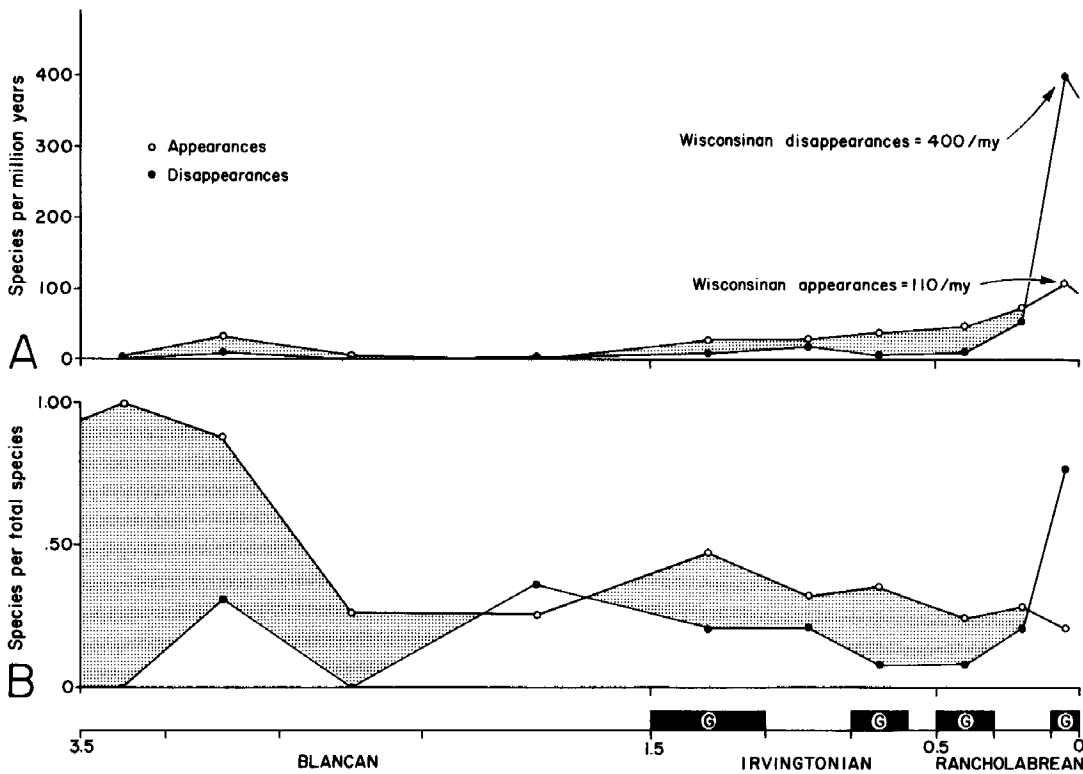


Figure 10.4. Patterns of change in the appearance and disappearance of large herbivorous species of North American Plio-Pleistocene mammals, expressed (A) in terms of species per million years or (B) species per total species. Note that Wisconsinan disappearances ("extinctions") exceeded Wisconsinan first appearances ("originations") by 290 species per million years, or 56 percent of the total number of species. (Based on data in Kurtén and Anderson 1980) (see Table 10.5 this chapter).

Cenozoic were equal to or only slightly greater than extinction rates until the Pleistocene. In the early Pleistocene, origination rates greatly exceeded extinction rates, whether these are calculated per million years or as a percentage of total genera. The rate of late Pleistocene extinctions was the highest of any subdivision of the Cenozoic, but this may be in part an artifact of a more completely known Pleistocene fossil record. When viewed in terms of genera per total genera, the rate of late Pleistocene extinctions was about average for earlier parts of the Cenozoic.

Given the equilibrium observed between origination and extinction throughout the Cenozoic, the high rate of late Pleistocene generic extinctions may be viewed as a natural sequel to an unusually high rate of originations in the early Pleistocene.

The high rate of early Pleistocene generic originations may be a response to increased environmental heterogeneity associated with the onset of continental glaciation in the early Pleistocene. If this explanation has merit, it should be possible to correlate levels of generic or species diversity (saturation), and the originations (appearances) and extinctions (disappearances) that control saturation, with glacial and interglacial stages within the Pleistocene: glacial intervals should have high standing diversity with increased rates of origination at the beginning balanced by increased rates of extinction at the end. If there is any lag between environmental change and its effect on diversity, glacial intervals might be expected to show high rates of origination and interglacial intervals high rates of extinction. This hypothesis is tested using the temporal ranges of North American species of Plio-Pleistocene mammals published by Kurtén and Anderson (1980).

Throughout the Pleistocene, as throughout the Cenozoic, rates of origination and extinction appear to be closely related. When all North American species are considered, the rate of appearance of new species in the Pleistocene exceeds the rate of disappearance of species, even during the late Rancholabrean (Wisconsinan) glacial interval so well known for its fauna of unusual mammals now extinct.

When large herbivorous North American species are considered in isolation, the rate of disappearance (extinction or emigration) of species during the Wisconsinan greatly exceeds their rate of appearance (origination or immigration). Some 56 percent of Wisconsinan artiodactyls, perissodactyls, and proboscideans disappeared from the North American fauna without replacement. Late Wisconsinan extinction of large mammals is certainly real, but much of the "unusually high mortality of the Pleistocene" cited by Simpson (1953) is best regarded as a natural consequence of high faunal turnover caused by major oscillations in climate and environmental heterogeneity.

Patterns within the Pleistocene are inadequate to test the general environmental heterogeneity hypothesis advanced here to explain high rates of early Pleistocene originations. Three out of four glacial intervals of the Pleistocene exhibit high rates of species appearances, as predicted, but the remaining interval has an unusually low rate. The rates of disappearance of Pleistocene species in different intervals show no obvious correlation with glacials or interglacials. The tendency for high rates of species appearances to coincide with glaciations is suggestive, but better sampling of appearances and disappearances at the beginning and end of glacial and interglacial stages is required. Diversification patterns within the Pleistocene do not yet provide an adequate test of the influence that increased environmental heterogeneity during continental glaciation may have had on the origination and extinction of genera and species of Pleistocene mammals.

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