ECOLOGY AND THE EXTINCTION OF THE DINOSAURS

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ABSTRACT: The first direct evidence of the process of dinosaur extinction comes from a sequence of vertebrate faunas in Montana, spanning the Cretaceous-Paleocene boundary. Much of the physical environment can be reconstructed. The extinction here lasted roughly 10^5 years and proceeded by ordinary community evolution.

Botanical evidence shows a decline in winter temperatures and a replacement of much of the original subtropical flora by a temperate flora. This southward-moving community lacked dinosaurs (and marsupials) and replaced the subtropical terrestrial community, apparently by diffuse competition. Mammals were common but subordinate in energy flow in the subtropical community; the temperate community included early members of the large Paleocene placental radiation. About seven dinosaur species persisted during the infiltration, but they gradually became rarer and then disappeared.

The process implies that dinosaur extinction occurred somewhat later in the tropics than in Montana. Some slight evidence supports this. The contemporaneous major extinction in the sea was also gradual and perhaps as long. It is also explicable by diffuse competition in an increasingly rigorous environment.

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Dinosaurs were spectacular animals. Although some were probably feathered and gave rise to birds (Ostrom, 1974), dinosaurs as dinosaurs had the misfortune to become extinct. Until recently (1) there has been effectively no actual evidence on the cause of this extinction, and speculation has been unbounded. We hope to show that the subject is amenable to serious scientific study and that the major process, at least, was ordinary community evolution.

Geology and geography

Fig. 1 is a rough map of North America and Eurasia just before the end of the Cretaceous. Europe and Asia were both probably connected to North America but South America was not, and a deep and broad seaway that had linked the Gulf of Mexico with the Arctic Ocean was about to be bisected by sediments eroded from the rising Rocky Mountains (2).

In the Hell Creek Field of east-central Montana, where we worked, land encroached into the seaway although it may not have reached the eastern boundary until after a brief (and perhaps worldwide) rise in sea level in the early Paleocene. Fig. 2 shows the stratigraphy diagrammatically.

The Hell Creek Field contains one of the best known terrestrial sequences in the world before the Pleistocene (3). The Paleocene beds have much lignitic coal, and many classic dinosaur specimens have come from the Cretaceous there. Plants have been studied extensively from both pollen and leaves, and the nearby and underlying marine sediments and their fossils have been the focus of detailed study also.

Sedimentation was cyclic and more or less continuous. Single cycles can be traced for many miles, especially in the Fort Union, and the coal geologists

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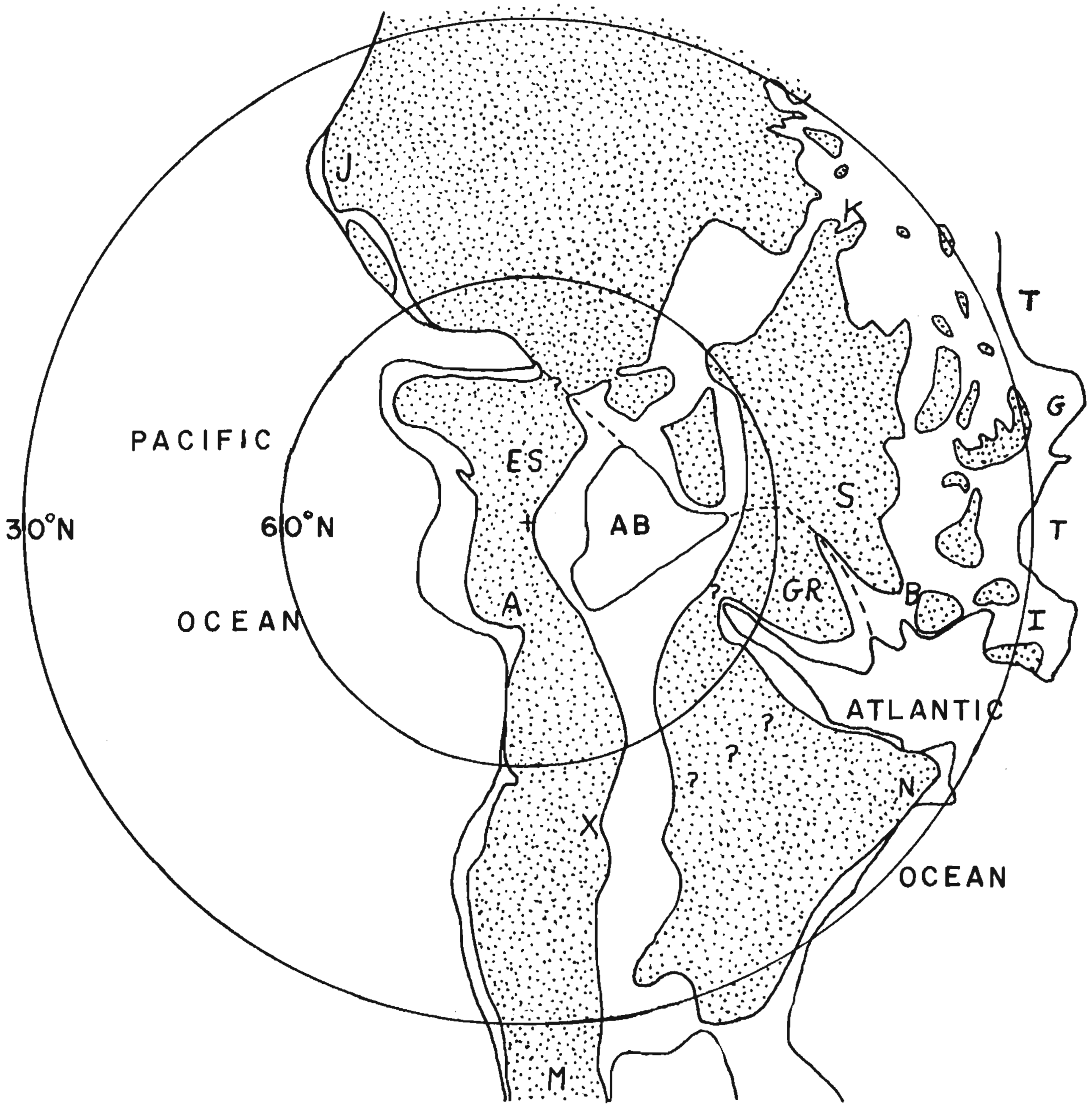

Fig. 1. Map of the northern part of the world in the early part of the late Maestrichtian, about 66 million years B.C., in polar stereographic projection. The continents are in their most likely configuration at that time and land is distinguished from ocean. The large circles are approximate paleolatitudes. The edges of the modern continental shelves are also shown; modern coastlines are omitted to avoid clutter and confusion. Turkey, Iran, and India were still separate from the Eurasian continent (and from each other), and fall outside the map area. Unfortunately two important land bridges are inadequately documented; on the possible seaway across eastern North America see Jeletzky (1971b). The data come from many sources. Dotted area : land. Dashed lines : future or intracontinental plate boundaries. X : Hell Creek Field. + : North Pole at 66 M.Y.B.C. ? : Possible seaways. A: Alaska. AB : Arctic Ocean Basin. B : British Isles. ES : Eastern Siberia. G : Greece. GR : Greenland. I : Iberia. J : Japan. K : Kazakhstan. M : Mexico. N : Newfoundland. S : Scandinavia. T : Tethys Sea.

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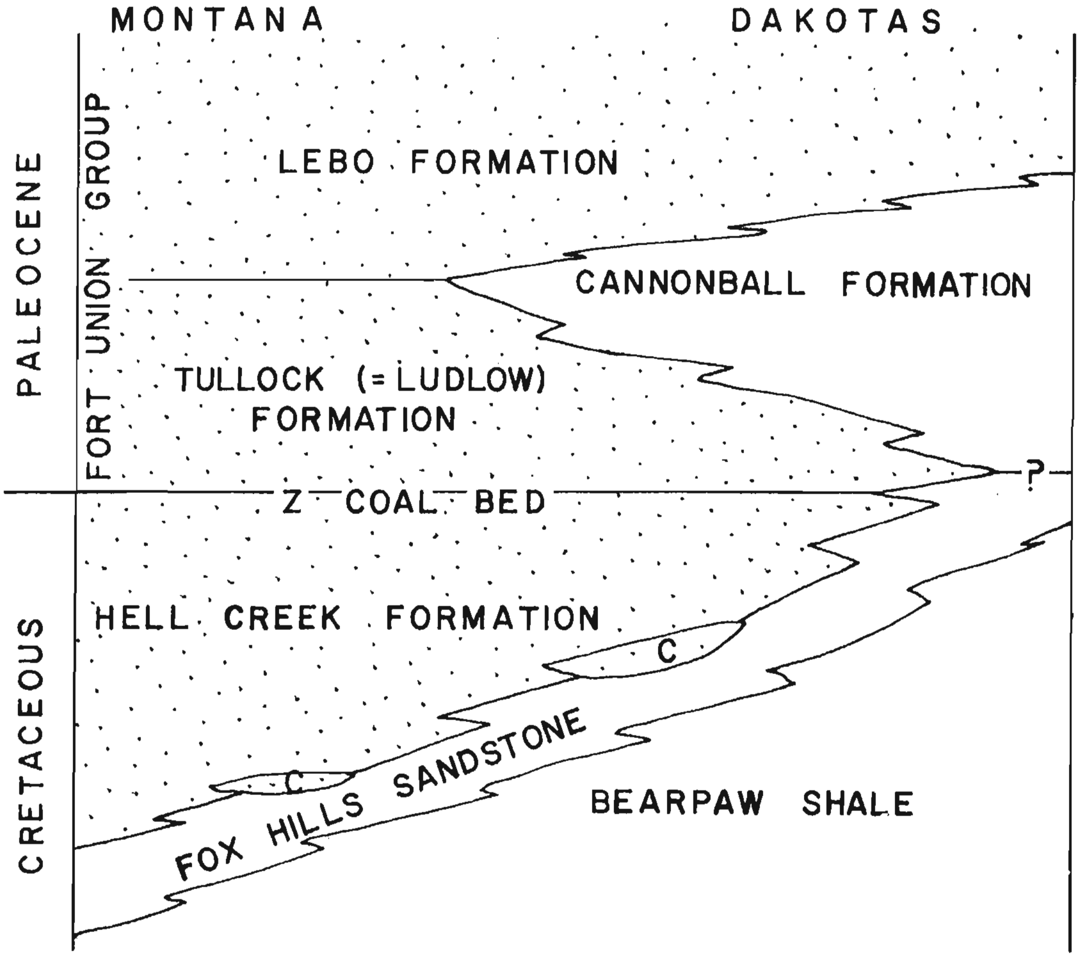

Fig. 2. Diagram of the stratigraphy in and near the Hell Creek Field. Nonmarine strata are dotted. C : lenses of Colgate Sandstone. ? : Continuity of marine strata is uncertain.

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have done so extensively. A single cycle is approximately synchronous throughout the region; the corresponding beds of two successive cycles are appreciably separated in time even if one bed is in one area and the other bed is elsewhere. Bentonites, the remains of volcanic ash falls, sometimes provide time markers even far into the marine sediments.

The Bearpaw Shale represents the open sea and grades laterally into the nearshore deposits of the Fox Hills Sandstone. In some areas land sediments are included in the Fox Hills, but often there is a beach-sand deposit, the Colgate Sandstone, that separates the Fox Hills from the fluviatile Hell Creek Formation. The Hell Creek consists of flood-plain deposits in which are interspersed sandy remnants of aggrading channels and point bars. The channels produce local disconformities. Carbonaceous shales, locally coally, represent times of relatively high sea level and low stream gradient.

The first regionally persistent coal, the Z bed of the coal geologists, conveniently marks the end of the Cretaceous in this area, as closely as a correlation can be made. The last dinosaurs occur a little below it. More than 20 potassium-argon dates from it and from stratigraphically related coals and bentonites to the north give the Z bed an age of 64 ± 1 million years (Folinsbee et al., 1965, 1970; Shafiqullah et al., 1968; Lambert, 1971 a, b). Sedimentation seems to continue regionally uninterrupted into the Paleocene Fort Union Group, of which the Tullock Formation is the lowest part, although locally there are disconformities near the boundary as at other times.

There were no hills nearby. Hills form either from uplift (including volcanism) or from erosion of pre-existing high land. Neither process operates on a delta-like wedge of sediment that is pushing its way into the sea. The land was low and flat, with braided or meandering streams filling their channels and cutting new ones. The streams flowed predominantly northeast; their sediment came from mountains rising near Yellowstone Park.

The height of land at any point can be estimated roughly by the vertical distance of that point above the Fox Hills. Regional subsidence and compaction of the sediments reduce this figure by a factor of perhaps 2, but limits can be set from the minimum stream gradient and the distance to the contemporaneous coastline. Sedimentation exceeded the joint effect of subsidence, compaction, and erosion, while the sea level presumably fell in the Cretaceous part of the sequence. From this analysis we predict that the Gulf of Mexico did not retreat more than about 200 or 300 km. from the site of the Fort Peck Reservoir in the Hell Creek Field, until well into the Paleocene. A very brief greater withdrawal, at the Cretaceous-Paleocene boundary, is nevertheless possible. A longer withdrawal would produce a large regional disconformity by erosion below the earlier base level.

The original animal communities

There are two more or less distinct animal communities in the lower part of the Hell Creek Formation. These are known from correlative and somewhat earlier strata from central Alberta to southeast Wyoming and South Dakota. Farther south there is a geographic replacement by ecologically similar but taxonomically somewhat distinct communities.

One community was aquatic or semi-aquatic. Estes and Berberian (1970), Estes, Berberian, and Meszoely (1969), and others have found the following taxa in this community: the bowfin Amia, two sturgeons, a gar and the garlike genus Belonostomus, a paddlefish, a tarpon and several other teleost fish, two freshwater rays, two freshwater sharks, three crocodiles (one, Brachychampsa, apparently a mollusc-eater), the crocodile-like eosuchian Champsosaurus, various poorly preserved shorebirds, a half dozen frogs, a half dozen aquatic and semiterrestrial salamanders, and a half dozen or more aquatic and semiaquatic turtles. Various unstudied molluscs also occur, and as usual softer-bodied invertebrates are not preserved. This community had been evolving slowly for millions of years, and it continued to do so until the Eocene. It underwent no appreciable change at the close of the Cretaceous (4).

The second community, the Triceratops community, was terrestrial, and also had been evolving slowly for millions of years. It contained 15 or 20 species of lizards (small to very large), two primitive snakes, a small cursorial crocodile, seven multituberculates (small, primitive, herbivorous mammals), about nine moderately common opossums, and four or five rare insectivorans.

The Triceratops community also contained dinosaurs. Triceratops and the duckbill Anatosaurus were most abundant (5). Other herbivores were the ornithopod Thescelosaurus, a bonehead (perhaps Pachycephalosaurus), and an armored ankylosaur or two. Two coelurosaurs were present: Paronychodon and Ornithomimus or a close relative. A spur-clawed dromaeosaurid represents a newly recognized group (Ostrom, 1969). Gorgosaurus was a larger predator, and the Hell Creek is the home of Tyrannosaurus.

Abundance and dominance

The calculation of relative abundance is a hazardous procedure. Elements other than teeth are not often preserved in an identifiable condition and, unlike the teeth of mammals, those of reptiles are replaced throughout the life of the animal. Some estimate must therefore be made of the mean rate at which dinosaur teeth were replaced. The value we have used is once a year, which is reasonable by analogy with recent reptiles (Edmund, 1960) but is not validated. The mean (not maximum) lifespan of individuals old enough to have recognizable teeth must also be guessed; for Anatosaurus and Triceratops we guess 25 years, although this value is irrelevant to some of the calculations, and for the mammals we guess 0.5 year. The number of teeth in a jaw and the relative number in the sediment are known (6). On this basis it is possible to estimate, with large error, that the mammals outnumbered the dinosaurs in the Triceratops community by something like 300 to 1, a reasonable figure by analogy with recent mammal communities. This suggests that the rarity of Cretaceous mammals in most collections is due to collecting or preservational bias rather than low population density.

Relative dominance (control of trophic energy: Van Valen, 1973b) is another matter. Ratios of weights based on the linear dimensions of load-supporting limbs (Bakker, 1972) give about the same values as more direct estimates based on modern mice and Colbert's (1962) weights for dinosaurs. The more common dinosaurs in the Hell Creek weighed about 5000 kg., or nearly 10^5 times as much as the average mammal underfoot.

Dinosaurs seem to have been active endotherms (e.g. Bakker, 1972; Ricqlès, 1974). If we take their metabolic rate to be that of mammals of the same size, the standard 0.75-power proportionality with body weight (e.g., Kleiber, 1961) gives a dinosaur about 4000 times the metabolic energy requirement of a contemporaneous mammal. From avian evidence this applies to active movement as well as to basal metabolism, but it excludes growth and reproduction.

By analogy with modern mammalian faunas (Bourlière, 1964), there were roughly 3 dinosaurs per square kilometer. The analogy is based on the assumption that gross trophic structure of a community type is stable, as suggested by similar trophic structure of communities of different origins and by return to earlier trophic structure but with taxonomically different organisms, after disturbance (e.g. D.E. Wilson, 1973; Lein, 1972; Walker, 1972; Heatwole and Levins, 1972; Paine, 1971; Olson, 1966). With a mean lifespan of 25 years, dinosaur growth was at a mean rate of roughly 600 $kg/km^2/yr$. The usual value of 2 kcal/g wet weight for animal tissue (Odum, 1971) makes this about 10^6 $kcal/km^2/yr$. By the standard relationships of metabolism to body size in the animal kingdom (Hemmingsen, 1960), endothermic dinosaurs used about 10^8 $kcal/km^2/yr$ for their activities and maintenance. Thus these calculations give about 1 percent of total energy use for growth. This value is indistinguishable from what is expected for mammals of the same large size (cf. Golley, 1968) and so adds independent plausibility to the numerical values we chose.

Net primary productivity (production of plant matter) was about 7×10^9 $kcal/km^2/yr$ (cf. Lieth, 1973; Rodin, Bazilevich, and Rozov, 1975). Dinosaurs used about 1 percent of this, and in the Triceratops community in Montana, at least, mammals used very roughly a tenth of the energy that dinosaurs did (7). This dominance ratio is derived independently from the value for the absolute energy used but assumes equal metabolic and assimilative efficiencies for mammals and dinosaurs. These efficiencies have no detectable dependence on body size for recent endotherms (Golley, 1968). Recent small female mammals approximately double their food intake during pregnancy and lactation (Sadleir, 1969); this correction is included in the ratio. Mammals were therefore an energetically subordinate part of the fauna.

Evolution of the animal communities

In the upper part of the Hell Creek Formation there are three faunas (Fig. 3) which contain the earliest record of the great Cenozoic diversification of

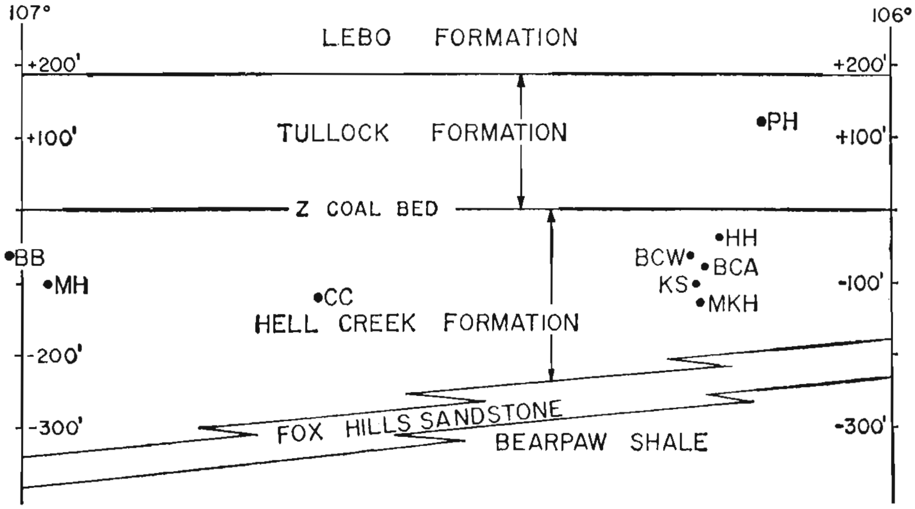

Fig. 3. Stratigraphic cross-section of the Hell Creek Field between 106° and 107° W, a distance of 72 km. Vertical distances are in feet from the _Z_ coal bed. From Sloan and Van Valen (1965). BCA (Bug Creek Anthills), BCW (Bug Creek West), HH (Harbicht Hill) and PH (Purgatory Hill) are localities with the _Protungulatum_ community. Other dots designate mammal localities with only the _Triceratops_ community.

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the placental mammals. There are the first ungulates (not yet with hoofs), the first primates, and new insectivorans as well as new multituberculates and poikilothermic vertebrates (Sloan and Van Valen, 1965; Van Valen and Sloan, 1965; Estes and Berberian, 1970). How did their entry affect the _Triceratops_ community?

The first thing to note is that the invaders were not rare. In Bug Creek Anthills (8), the earliest and richest in specimens of the three faunas, the invading mammals outnumber the indigenes by 20 to 1. However, almost every species in the _Triceratops_ community occurs at Bug Creek Anthills. It is not clear whether the two groups were always physically separated by habitat differences, but it is convenient to refer to the invaders as the _Protungulatum_ community. This community occupied only suitable parts of the Hell Creek Field, as it is absent from Brownie Butte and some other faunas later than Bug Creek Anthills. We will refer to the time from the deposition of Bug Creek Anthills to that of the _Z_ coal bed as Bug Creek time.

There were no dinosaurs in the _Protungulatum_ community, although several of the original salamanders and multituberculates (and the terrestrial crocodile) changed in frequency like the invaders and so presumably were adaptable in relevant ways. The new community also lacked marsupials.

At Bug Creek Anthills placentals already comprise a major, although not preponderant, part of the fauna. In the unlikely event that the preserved specimens quantitatively represent those dying in the general region, the mammals were already more or less as dominant as the dinosaurs, and the placentals had a major role in this increase. More likely there is a local bias toward the placentals and other newcomers, perhaps a large bias, but their role in the regional energy flow in the Bug Creek area was already large and became larger.

The _Protungulatum_ community gradually changed through time (Fig. 4). The two species of ungulates initially present, one exceedingly rare, were joined by three others. These other species are closely related to the original two, but we can only speculate as to where they originated. The first primate

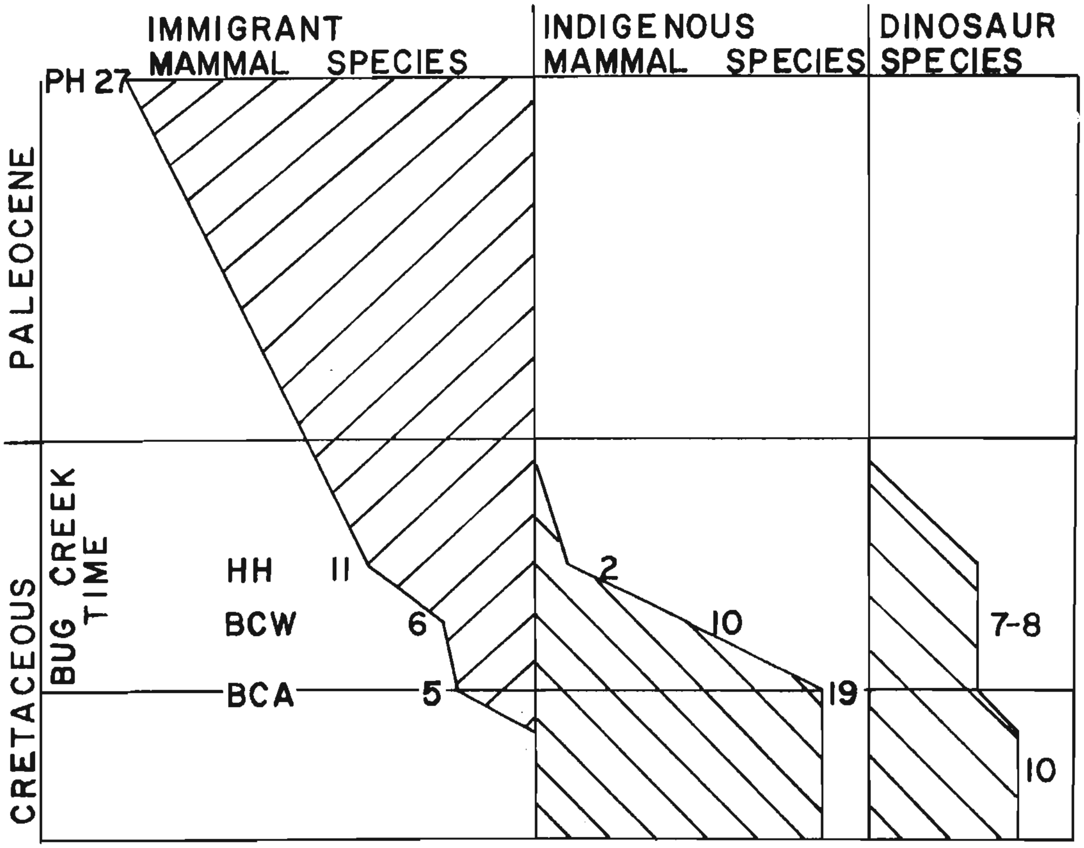

Fig. 4. Change in observed numbers of species of different groups in Bug Creek time. The vertical axis is proportional to thickness of sediments and so, roughly, to time. Many more specimens are known from Bug Creek Anthills than from the later faunas, so later absence of some rarer species may spuriously contribute to a declining trend in the indigenes. The overall picture is, however, unambiguous for each group. Abbreviations as in Fig. 3.

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appeared, as did a new multituberculate. Two multituberculates evolved into new species, and other lineages also changed morphologically. This community was evolving quite rapidly. In fact it seems to have given rise to most later placental mammals. The surviving multituberculates also diversified in the first half of the Paleocene before becoming extinct (Van Valen and Sloan, 1966; Sloan, unpublished). At the nearby localities Purgatory Hill and Garbani (Van Valen and Sloan, 1965; Clemens, 1974), the former of which we believe to be of late early Paleocene (about middle Danian) age on the basis of lineages of the condylarths and multituberculates, a normal Paleocene fauna like those known from areas to the south and west coexists with some ancestral genera that survived from the Cretaceous. The community change apparently occurred by both immigration and local evolution.

While the Protungulatum community gradually expanded, the Triceratops community gradually contracted. A bone that may represent the last known pterosaur occurs in the Lance Formation of eastern Wyoming (Estes, 1964; cf. Lawson, 1975), which is at least faunally correlative with the lower part of the Hell Creek Formation. Two or three of the insectivorans seem to drop out, as do all but perhaps one of the nine marsupials, some of the lizards, and two or three multituberculates.

The top carnivore, Tyrannosaurus, was rare in the lower part of the Hell Creek Formation and does not occur at all in the channel of Bug Creek Anthills.

However, one specimen has been found by others in later sediments. Ankylosaurs and perhaps the bonehead had also become at least locally extinct. The other dinosaurs persist at least to Bug Creek Anthills, and about seven species beyond it, but they become rarer. By the time of the latest of the Bug Creek faunas, Harbicht Hill, the relative abundance of Triceratops was a tenth that at Bug Creek Anthills. Mammals were by then the dominant vertebrates in community energy flow. The increasing scarcity of dinosaurs is also observable in the remains scattered in floodplain sediments, at least in the Bug Creek area, and gives quantitatively similar results.

It is apparent that the gradual change of these communities immediately precludes all possible catastrophist explanations for dinosaur extinction. The change was geologically rapid, but ecologically very slow. The time involved can't as yet be estimated directly, but as a first approximation we can assume that the net rate of sedimentation was the same for the Hell Creek Formation and the overlying Fort Union Group. The latter effectively spans Paleocene time, about 10 million years, and in the Hell Creek Field is about 450 m. thick. Bug Creek time, or the duration of dinosaur extinction in Montana, was then, very roughly, 400,000 years (9).

Plants and climate

Several studies (10) have been made of the leaves and pollen of the Hell Creek Field, with some attention paid also to fruits and wood. Appreciable work has also been done on the plants of stratigraphically related beds in nearby areas. It is possible to make a coherent picture of these studies, although there is some conflict among the interpretations of the original workers. We must accept responsibility for the following synthesis, some aspects of which are new although based on published data.

Before Bug Creek time, the deltaic environment of the Hell Creek Field existed in an equable, moist, subtropical climate, although there were major storms (Erickson, 1974). Shoemaker (1969) has compared the flora favorably with the mid-montane forests of Costa Rica and Sabah. It is, however, unknown how open the canopy was, i.e. where it lay on the forest-savanna continuum (11). Both leaves and pollen show appreciable differences among nearby localities in their flora, even when studied by the same workers. The nature of this local heterogeneity is unclear. Larger-scale heterogeneity, including latitudinal gradients, also existed: palms reached their northern limit near the southern part of the Hell Creek Field, although they extended into British Columbia on the Pacific coast (12).

In the transition to the Paleocene, this flora underwent major changes. At least in some localities the flora in Bug Creek time is intermediate between the earlier and later floras. There are several ways of looking at the changes, and almost all give a single conclusion. The diversity of pollen decreases markedly in the transition. There is more than a 50 percent turnover in the species of both pollen and leaves. Gymnosperms (and ferns) increase at the expense of both monocots and dicots. Most taxa are either poorly identified with recent taxa or the latter occur in diverse environments, but of those for which some comparison is possible most are tropical or subtropical indicators before Bug Creek time, while afterwards more than two thirds are temperate indicators. The proportion of species with entire-margined leaves decreases, but the proportion with large leaves increases. A flora where most dicots were evergreen gives way to one where there is a preponderance of deciduous species among the remaining dicots.

Except for leaf size, all these lines of evidence favor a decrease in winter temperature. That is, winters became more severe. The continued occurrence

Fig. 5. Hypothetical reconstruction of a typical scene in the Hell Creek Field before Bug Creek time. Note a 10-meter-long Triceratops skulking in the undergrowth.

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of rather large crocodiles, turtles, and champsosaurs in Montana and Alberta somewhat suggests the continued occurrence of winters without much frost. Stream drainage may also have become poorer. Because the northern limit of temperature-controlled distributions is set by the winter temperature and related effects, nothing can be said about any change in the summer temperature from shifts in northern limits.

Southern limits of temperature-controlled distributions are more ambiguous, but the immigration of some more northerly species suggests, if anything, a lower summer temperature (Conolly and Dahl, 1970). Therefore Axelrod and Bailey's (1968) conclusion (on much less evidence than ours) that the equability (13) decreased is an unsupported possibility. Figs. 5 and 6 depict visually the general habitat change.

There is much other evidence, of diverse kinds, that bears on climatic change at the close of the Cretaceous (e.g. Saito and Van Donk, 1974; Krassilov, 1975). We defer its presentation and evaluation to our longer treatment, as we do much else, but it predominantly supports the picture we give here and extends it worldwide.

Fig. 6. Reconstruction of an early Paleocene scene in the Hell Creek Field. The spacing of trees is based on a plane-table mapping of a petrified forest in the Tullock Formation. Drawn to the same scale as Fig. 5.

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Dinosaur extinction in Montana

So what happened?

Winter temperatures became more severe. This caused the local extinction of many subtropical plants, and a temperate forest moved south. This forest lacked dinosaurs, and as it infiltrated the existing biota the dinosaurs found it progressively less easy to cope (14) with their new biotic environment.

But why did the temperate forest lack dinosaurs? This is unclear and perhaps will remain so until the origin of this community is discovered. We will nevertheless evaluate four hypotheses.

Perhaps the lower productivity of a temperate forest couldn't support dinosaurs. But the difference today is relatively small (Golley, 1972; Lieth, 1973; Rodin, Bazilevich, and Rozov, 1975), so some species should survive (15).

Perhaps the dinosaurs couldn't eat the temperate vegetation. Moreover, the increase in deciduous trees would make less food available in winter. But the teeth of the herbivores comprised batteries anatomically effective for crushing, and Anatosaurus is known to have eaten conifer needles. Presumptively deciduous tress didn't come to dominate the vegetation. With respect to digestion, chemical defenses at least today seem to be more characteristic of tropical vegetation than of temperate (Levin, 1976). Moreover, dinosaurs lived all over the world, in widely diverse floras, and had survived without noticeable harm through one of the great floral turnovers of the history of the earth. About 30 million years earlier the angiosperms had diversified and spread worldwide, replacing a world flora dominated by cycads and other pre-existing groups. That dinosaurs flourished and radiated exhuberantly throughout this transition makes implausible a dietary explanation for their absence from a temperate forest.

Perhaps dinosaurs were excluded from the temperate forest by a direct effect of temperature, an insuperable physiological threshold. Reptiles today, especially ones too large to burrow, are concentrated in warmer areas. But the probable endothermy of dinosaurs makes an argument by analogy suspect here. Although a few probably had feathers (Ostrom, 1974), just as pterosaurs had hairlike insulation (Sharov, 1971), Anatosaurus, at least, had neither. But neither do whales that live in icy water, which is a much better heat conductor than air. The presence of insulation like that of whales, or an analogous adaptation, can't yet be tested for dinosaurs (particularly for young ones, for whom it would be most useful).

Although the Arctic is poorly known paleontologically, the dinosaurs farthest north by Cretaceous latitudes seem to be from northeastern Yukon (Rouse and Srivastava, 1972), at about 75° N paleolatitude (16). 75° N today is well north of Baffin Land, Alaska, and all but the Taimyr Peninsula of Siberia. Late Cretaceous floras from Alaska and Siberia suggest that a moderately large area was temperate (e.g. Samoilovich, 1967; Zaklinskaya, 1970; Smiley, 1972; Stanley, 1972; Krassilov, 1975). However, the Cretaceous flora of the Yukon and nearby was more similar to the Cretaceous flora of Montana than to the Montana Paleocene flora (Rouse and Srivastava, 1972; Bihl, 1973).

The Triceratops community survived for an ecologically very long time on flat terrain in close proximity to the invading Protungulatum community with its flora. If the invasion was climatically caused, the Triceratops community was able to tolerate the climate causing that infiltration. And the marsupials of the Triceratops community became almost as extinct as the dinosaurs; some indigenous placentals and multituberculates also disappeared.

Most importantly, perhaps, the hypothesis of a direct effect of temperature can't easily explain the extinction of dinosaurs in areas which remained tropical.

A fourth and final hypothesis is primarily historical rather than functional. Perhaps in the formation of the Protungulatum community no dinosaurs happened to participate even though they could have done so. In other words, their exclusion was due to local effects and what species were available rather than to overall properties of dinosaurs (17). This hypothesis is hard to test in the absence of a record of the earlier history of the Protungulatum community, and it lacks direct evidence. It nevertheless is the only hypothesis that seems plausible.

A perhaps relevant item is that all the placental mammals in the Protungulatum community seem closely related to each other. This is true despite their being classified into three orders because of the evolution of their descendants. By themselves, the insectivoran Procerberus, the primate Purgatorius, and the condylarth Protungulatum could justifiably be placed in the same family.

It may be that, a geologically short time earlier, a common ancestor of these placentals developed some kind of adaptation that permitted more effective use of a temperate forest. Perhaps it was chance that this happened to a placental instead of to a marsupial, a multituberculate, or a dinosaur. (The temperate community did share some multituberculates with the subtropical community.) Or it may have been related to a peculiarity of placentals, or to an immigration of a lucky species from the continent of Europe plus eastern North America or from elsewhere (18). Nothing requires that every community contain dinosaurs (19).

A more effective use of the resource space by these small mammals may well have prevented the invasion of the community by other vertebrates and may have caused the extinction of some already present. Presumably such effects would be by diffuse competition rather than by one-to-one face-offs. Such trophic competitive processes require that the ultimate regulation of the density of at least most of the competitors be by food. Hairston, Smith, and Slobodkin (1960) have argued that this is unlikely for most herbivores, but we have given generally applicable evidence that even the herbivore trophic level is ultimately regulated by food (Van Valen and Sloan, 1966; Van Valen, 1973a).

Just how competition ordinarily occurs among herbivores remains mysterious, and this is quite as true for the end of the Cretaceous as it is for communities today. A major part of the flora can't be adequately reconstructed, so reconstruction of diets on the basis of dental adaptations by analogy with recent mammals is even more tenuous than usual (20). Most resource use should have no necessary relationship to body size; Webb (1969) has in fact suggested a partial replacement of ungulates by rodents in the late Cenozoic, Stone et al. (1957) gave evidence for competition between rats and Drosophila, and Brown et al. (1975) do so for rodents and ants (21). Possibly competition with young dinosaurs or even baby ones was critical.

If dinosaurs kept mammals from radiating widely and from becoming dominant in energy flow during their 130-million-year coexistence (a piece of conventional wisdom which nevertheless seems likely), this requires that the two groups were marginally in competition for that long interval. Predation is unlikely to have been critical because mammals could have become energetically dominant while remaining small, as insects have done. There is therefore no conceptual difficulty in thinking of mammals outcompeting dinosaurs when the mammals became better by their rapid evolution at the end of the Cretaceous.

The extinction process was similar to an ecological succession. One community gradually infiltrated and replaced another. The replacement doesn't satisfy all of Odum's (1969) or Margalef's (1968) criteria of successions, but neither do many ordinary successions. No mysterious processes need to be postulated. The extinction rates were much slower than those of the drastic extinction of large terrestrial vertebrates after the latest glaciation (Martin, 1968), slower by a factor of perhaps 100 to 1000.

The minimum density consistent with survival is a greater proportion of the usual density for large animals than for small ones. Large animals are scarcer and breed more slowly. And so for the dinosaurs: they could maintain only progressively sparser populations in the face of a community infiltrating and replacing the vegetation they had eaten for millions of years. Eventually some minor crisis was too much. What crisis this was may have been different for different species, or it may have been something like the coincidental supernova postulated by Russell and Tucker (1971) and others. It doesn't matter much; competition doomed their death and any final executioner would do.

Dinosaur extinction elsewhere

The area of the present-day tropics obviously didn't lose its dinosaurs in quite the same way Montana did. A temperate forest has never reached Brazil or central Africa. As with the origin of the temperate forest community, we won't really know what happened in the tropics until someone finds an appropriate sequence there and studies it ecologically.

But here, at least, there are some facts. One fact is that no dinosaurs have been found in sediments definitely known to have been deposited after the end of the Cretaceous. Another fact is that all over the world, except on islands (22), diverse placental mammals occur in the first post-Cretaceous sediments that contain terrestrial vertebrates. And everywhere many of them are of kinds that seem descended from members of the Protungulatum community.

In most places, unfortunately, the gap between the end of the Cretaceous and the first Cenozoic vertebrates is large. The Hell Creek Field is the only known area with a more or less continuous sequence, and even here the first Cenozoic faunas are not much less than a million years after the boundary. The gaps elsewhere between the last known dinosaurs and the first known terrestrial Cenozoic vertebrates range from 1 or 2 million years in New Mexico and Utah, and not much if any longer in western Europe, to about 15 million years in all of Africa (on which see Gevin et al., 1975).

It is almost necessary to infer that the rapidly evolving placentals escaped the limits of their temperate forest and expanded worldwide in a geologically short time. In doing so, they may well have outcompeted the dinosaurs in the dinosaurs' home grounds.

This hypothesis requires, and it may be taken as a prediction, that dinosaurs survived longer in the tropics than in Montana (23). Two flimsy data support the prediction.

The only hadrosaurian dinosaur described from the Southern Hemisphere (Casamiquela, 1965) was found in beds dated provisionally as Danian (early Paleocene). Cox (1974) has noted that this is the only Southern Hemisphere record of a dinosaur of any of the several characteristically Northern Hemisphere families. Other dinosaurs are, however, well known from the Southern Hemisphere. Many nonmarine molluscs entered South America in the early Paleocene (Parodiz, 1969) and a diversity of ungulates derivable from <u>Protungulatum</u> occur in the first definitely Cenozoic vertebrate deposits of South America a few million years later. The Bombacaceae arrived, apparently from North America (Wolfe, 1975), by the middle Paleocene (Germeraad, Hopping, and Muller, 1968). The South American crustal plate was at the end of the Cretaceous probably overthrusting the Caribbean (24), whose geological history is still very poorly known. The hadrosaur may well have entered South America from North America at this time of relative approach (and perhaps junction) of the two continents, together with the molluscs and mammals (25). It did not survive long with the invading mammals.

The second flimsy datum concerns a mammalian fauna from Laguna Umayo, Peru (Grambast et al., 1967; Sigé, 1968, 1971, 1973). This fauna contains eggshells reported to be those of dinosaurs, charophyte oogonia dated as late Cretaceous, several marsupials, and a placental. The placental, <u>Perutherium</u>, is an ungulate decidedly more advanced than <u>Protungulatum</u>; by North American standards it is of about the grade present in the late part of the early Paleocene or a little later. At least one of the marsupials is similar to those that had been present in North America for millions of years in the <u>Triceratops</u> community and before (Fox, 1971b; Sahni, 1972), and Sigé's identifications of the other marsupials support this view. Unless there was a long-lasting or repeated land connection between North and South America, which is unlikely on both geological and zoogeographic grounds, the ancestors of these marsupials immigrated to South America with the placentals. We prefer the evidence of <u>Perutherium</u> to the reportedly much more ambiguous evidence of the charophytes in determining the age of the Laguna Umayo Fauna, and so assign it a Paleocene age. If the eggshells there really came from dinosaurs, the dinosaurs were then Paleocene (26).

The absence of marsupials from the temperate forest (and from known Cretaceous faunas in Asia and Europe, unless <u>Deltatheridium</u> really was a marsupial), and their restriction to subtropical and presumably tropical communities, helps explain the present distribution of marsupials. Unless marsupials had been evolving in South America (Tedford, 1974), as is possible if unlikely, they came from the geographically adjacent part of North America, where they were the predominant therian mammals. The Australian marsupials are also derivable from those known in North America at the end of the Cretaceous (Clemens, 1968), so a further expansion into Antarcticaustralia is plausible. If separation from South America occurred shortly afterwards, as may have happened (22), the placentals of South America were still perhaps too rare or local to have followed, or the marsupials may have crossed a water gap. Possibly the placentals followed anyway and were later exterminated before the first (about late Oligocene) known mammal fossils of Australia (27), but otherwise the dominance of marsupials in Australia is both provisionally explained and relevant to the extinction of dinosaurs there. An immigrating wave of marsupials could perhaps do as much damage to a coadapted fauna of dinosaurs as could a wave of placentals. But we won't know what really did happen there, and when, until evidence from the Australian record is available.

Extinctions in the sea

The great dying affected also organisms that lived in the sea. In fact extinction here was at least as severe as that on land. About 90 percent of the specific lineages of coccolithophores (the dominant planktonic algae) became extinct (Bramlette and Martini, 1964; Perch-Nielsen, 1969, 1972). So did 13 of the 18 generic lineages of planktonic foraminiferans, the next level in the food chain (original analysis). Most groups of marine reptiles and all ammonites completely vanished. And many other organisms did too, although not all at quite the same time (Kauffman, 1973b). Very roughly half the generic or familial lineages of marine organisms disappeared in the last 5 million years or less of the Cretaceous.

This extinction has some ecological regularities, each with exceptions. The plankton and the whole pelagic food chain, which depends on them, suffered severely. So did filter-feeders on the sea bottom. But sea-bottom predators and detritus-feeders in the mud had little loss, and groups usually resistant to physical stresses fared better than those with a narrow tolerance. The pattern differs from that of the late Permian, when a restriction of the area of shallow seas seems to have been the main control (Newell, 1963; Ruzhentsev and Sarycheva, 1965; Schopf, 1974; but see Bowen, 1975).

Although some of the late Cretaceous extinctions took place over a few million years, both on land and in the sea there was a geologically short but ecologically long interval where a major crisis occurred. For the sea this is best shown in work by Percival (1972; Percival and Fischer, 1977), who studied an apparently continuous section at Zumaya in northern Spain (see also Hillebrandt, 1965, and Herm, 1965, for Zumaya foraminiferans, and Worsley, 1970, pp. 28-29, for a generally similar result in Alabama).

The time scale is 10^4 or 10^5 years, like that for the dinosaurs in Montana. The planktonic foraminiferans gradually decreased in size and all the larger species gradually became extinct. The absolute number of planktonic foraminiferans, estimated from the ratio of planktonic to benthonic individuals (28), decreased gradually by a factor of 1000 if the number of benthonic individuals remained constant.

Somewhat after the start of the foraminiferal decline, there was a more rapid but gradual decline in the number of species of coccolithophores. It is unknown whether there was a concomitant or antecedent decline in the number of individuals (29). For both foraminiferans and coccolithophores, some of the species of the early Paleocene were present but rare before the end of the crisis. Both groups took a million or more years to recover, as was the case in Montana for the re-establishment of a more or less balanced terrestrial community (30).

Synthesis

As normally happens during a regression of the sea (Kauffman, 1970), there were many marine extinctions during the last few million years of the Cretaceous. About 10^5 years before the end, there was a geologically sudden decline in temperature, apparently worldwide. The cause of this is unknown although several possibilities exist (31). Other physical or chemical changes in the sea occurred at about the same time and may well be interrelated (Tappan, 1968; Worsley, 1970, 1971). Perhaps cold bottom water reappeared briefly (32). The plankton and species dependent on the plankton were drastically affected; most others in the sea were not.

On land, the fall in temperature caused a southward movement of communities. One of these, which had placental mammals instead of dinosaurs for perhaps historical reasons, slowly replaced a dinosaur-dominated community. The diversifying placentals soon escaped and outcompeted the dinosaurs everywhere.

So how did the world end? Not with a bang, not even with a whimper, but with, of all things, a slow plant succession, which permitted the placental mammals to diversify. And soon they took over the earth.

NOTES

(1) This presentation is abstracted from a much longer and documented version, most of which was done by about 1964. (The lack of publication is due to the unavailability of a way for persons without the right institutional connections to publish monographs in this country. The problem may possibly be solved now for this monograph.) We have presented our results on many occasions, publicly and privately, in this interval. The only published abstracts are Sloan (1964) and Van Valen and Sloan (1972), but a summary of our results (attributed to another paleontologist) was given on the BBC television documentary The Dinosaur Hunters (1972).

Our work in Montana, at first independent but soon coalesced, had two main purposes: to find Cretaceous ancestors for the Cenozoic radiation of the placental mammals, and to look, from the viewpoint of modern ecology, at what really happened at the dinosaur extinction. Both purposes were satisfactorily realized (cf. Sloan, 1970).

Many people have helped us in our work. We thank them all here, and will try to do so individually and more adequately in the longer version.

(2) Perhaps other causes also operated, but Jeletzky (1974) has concluded that local events predominated at least in Canada in the Cretaceous.

(3) Aspects of the geology of the Hell Creek Field and nearby areas have been given in the following publications, in addition to our own work and papers mentioned elsewhere: Bauer (1924), B. Brown (1907, 1914), R.W. Brown (1938, 1952), R.W. Brown and Lindvall (1953), Collier (1919), Colton (1955), Colton and Bateman (1956), Dobbin and Reeside (1929), Feldman (1972), Fox and Olsson (1969), Frye (1967, 1969), Gerhard (1963, 1967), Gill and Cobban (1973), Jensen (1951), Jensen and Varnes (1964), Johnson and Smith (1964), Knowlton (1909), Leonard (1911), Lindberg (1944), Mallory (1972), Miner (1935), Perry (1935), Stanton (1909), Thom and Dobbin (1924), Waage (1968), and Yen (1948). References to several dozen reports on coal geology can be found in Bryson and Bass (1973).

(4) Bug Creek represents the last recorded occurrence of *Belonostomus* and its small order; this is ordinary slow community change.

(5) *Anatosaurus* seems to have been partly aquatic, as shown by the webbed feet of mummies and the ducklike bill in soft tissue as well as bone (Morris,

1970, 1971). However, the only reported stomach contents are conifer needles and other remains of land plants (Kräusel, 1922), and Ostrom (1964) has given other evidence for an important terrestrial component in its life.

(6) The estimates are based on specimens collected by washing from channel deposits. They are therefore subject to the biases of stream sorting. However, minute multituberculate teeth are much commoner than the more conspicuous large bone fragments, so the overall bias here is presumably not large relative to other sources of error.

(7) Unpublished calculations by Van Valen for various recent mammal communities give values on both sides of 10 for the ratio of energy used by large mammals to that used by small mammals. This ratio was not used in deriving that for the Cretaceous.

(8) Bug Creek was named by a local rancher after Barnum Brown took out some big bug in 1906. The namesake "bug" happens to be the mounted skeleton of *Tyrannosaurus* in the American Museum. Harvester ants (*Pogonomyrmex owyheei* at Bug Creek) decorate their anthills with small mammal teeth as well as other resistant objects.

The 20:1 ratio of invaders to indigenes is based on the ratio of specimens of invading mammal species, to specimens of mammal species that are restricted to the *Triceratops* community. The data are in Sloan and Van Valen (1965) and are for thousands of specimens from Bug Creek Anthills. The invaders are *Stygimys*, *Catopsalis*, *Procerberus*, and *Protungulatum*, which constitute 53.32 percent. The indigenes total 2.95 percent. (*Mesodma* and *Cimexomys*, which occur in both communities, are excluded.) The ratio is 18:1, which we round to 20:1 because of probable inaccuracy.

(9) Although some Fort Union coals are thick and surprisingly free of transported sediment, a decrease in the estimated duration of Bug Creek time by as much as a factor of 10 is unlikely. Perhaps 100,000 years would be a better estimate than 400,000; this is also more consonant with an estimate from marine strata (Worsley, 1970).

(10) Some relevant botanical studies of the Hell Creek Field are the following: R.W. Brown (1939, 1962), Dorf (1942), Shoemaker (1966), Hall and Norton (1967), Norton and Hall (1967, 1969), Oltz and Hall (1968), Oltz (1969, 1971), Tschudy (1971).

(11) What the herbaceous stratum was at this time, aside from ferns and a few nongrassy monocots, remains a mystery. Most recent herbaceous angiosperms seem to have originated later (Muller, 1970), and almost none occur in the Hell Creek Field. Possibly the reputedly extinct Normapolles, a diverse pollen group largely restricted to the contiguous land of Europe and eastern North America, was largely herbaceous, but this doesn't help much in Montana. Possibly such extinct genera as the abundant *Aquilapollenites* provided the missing stratum, but there is no positive evidence. Pollen of herbaceous plants is normally rare in sediments. This may affect Muller's stratigraphic records as well as the observed floras from Montana. Monocots were, however, well established, and their basic adaptation is to a herbaceous habit (Cronquist, 1974).

(12) The latitudinal difference between British Columbia and Montana was greater than it is today, so the greater northward extent of palms on the Pacific Coast implies greater equability there in the Cretaceous as well as today.

(13) Bailey's (1960) measure of temperateness or equability, based on departure from the mean temperature of the earth's surface in the first half of the twentieth century, is inappropriate for most biological applications. It can be replaced by a direct measure of temperature variation, such as the annual variance. The annual mean and extremes are of course also often important, but different organisms are adapted differently.

(14) Even outside the Marshes.

(15) Today the vertebrates of rain forests live almost entirely on the production of the canopy rather than on that of the toxic understory (Bourlière, 1973). We don't know the situation in the Cretaceous, but we suspect that Triceratops wasn't arboreal.

(16) Dinosaurs occur in Spitzbergen in early Cretaceous rocks (de Lapparent, 1960, 1962), but tectonic reconstruction places Spitzbergen at a latitude of 50° or 60° then.

(17) What species were available for inclusion in the temperate community could nevertheless be related to their average properties. Both marsupials and dinosaurs may have been predominantly tropical and subtropical, and therefore less likely to participate in a temperate community than placentals. There is, however, no positive evidence for dinosaurs being more important in tropical areas. And marsupials, at least, are able to overcome such restrictions, which are at least for marsupials as a whole ecological rather than inherently physiological.

(18) It is possible, if unlikely, that the water gap between North America and most of Asia, the deep-water part of which now lies in the Verkhoyansk Mountains of Siberia, didn't close until the Cenozoic, although the orogeny there was in the early Cretaceous (on the latter, see Churkin, 1972, and Herron, Dewey, and Pitman, 1974). Each possible result here would be incompatible with some of the recent anti-ecological zoogeographical speculation on Cretaceous interchange across this region. (It is also relevant to such speculation that the Turgai Straits in Kazakhstan were only episodic in the early Cenozoic and so weren't a complete barrier [Vinogradov, 1967, 1968, 1975]). Possibly the Okhotskian Belt of Nalivkin (1962), which lies farther east but extends farther south, is associated with later movement in conjunction with the Pacific plate. The northern boundary of this plate seems to have shifted south to the Aleutian Trench at about the end of the Cretaceous (Scholl, Buffington, and Marlow, 1975). Our reconstructed plate movements, based on evidence from the Atlantic, fit eastern Siberia awkwardly. Its geographical history needs further study, integrated with evidence from other regions.

(19) That placentals were in some way preadapted to the temperate forest is suggested by a roughly simultaneous diversification of placentals in southern Alberta. Such preadaptation could be related to temperature, the lower productivity of northern floras with less annual sunlight, possibly greater adaptability of placentals, or various other untestable causes. At least most of the lineages in Alberta differed from those entering Montana, and in this case also most of the lineages are interrelated (Lillegraven, 1969). They too diversified into the Cenozoic. However, the putative ancestors of the Alberta radiation were already present in the Triceratops community earlier, and they were able to adapt rapidly to a possibly changing flora. (The botanical evidence from Alberta is too poor for a stronger statement, and more work needs to be done there.) Censuses of specimens by locality aren't available for Alberta, but a total count from Lillegraven's paper gives 286 placentals, 322 marsupials, and 255 multituberculates. Probably the radiation of placentals in Alberta occured before the Protungulatum community immigrated. Possibly it was a parallel response to the appearance of a temperate forest. This line of speculation can be carried further but seems too insecurely based for elaboration.

A montane origin for the temperate forest in Montana is unlikely because this forest occurs perhaps 100 km. from the epicontinental seacoast before it occurs farther inland, on the basis of a few localities. Perhaps it came from Greenland. The evidence for a southward movement of the Protungulatum community is the strong spatiotemporal coincidence of its appearance with the appearance of a cooler flora.

(20) Thus hadrosaurs and ceratopsians were dentally adapted to resistant food, but Protungulatum and Stygimys might have been too because small mammals have less need for a special adaptation here than do large ones, partly because of the allometric relations between tooth size, body size, and food intake, and partly because of their shorter lives (Van Valen, 1960). More likely, the dinosaurs were eating more resistant parts of plants than were the mammals. The opal phytoliths that make grass leaves so abrasive presumably were absent before grasses and sedges originated in the Cenozoic. If dinosaurs crunched branches or stems as well as leaves, this may itself explain the difference in dental adaptation. Such a difference in diet would be irrelevant to competition if both groups ate the same plants. Such arguments as this can merely establish plausibility rather than probability, but a plausible interpretation of superficially contrary evidence is helpful.

(21) Van Valen (1975) nevertheless gives evidence suggesting that, despite individual counterexamples and contrary theory, most interactions of at least mammals and foraminiferans are with species of a generally similar size.

(22) Australia and Antarctica, still connected to each other in the Paleocene, were far from Asia and Africa. They were an "island" in the sense that South America was one for most of the Cenozoic, being isolated from evolution elsewhere. The time of the separation of Antarcticaustralia from South America is still unclear (Dalziel et al., 1973). South America and Antarctica are now farther apart than they were in the early Cenozoic and Cretaceous (Dalziel and Elliot, 1973). The initial bending of the Scotia Arc, which joins these continents, was also no earlier than latest Cretaceous (Dalziel and Elliot, 1973). The presumptively earliest Cenozoic mammalian fauna of South America, that of Laguna Umayo, Peru (on which see Sigé, 1973), consists largely of species of marsupials, with an even greater preponderance in numbers of individuals. (The lack of multituberculates here as in Australia is, however, striking.) It is therefore plausible but unproved that a path to Australia was open long enough for southern derivatives of the tropically concentrated marsupials to come but closed before placentals diversified in South America. Sweepstakes dispersal via islands is also possible.

The Protungulatum community was very probably absent from the South American Cretaceous. Apart from its not having been found, its descendants are diverse in Holarctica but in South America come from only one of its lineages until the Oligocene immigration of primates.

(23) Stone and Langston (1975) have just reported a dinosaur from southwest Texas that is associated with a Paleocene-like pollen flora. This could well be a southern extension of the flora that invaded Montana, but presumably is slightly later. If so, dinosaurs survived longer even in Texas than in Montana. "The discovery of dinosaurian remains in Tertiary deposits, or of trilobites in the Permian, should give far less cause for surprise than a positive announcement that they did nowhere so occur" (Heilprin, 1887, p. 204).

(24) Tectonic references on the relative approach of North and South America at the end of the Cretaceous are Beets (1972), Bell (1972), Bellizzia (1972), Freeland and Dietz (1972), Harvey (1972), Malfait and Dinkelman (1972), and Maresch (1974). Shagam (1972) in particular notes that at the Cretaceous-Cenozoic boundary the tectonic environment changed from tensional to compressional across the entire northern boundary of South America. The isthmus-forming position of southern Central America is unlikely to be simply chance, and a similar relationship might have appeared at the end of the Cretaceous, perhaps in relation to the colliding borderland of Maresch (1974). An Antillean connection is,however, also possible. Fox and Heezen (1975) note that there was "significant plate consumption" north and south of the Caribbean until the Eocene, and that the whole Caribbean basin may have been epeirogenically

uplifted to some extent in the late Cretaceous and early Cenozoic. The major orogeny in southern Central America began about the end of the Cretaceous (Dengo, 1973).

Scotese (1975), in a set of computerized reconstructions of continental segments, shows a distance between North and South America at 60 million years similar to that today. Kauffman (1973a), finding a progressively increasing endemism of clams on each side of the present Central America as the Cretaceous neared its end, postulated a land barrier there. And, if serum albumin evolved at a constant average rate, the best estimate for the time of divergence of North and South American hyline treefrogs is 65 million years (Maxson and Wilson, 1975), very close to the time suggested for migration of mammals and land molluscs.

(25) Hadrosaurs may of course have been in South America for a long time, although they originated near the time of the separation of South America from Africa. However, they are quite unknown in the definitely Cretaceous dinosaur faunas from South America.

The partly archaic nature of the Edentata (including Pholidota), and their southern distribution, suggests that they may represent a southern radiation of primitive placentals that started before South America left Africa. If so, some Palaeanodonta probably moved to North America from South America at the beginning of the Paleocene, perhaps even before the Xenarthra originated from them in South America. Edentata thus may well have inhabited Australia before the marsupial invasion, and perhaps well into the Cenozoic.

(26) According to current ideas India was rafting merrily along to the north by itself at the end of the Cretaceous, out of sight of other land, although the immense lava flows of the Deccan Traps, of latest Cretaceous and Paleocene age, might suggest some degree of external interaction. Unless advanced mammals arrived from elsewhere before India collided with Asia at about the middle Eocene, we predict that the known late Cretaceous dinosaur fauna of India survived through the Paleocene into the Eocene.

(27) A placental of the family Anthracotheriidae seems somehow to have arrived on Timor in the Eocene (von Koenigswald, 1967). Anthracotheres are unknown in South America, as are any other artiodactyls before the connection to North America in the Pliocene, and Timor has been associated with Australia at least since the Paleozoic (e.g. Audley-Charles, 1973; Veevers and Evans, 1973). However, a water gap did appear to separate Timor from Australia then as now, and the first collision of Timor with an Indonesian microplate reportedly was in the Paleocene (Audley-Charles, 1973), before Australia had separated from Antarctica and while it was still far from Asia. This explanation is unsatisfactory, but so are others.

(28) The ratio of planktonic to benthonic foraminiferans can also be affected by dissolution of planktonic tests and by adverse bottom conditions (Sliter, 1975). Because the carbonate compensation depth seems to have risen remarkably high at the end of the Cretaceous, selective dissolution must be considered possible until the planktonic specimens are examined for evidence of partial dissolution. However, the rise itself may have been caused by a decrease in productivity of carbonate-secreting plankton, mostly foraminiferans.

(29) We predict that a decline in number of individuals of coccolithophores occurred together with that of the foraminiferans, and that the algae, being more numerous and smaller, were able to maintain their full complement of species longer than could the protozoans.

(30) There are no known land vertebrates in the early Paleocene (or in the _Protungulatum_ community other than the cursorial crocrodile and ordinary heron-like birds) that could easily have preyed on other vertebrates. Triisodontine arctocyonids may have done so ineffectively and soon evolved into predaceous

mesonychids, and crocodiles and Champsosaurus could perhaps forage on land sometimes. Additionally, no known land vertebrate of the early Paleocene was more than a meter long, unlike the situations immediately earlier and later.

Early Paleocene land vertebrates are known only from North America and Europe. Probably elsewhere there were effective predators, such as sebecoid crocodiles in South America and ratite birds on all continents of the Southern Hemisphere. There is good if indirect evidence that these groups were present there through the Paleocene.

(31) The geologically rapid climatic change and the changes in movements of continental and oceanic plates may have been coincidental, but there are at least two possible causal connections. The more likely is the induction of unusual amounts of volcanism. As for the second, the postulated temporary Central American land bridge would have interrupted any worldwide equatorial flow of "Tethys" warm water. This should reduce the temperature of the tropical seas, because their warmth comes from their residence time in highly isolated regions. However, indirect effects would be required for a reduction in total surface insolation and for the temperature decrease at higher latitudes, and the maps of Smith, Briden, and Drewry (1973) suggest that Europe and Africa were close enough together in the Cretaceous to preclude a major worldwide flow, although an epicontinental flow may have been wider (Gordon, 1973).

(32) The possibility of Antarctic glaciation at the Cretaceous-Paleocene boundary can be tested by oxygen-isotope measurements of benthic foraminiferans in a sufficiently complete deep-water section, if any exist. Perhaps the Zumaya sediments were deposited in deep enough water. The probable sudden eustatic regression of the sea at the boundary, culminating a more gradual but perhaps not worldwide retreat, is most easily explained by such a glaciation. The temperature drop at the boundary would provide a cause. A glaciation would, however, increase the difficulty of marsupials getting to Australia at this time, especially without placentals.

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