

DINOSAUR RENAISSANCE

The dinosaurs were not obsolescent reptiles but were a novel group of “warm-blooded” animals. And the birds are their descendants

by Robert T. Bakker

The dinosaur is for most people the epitome of extinctness, the prototype of an animal so maladapted to a changing environment that it dies out, leaving fossils but no descendants. Dinosaurs have a bad public image as symbols of obsolescence and hulking inefficiency; in political cartoons they are know-nothing conservatives that plod through miasmatic swamps to inevitable extinction. Most contemporary paleontologists have had little interest in dinosaurs; the creatures were an evolutionary novelty, to be sure, and some were very big, but they did not appear to merit much serious study because they did not seem to go anywhere: no modern vertebrate groups were descended from them.

Recent research is rewriting the dinosaur dossier. It appears that they were more interesting creatures, better adapted to a wide range of environments and immensely more sophisticated in their bioenergetic machinery than had been thought. In this article I shall be presenting some of the evidence that has led to reevaluation of the dinosaurs' role in animal evolution. The evidence suggests, in fact, that the dinosaurs never died out completely. One group still lives. We call them birds.

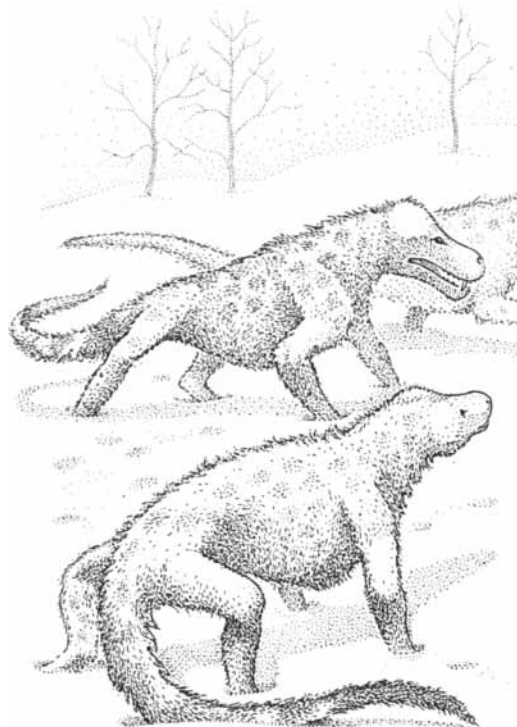
Ectothermy and Endothermy

Dinosaurs are usually portrayed as “cold-blooded” animals, with a physiology like that of living lizards or crocodiles. Modern land ecosystems clearly show that in large animals “cold-bloodedness” (ectothermy) is competitively inferior to “warm-bloodedness” (endothermy), the bioenergetic system of birds and mammals. Small reptiles and amphibians are common and diverse, particularly in the Tropics, but in nearly all habitats the overwhelming majority of land vertebrates with an adult weight of

10 kilograms or more are endothermic birds and mammals. Why?

The term “cold-bloodedness” is a bit misleading: on a sunny day a lizard's body temperature may be higher than a man's. The key distinction between ectothermy and endothermy is the rate of body-heat production and long-term temperature stability. The resting metabolic heat production of living reptiles is too low to affect body temperature significantly in most situations, and reptiles of today must use external heat sources to raise their body temperature above the air temperature—which is why they bask in the sun or on warm rocks. Once big lizards, big crocodiles or turtles in a warm climate achieve a high body temperature they can maintain it for days because large size retards heat loss, but they are still vulnerable to sudden heat drain during cloudy weather or cool nights or after a rainstorm, and so they cannot match the performance of endothermic birds and mammals.

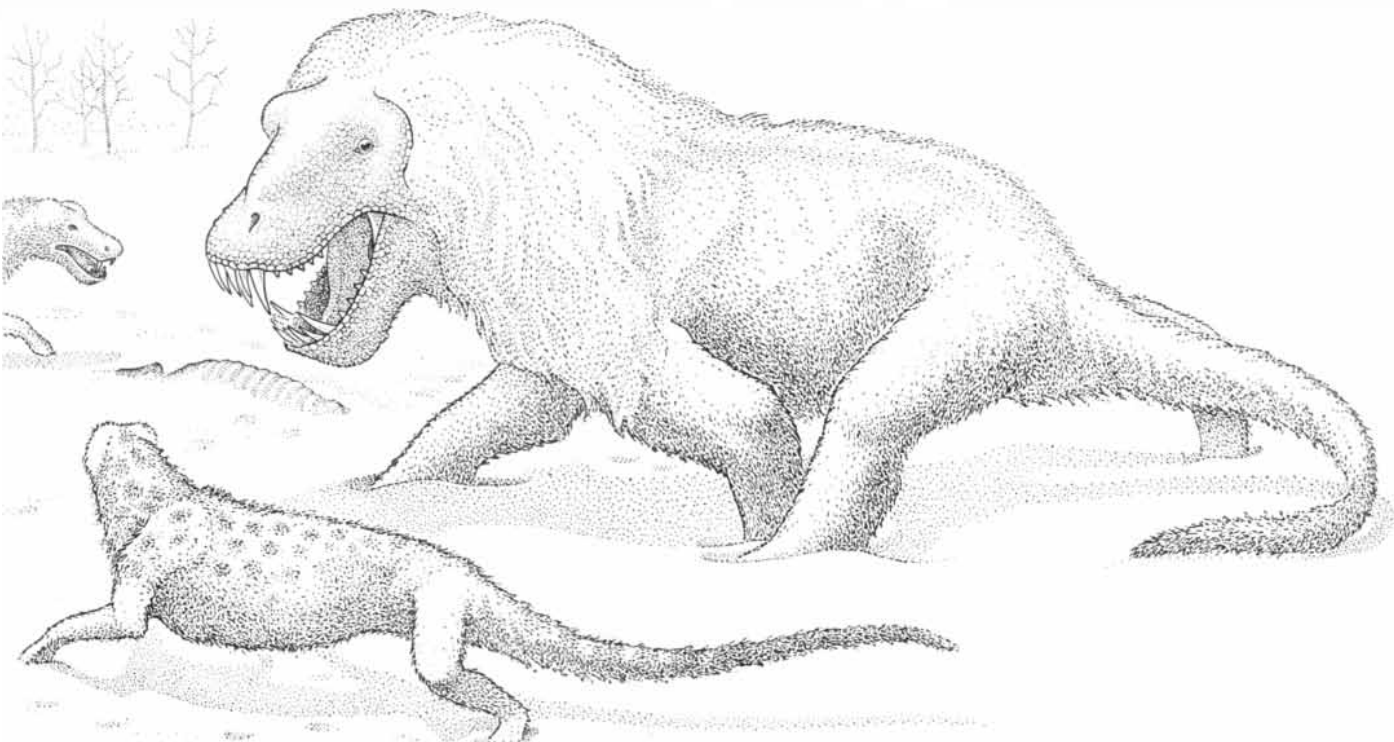
The key to avian and mammalian endothermy is high basal metabolism: the level of heat-producing chemical activity in each cell is about four times higher in an endotherm than in an ectotherm of the same weight at the same body temperature. Additional heat is produced as it is needed, by shivering and some other special forms of thermogenesis. Except for some large tropical endotherms (elephants and ostriches, for example), birds and mammals also have a layer of hair or feathers that cuts the rate of thermal loss. By adopting high heat production and insulation endotherms have purchased the ability to maintain more nearly constant high body temperatures than their ectothermic competitors can. A guarantee of high, constant body temperature is a powerful adaptation because the rate of work output from muscle tissue, heart and lungs is greater at



HAIRY THERAPSIDs, mammal-like reptiles of the late Permian period some 250 million years ago, confront one another in the snows of southern Gondwanaland, at a site that is now in South Africa. *Anteosau-*

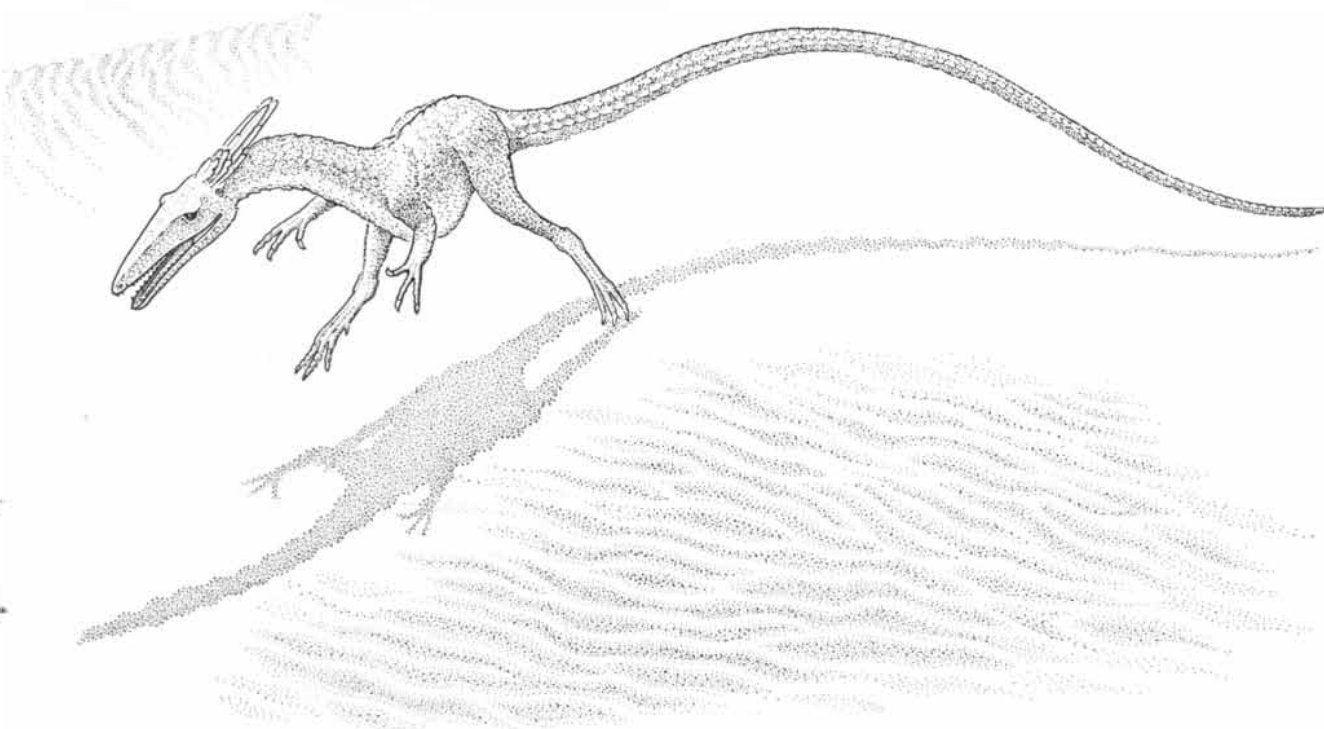


FEATHERED DINOSAUR, *Syntarsus*, pursues a gliding lizard across the sand dunes of Rhodesia in the early Jurassic period some 180 million years ago. This small dino-



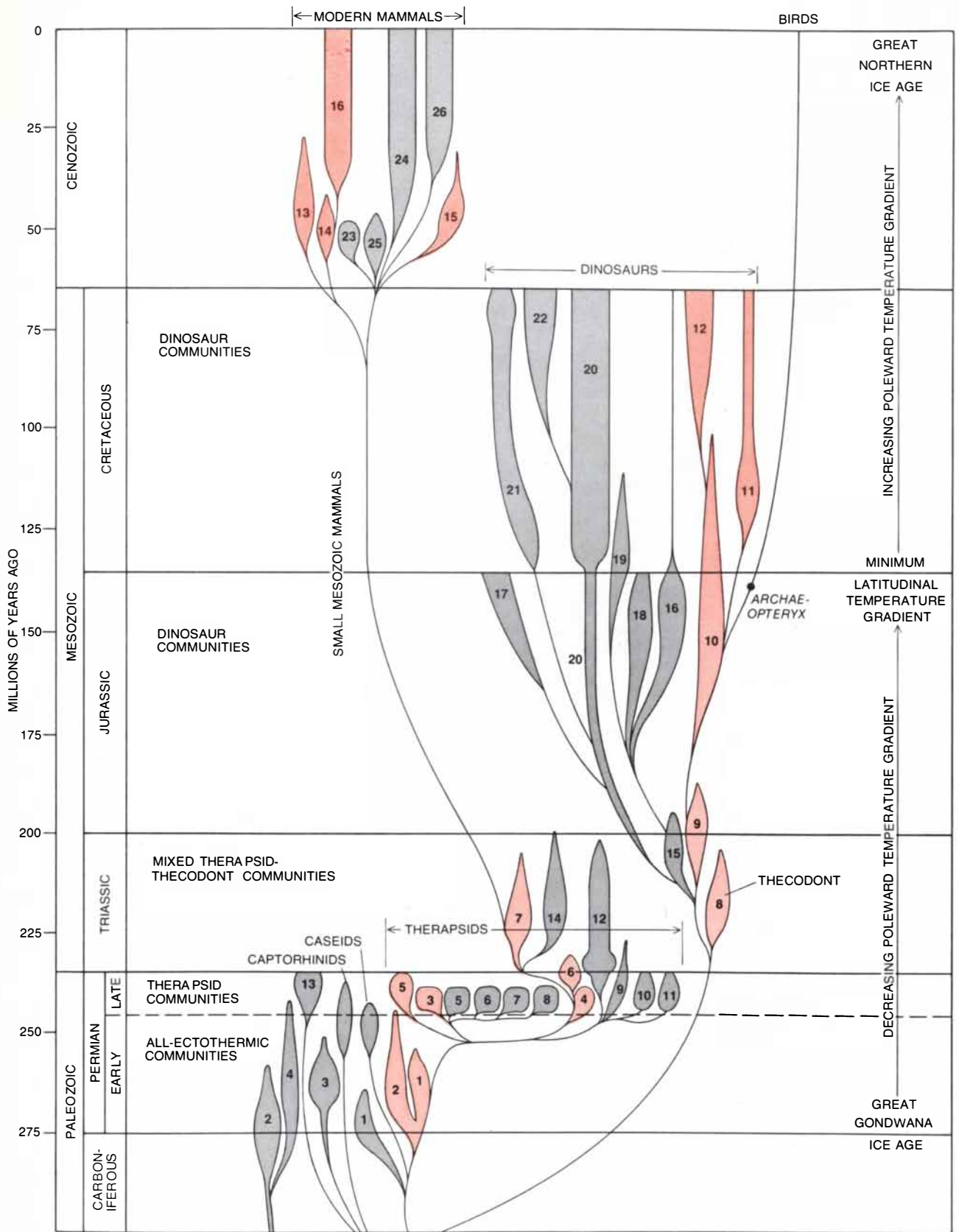
rus (right), weighing about 600 kilograms, had bony ridges on the snout and brow for head-to-head contact in sexual or territorial behavior. Pristerognathids (left) weighed about 50 kilograms and represent a group that included the direct ancestors of mammals. The reconstructions were made by the author on the basis of fossils

and the knowledge, from several kinds of data, that therapsids were endothermic, or "warm-blooded"; those adapted to cold would have had hairy insulation. The advent of endothermy, competitively superior to the ectothermy ("cold-bloodedness") of typical reptiles, is the basis of author's new classification of land vertebrates.



saur (adult weight about 30 kilograms) and others were restored by Michael Raath of the Queen Victoria Museum in Rhodesia and the author on the basis of evidence that some thecodonts, ancestors of the dinosaurs, had insulation and on the basis of close anatomi-

cal similarities between dinosaurs and early birds. Dinosaurs, it appears, were endothermic, and the smaller species required insulation. Feathers would have conserved metabolic heat in cold environments and reflected the heat of the sun in hot climates such as this.



PREDATOR-PREY SYSTEMS of land vertebrates and the paths of descent of successive groups are diagrammed with the predators (*color*) and the prey animals (*gray*) numbered to refer to the

groups named and pictured in the illustrations on pages 64 through 67. The relative importance of the live biomass represented by the fossils is indicated by the width of the gray and colored pathways.

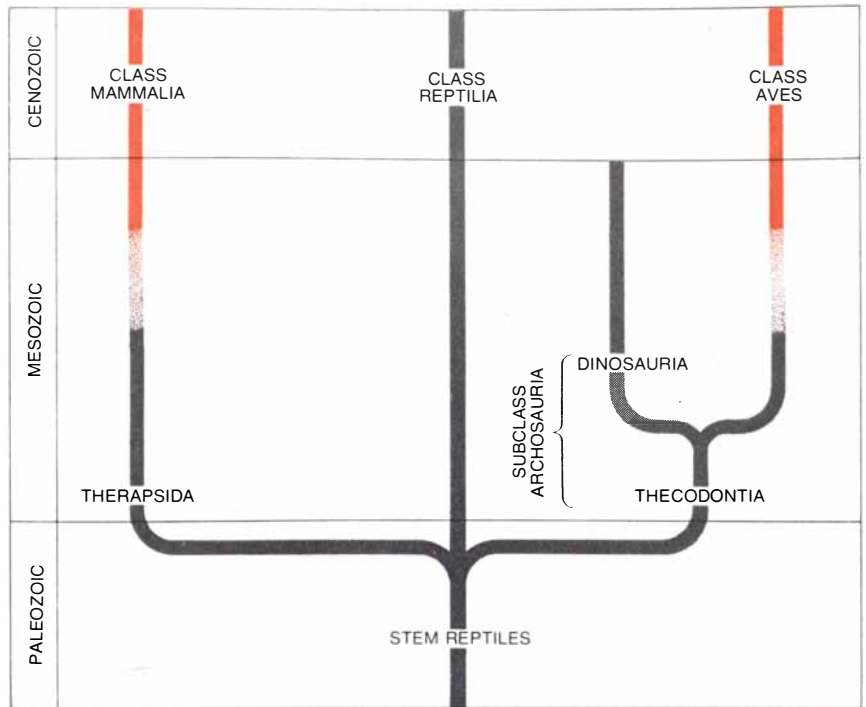
high temperatures than at low temperatures, and the endothermic animal's biochemistry can be finely tuned to operate within a narrow thermal range.

The adaptation carries a large bioenergetic price, however. The total energy budget per year of a population of endothermic birds or mammals is from 10 to 30 times higher than the energy budget of an ectothermic population of the same size and adult body weight. The price is nonetheless justified. Mammals and birds have been the dominant large and medium-sized land vertebrates for 60 million years in nearly all habitats.

In view of the advantage of endothermy the remarkable success of the dinosaurs seems puzzling. The first land-vertebrate communities, in the Carboniferous and early Permian periods, were composed of reptiles and amphibians generally considered to be primitive and ectothermic. Replacing this first ectothermic dynasty were the mammal-like reptiles (therapsids), which eventually produced the first true mammals near the end of the next period, the Triassic, about when the dinosaurs were originating. One might expect that mammals would have taken over the land-vertebrate communities immediately, but they did not. From their appearance in the Triassic until the end of the Cretaceous, a span of 140 million years, mammals remained small and inconspicuous while all the ecological roles of large terrestrial herbivores and carnivores were monopolized by dinosaurs; mammals did not begin to radiate and produce large species until after the dinosaurs had already become extinct at the end of the Cretaceous. One is forced to conclude that dinosaurs were competitively superior to mammals as large land vertebrates. And that would be baffling if dinosaurs were "cold-blooded." Perhaps they were not.

Measuring Fossil Metabolism

In order to rethink traditional ideas about Permian and Mesozoic vertebrates one needs bioenergetic data for dinosaurs, therapsids and early mammals. How does one measure a fossil animal's metabolism? Surprising as it may seem, recent research provides three independent methods of extracting quantitative metabolic information from the fossil record. The first is bone histology. Bone is an active tissue that contributes to the formation of blood cells and participates in maintaining the calcium-phosphate balance, vital to the proper functioning of muscles and nerves. The low rate of



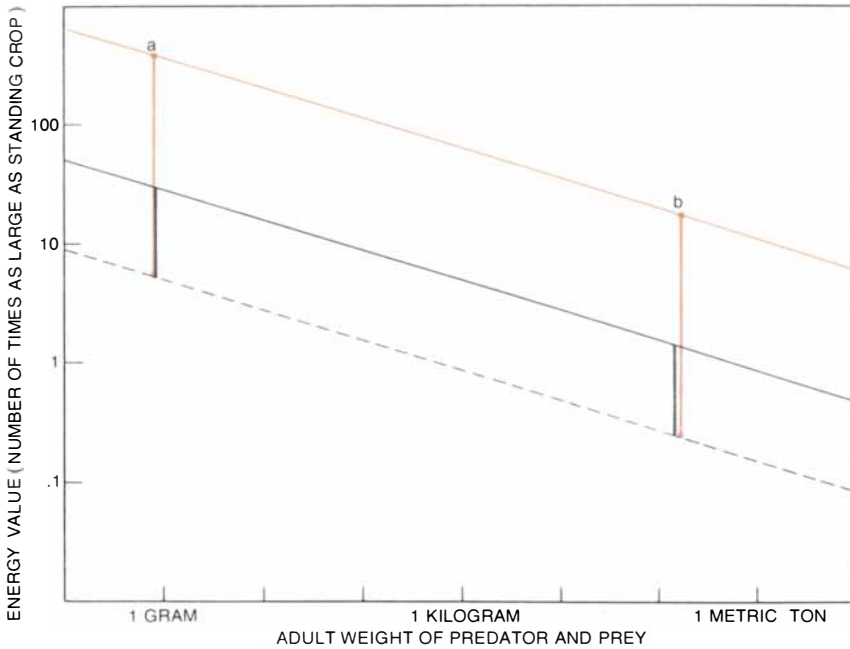
USUAL CLASSIFICATION of land vertebrates (excluding the Amphibia) is diagrammed here in a highly simplified form. The classes are all descended from the original stem reptiles. Birds (class Aves) were considered descendants of early thecodonts, not of dinosaurs, and endothermy (color) was thought to have appeared gradually, late in the development of mammals and birds. The author proposes a reclassification (see illustration on page 77).

energy flow in ectotherms places little demand on the bone compartment of the blood and calcium-phosphate system, and so the compact bone of living reptiles has a characteristic "low activity" pattern: a low density of blood vessels and few Haversian canals, which are the site of rapid calcium-phosphate exchange. Moreover, in strongly seasonal climates, where drought or winter cold forces ectotherms to become dormant, growth rings appear in the outer layers of compact bone, much like the rings in the wood of trees in similar environments. The endothermic bone of birds and mammals is dramatically different. It almost never shows growth rings, even in severe climates, and it is rich in blood vessels and frequently in Haversian canals. Fossilization often faithfully preserves the structure of bone, even in specimens 300 million years old; thus it provides one window through which to look back at the physiology of ancient animals.

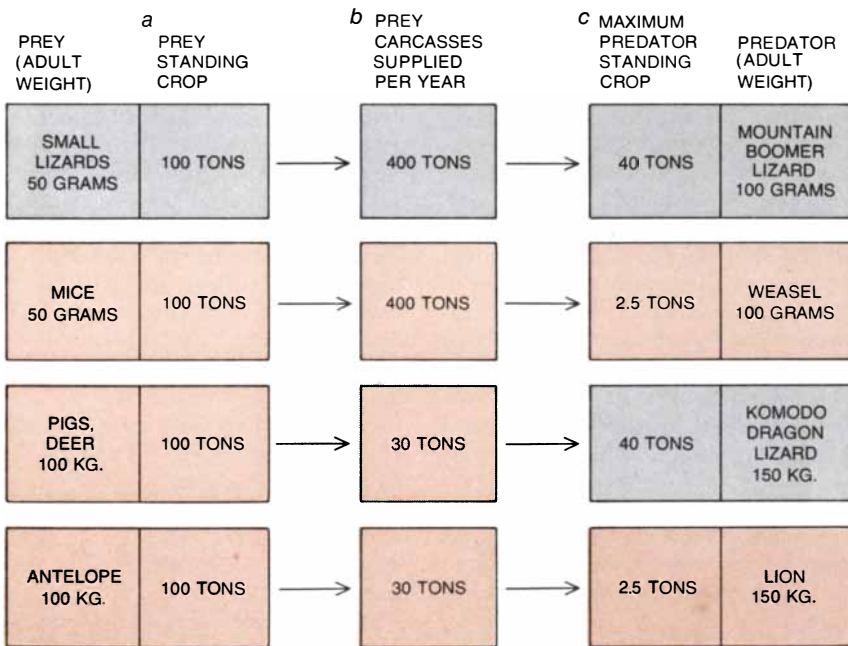
The second analytic tool of paleobiogenetics is latitudinal zonation. The present continental masses have floated across the surface of the globe on lithospheric rafts, sometimes colliding and pushing up mountain ranges, sometimes pulling apart along rift zones such as

those of the mid-Atlantic or East Africa. Paleomagnetic data make it possible to reconstruct the ancient positions of the continents to within about five degrees of latitude, and sedimentary indicators such as glacial beds and salt deposits show the severity of the latitudinal temperature gradient from the Equator to the poles in past epochs. Given the latitude and the gradient, one can plot temperature zones, and such zones should separate endotherms from ectotherms. Large reptiles with a lizardlike physiology cannot survive cool winters because they cannot warm up to an optimal body temperature during the short winter day and they are too large to find safe hiding places for winter hibernation. That is why small lizards are found today as far north as Alberta, where they hibernate underground during the winter, but crocodiles and big lizards do not get much farther north than the northern coast of the Gulf of Mexico.

The third meter of heat production in extinct vertebrates is the predator-prey ratio: the relation of the "standing crop" of a predatory animal to that of its prey. The ratio is a constant that is a characteristic of the metabolism of the predator, regardless of the body size of the animals of the predator-prey system. The reason-



PREDATOR-PREY RATIO remains about constant regardless of the size of the animals involved because of the scaling relations in predator-prey energy flow. The yearly energy budget, or the amount of meat required per year per kilogram of predator, decreases with increasing weight for endotherms (*colored curve*) and for ectotherms (*solid black curve*). The energy value of carcasses provided per kilogram by a prey population decreases with increasing weight at the same rate (*broken black curve*). The vertical lines are proportional to the size of the prey "standing crop" required to support one unit of predator standing crop: about an order of magnitude greater for endothermic predators (*color*) than for ectothermic ones (*gray*), whether for a lizard-size system (*a*) or a lion-size one (*b*).



ENERGY FLOW and predator-prey relation are illustrated for predator-prey systems of various sizes. Standing crop is the biomass of a population (or the potential energy value contained in the tissue) averaged over a year. For a given adult size, ectothermic prey (*gray*) produce as much meat (*b*) per unit standing crop (*a*) as endotherms (*color*). Endothermic predators, however, require an order of magnitude more meat (*b*) per unit standing crop (*c*). The maximum predator-prey biomass ratio (*c/a*) is therefore about an order of magnitude greater in an endothermic system than it is in an ectothermic one.

ing is as follows: The energy budget of an endothermic population is an order of magnitude larger than that of an ectothermic population of the same size and adult weight, but the productivity—the yield of prey tissue available to predators—is about the same for both an endothermic and an ectothermic population. In a steady-state population the yearly gain in weight and energy value from growth and reproduction equals the weight and energy value of the carcasses of the animals that die during the year; the loss of biomass and energy through death is balanced by additions. The maximum energy value of all the carcasses a steady-state population of lizards can provide its predators is about the same as that provided by a prey population of birds or mammals of about the same numbers and adult body size. Therefore a given prey population, either ectotherms or endotherms, can support an order of magnitude greater biomass of ectothermic predators than of endothermic predators, because of the endotherms' higher energy needs. The term standing crop refers to the biomass, or the energy value contained in the biomass, of a population. In both ectotherms and endotherms the energy value of carcasses produced per unit of standing crop decreases with increasing adult weight of prey animals: a herd of zebra yields from about a fourth to a third of its weight in prey carcasses a year, but a "herd" of mice can produce up to six times its weight because of its rapid turnover, reflected in a short life span and high metabolism per unit weight.

Now, the energy budget per unit of predator standing crop also decreases with increasing weight: lions require more than 10 times their own weight in meat per year, whereas shrews need 100 times their weight. These two bioenergetic scaling factors cancel each other, so that if the adult size of the predator is roughly the same as that of the prey (and in land-vertebrate ecosystems it usually is), the maximum ratio of predator standing crop to prey standing crop in a steady-state community is a constant independent of the adult body size in the predator-prey system [see top illustration at left]. For example, spiders are ectotherms, and the ratio of a spider population's standing crop to its prey standing crop reaches a maximum of about 40 percent. Mountain boomer lizards, about 100 grams in adult weight, feeding on other lizards would reach a similar maximum ratio. So would the giant Komodo dragon lizards (up to 150 kilograms in body weight) preying on deer, pigs and monkeys. Endothermic

mammals and birds, on the other hand, reach a maximum predator-prey biomass ratio of only from 1 to 3 percent—whether they are weasel and mouse or lion and zebra [see bottom illustration on opposite page].

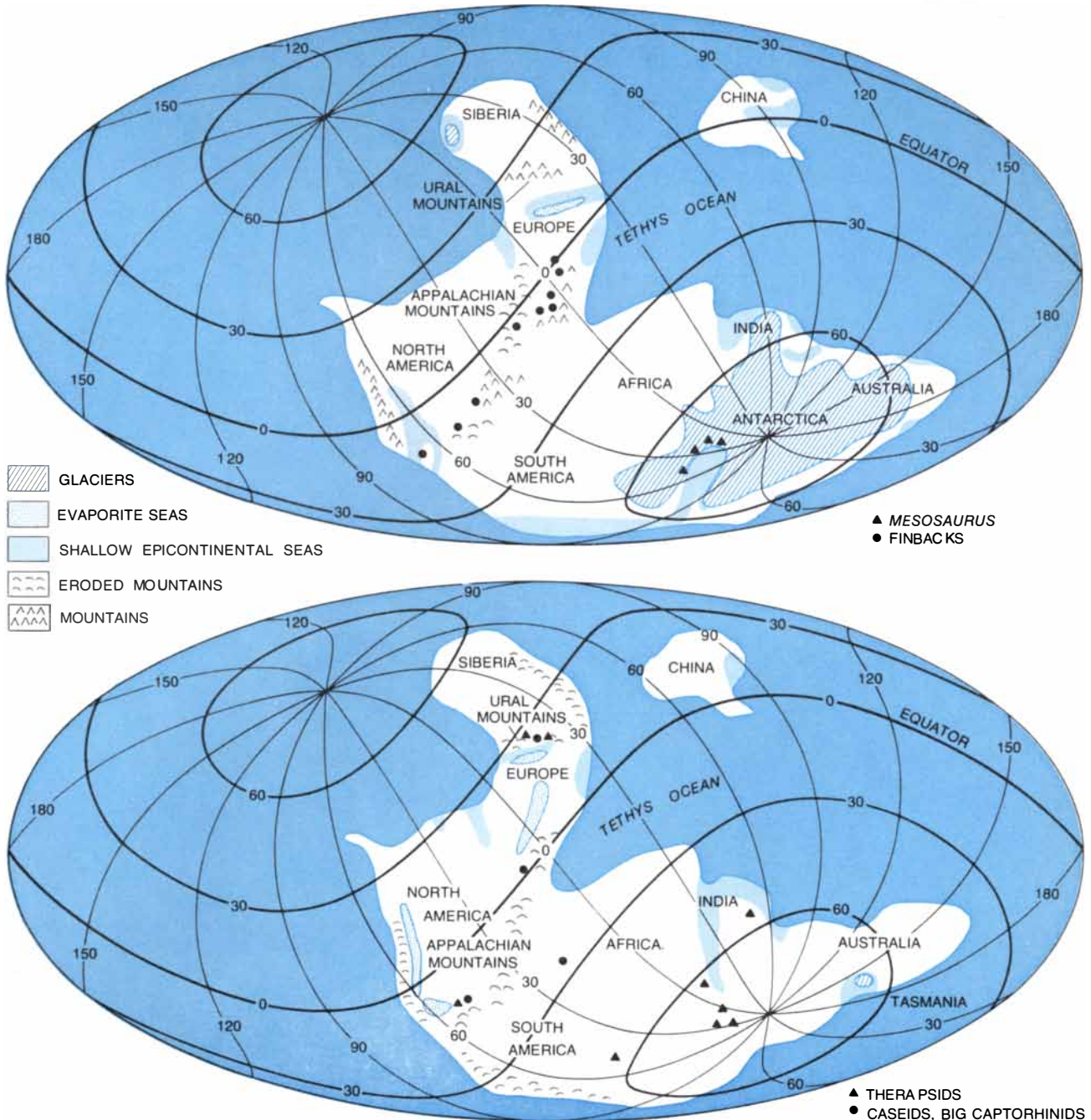
Some fossil deposits yield hundreds or

thousands of individuals representing a single community; their live body weight can be calculated from the reconstruction of complete skeletons, and the total predator-prey biomass ratios are then easily worked out. Predator-prey ratios are powerful tools for paleophysiology

because they are the direct result of predator metabolism.

The Age of Ectothermy

The paleobioenergetic methodology I have outlined can be tested by analyzing



PERMIAN WORLD is reconstructed here (on an oblique Mollweide projection, which minimizes distortion of area) on the basis of paleomagnetic and other geophysical data. All major land masses except China were welded into a supercontinent, Pangaea. In the early Permian (*top*) the Gondwana glaciation was at its maximum, covering much of the southern part of the continent. Big finback pelycosaurs and contemporary large reptiles and amphibians were confined to the Tropics; they had ectothermic bone and high predator-prey ratios. The only reptile in cold southern

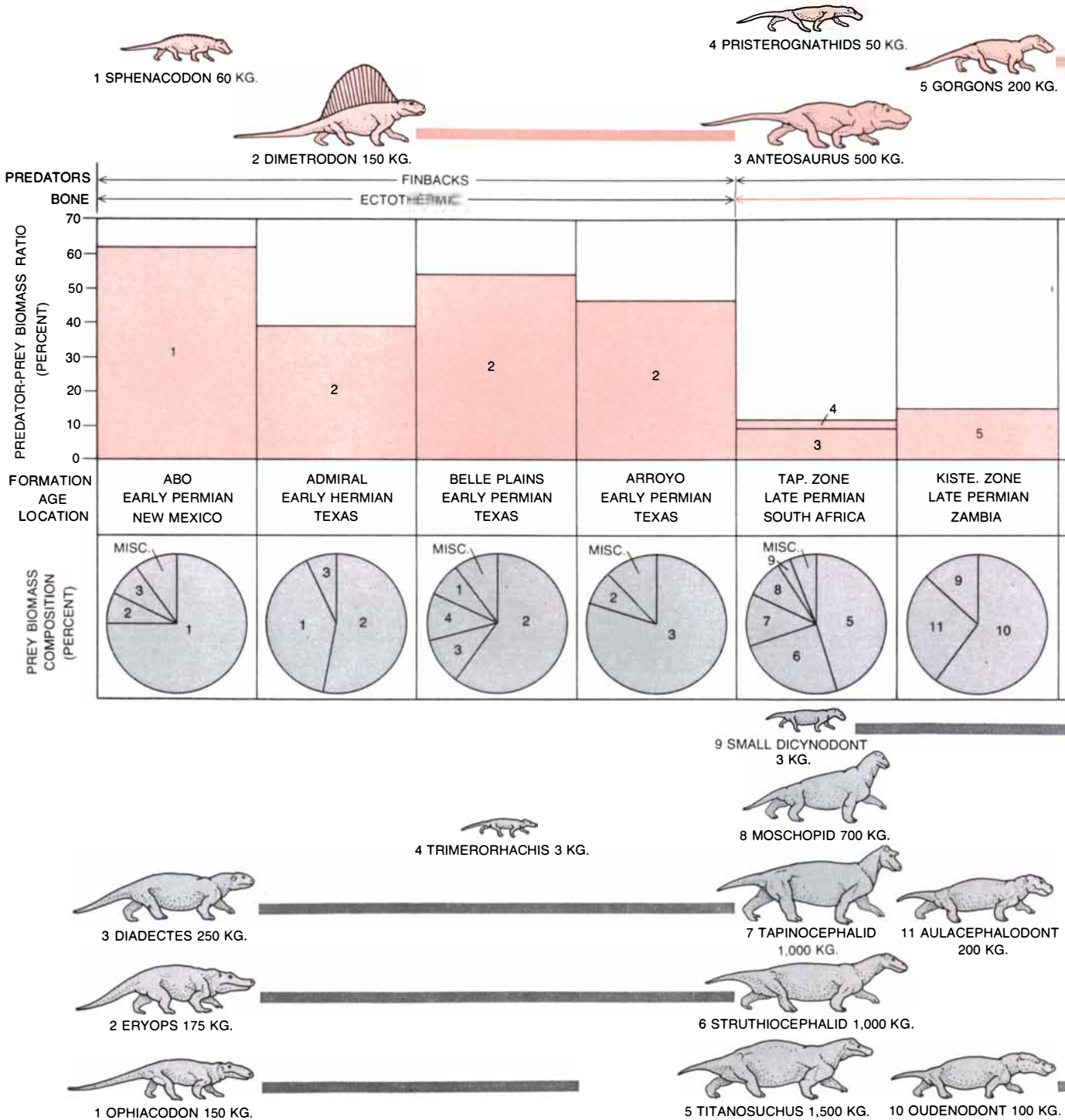
Gondwanaland was the little *Mesosaurus*, which apparently hibernated in the mud during the winters. The late Permian world (*bottom*) was less glaciated, but the south was still cold and the latitudinal temperature gradient was still steep. Big reptiles with ectothermic bone, caseids and captorhinids, were restricted to the hot Tropics, as large reptiles had been in the early Permian. By now, however, many early therapsids, all with endothermic bone and low predator-prey ratios, had invaded southern Gondwanaland. They must have acquired high heat production and some insulation.

the first land-vertebrate predator-prey system, the early Permian communities of primitive reptiles and amphibians. The first predators capable of killing relatively large prey were the finback pelycosaurs of the family Sphenacodontidae, typified by *Dimetrodon*, whose tall-spined fin makes it popular with car-

toonists. Although this family included the direct ancestors of mammal-like reptiles and hence of mammals, the sphenacodonts themselves had a very primitive level of organization, with a limb anatomy less advanced than that of living lizards. Finback bone histology was emphatically ectothermic, with a low den-

sity of blood vessels, few Haversian canals and the distinct growth rings that are common in specimens from seasonally arid climates.

One might suspect that finbacks and their prey would be confined to warm, equable climates, and early Permian paleogeography offers an excellent op-



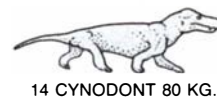
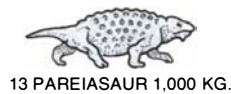
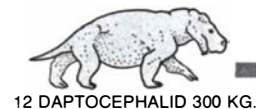
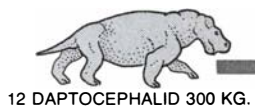
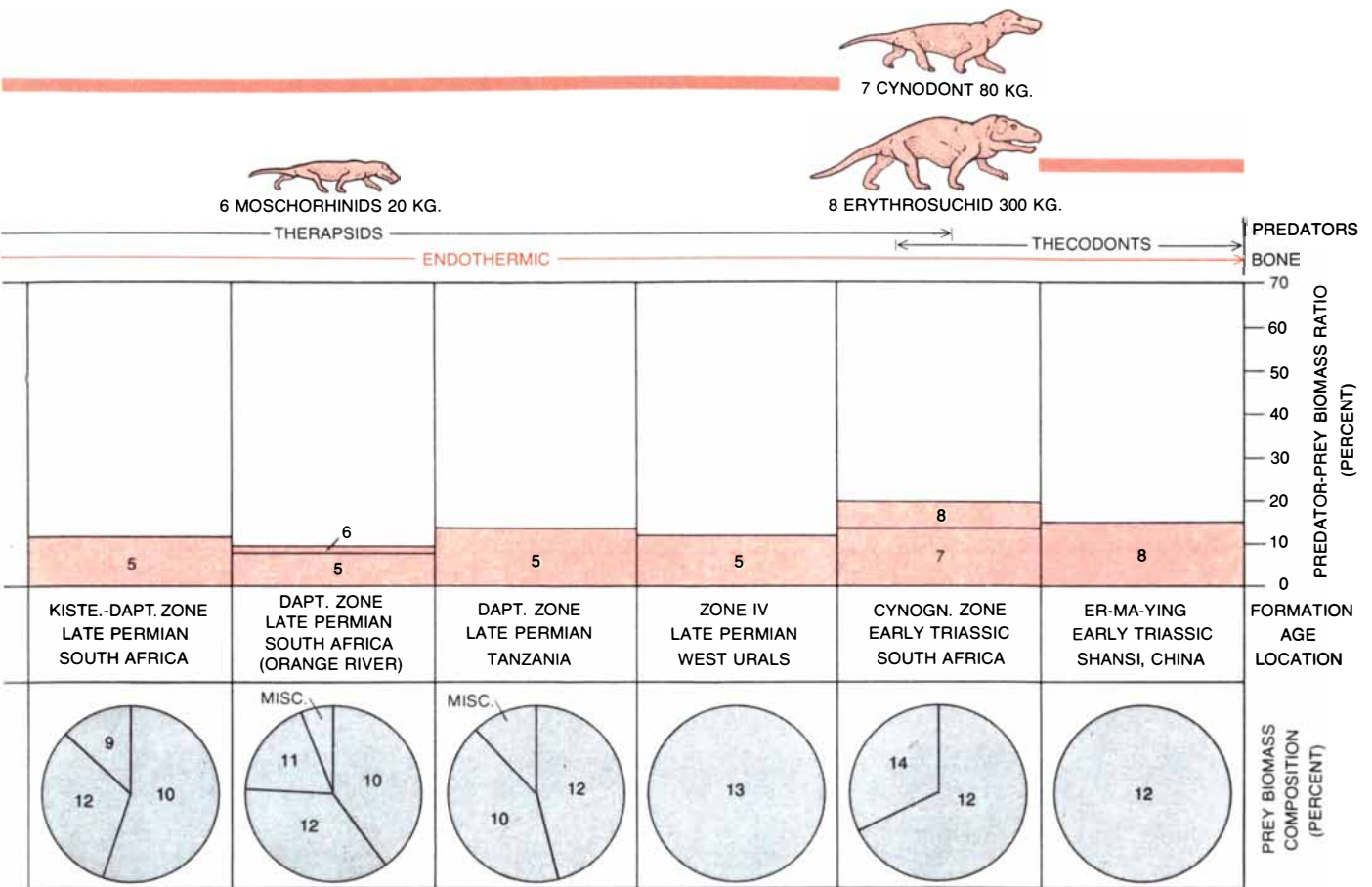
PREDATOR-PREY RATIO AND PREY COMPOSITION are shown on these two pages and the next two pages for a number of fossil communities, each representing a particular time zone and

depositional environment. The predator (top) and prey (bottom) animals involved at each site are illustrated. For each deposit the histogram (color) gives the predator biomass as a percent of the

portunity to test this prediction. During the early part of the period ice caps covered the southern tips of the continental land masses, all of which were part of the single southern supercontinent Gondwanaland, and glacial sediment is reported at the extreme northerly tip of the Permian land mass in Siberia by Rus-

sian geologists [see illustration on page 63]. The Permian Equator crossed what are now the American Southwest, the Maritime Provinces of Canada and western Europe. Here are found sediments produced in very hot climates: thick-bedded evaporite salts and fully oxidized, red-stained mudstones. The lati-

tudinal temperature gradient in the Permian must have been at least as steep as it is at present. Three Permian floral zones reflect the strong poleward temperature gradient. The Angaran flora of Siberia displays wood with growth rings from a wet environment, implying a moist climate with cold winters. The



total prey biomass, in other words, the predator-prey ratio. The pie charts give the composition of the available prey. Note the sudden drop in the predator-prey ratios during the transition from the

finback pelycosaur to the early therapsids, which coincided with the first appearance of endothermic bone and also with the invasion of cold southern Gondwanaland by early therapsids of all sizes.

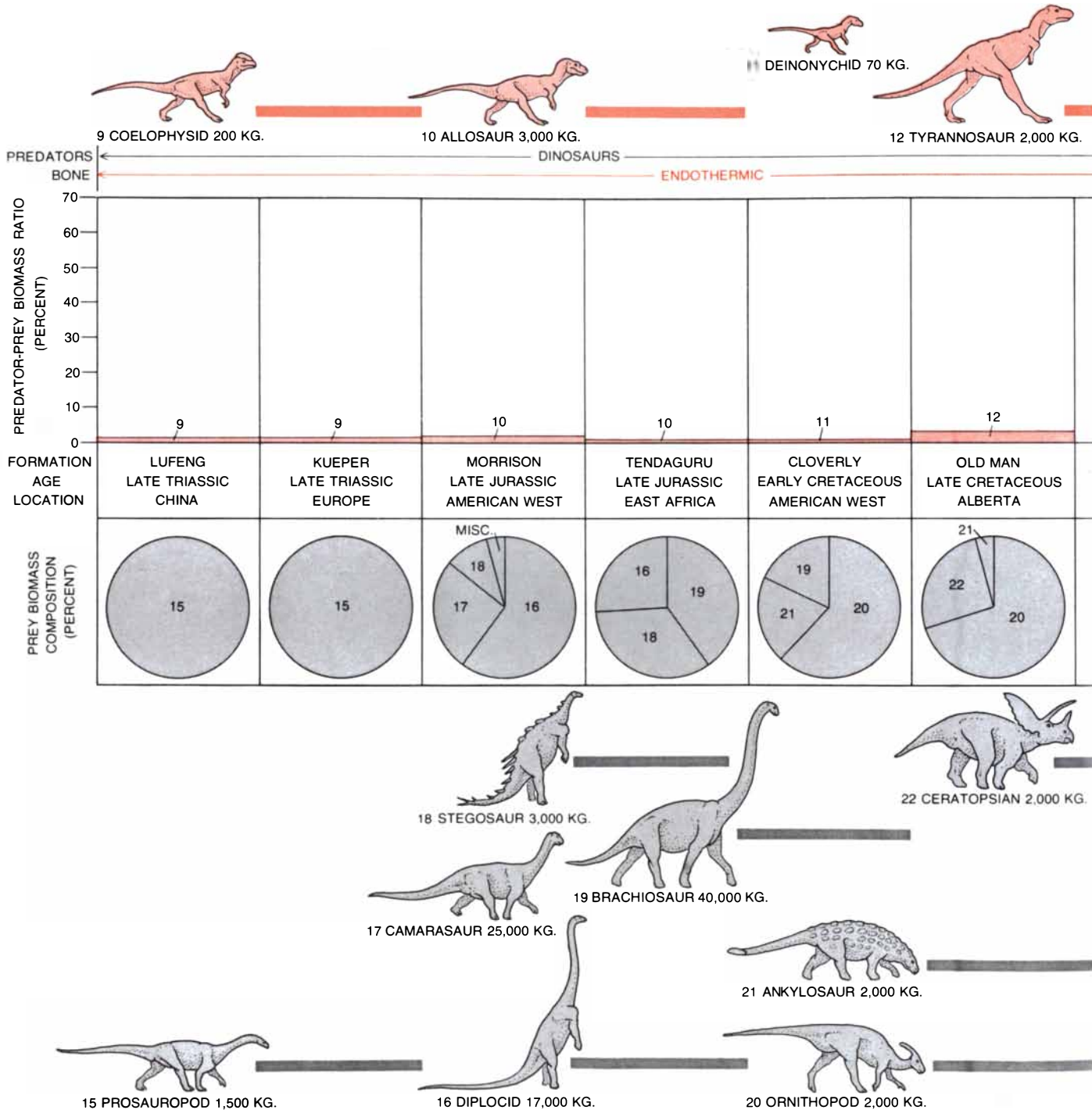
Euramerian flora of the equatorial region had two plant associations: wet swamp communities with no growth rings in the wood, implying a continuous warm-moist growing season, and semiarid, red-bed-evaporite communities with some growth rings, reflecting a tropical dry season. In glaciated Gondwanaland the peculiar *Glossopteris* flora dominated,

with wood from wet environments showing sharp growth rings.

The ectothermy of the finbacks is confirmed by their geographic zonation. Finback communities are known only from near the Permian Equator; no large early Permian land vertebrates of any kind are found in glaciated Gondwanaland. (One peculiar little fish-eat-

ing reptile, *Mesosaurus*, is known from southern Gondwanaland, and its bone has sharp growth rings. The animal must have fed and reproduced during the Gondwanaland summer and then burrowed into the mud of lagoon bottoms to hibernate, much as large snapping turtles do today in New England.)

Excellent samples of finback commu-



EVIDENCE FROM FOSSIL COMMUNITIES is continued from the preceding two pages. The animals are of course not all drawn

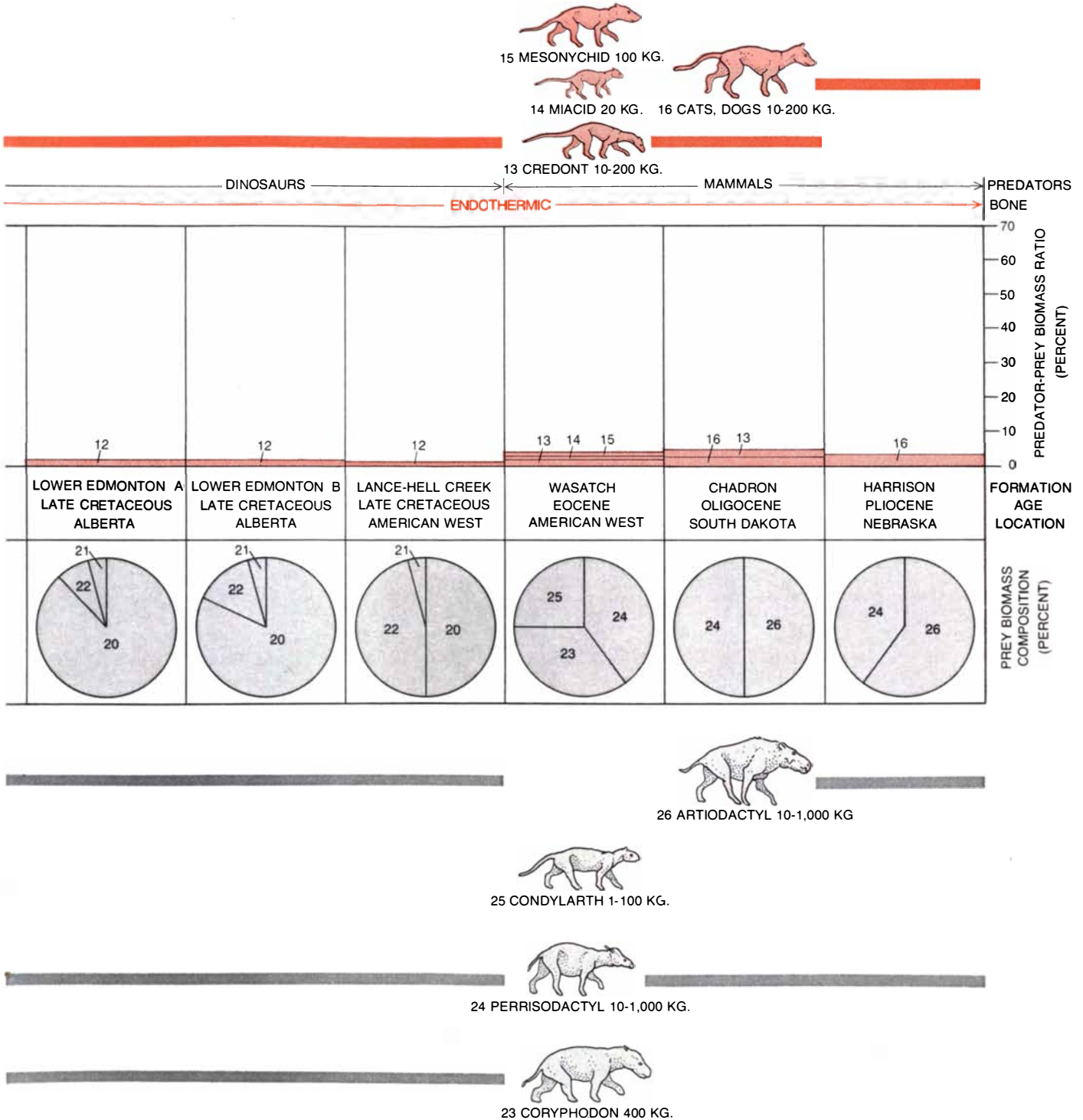
to the same scale; their adult weights are given. The drawings are presented with the same limb-stride positions in each to emphasize

nities are available for predator-prey studies, thanks largely to the lifework of the late Alfred Sherwood Romer of Harvard University. In order to derive a predator-prey ratio from a fossil community one simply calculates the number of individuals, and thus the total live weight, represented by all the predator and prey specimens that are found to-

gether in a sediment representing one particular environment. In working with scattered and disarticulated skeletons it is best to count only bones that have about the same robustness, and hence the same preservability, in both predator and prey. The humerus and the femur are good choices for finback communities: they are about the same size with

respect to the body in the prey and the predator and should give a ratio that faithfully represents the ratio of the animals in life.

In the earlier early Permian zones the most important finback prey were semi-aquatic fish-eating amphibians and reptiles, particularly the big-headed amphibian *Eryops* and the long-snouted

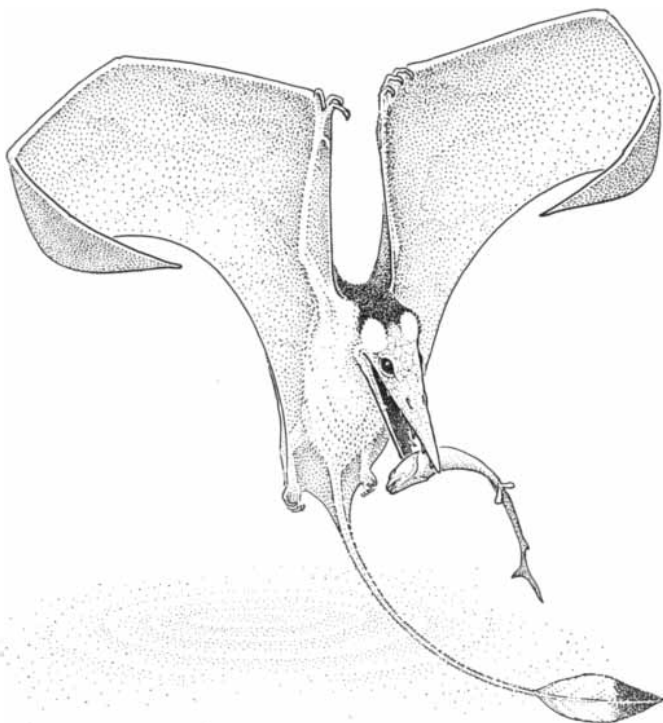


relative limb length. Long-limbed, fast-sprinting vertebrates of large size appeared only with the dinosaurs, in the middle Triassic.

Note the remarkably low predator-prey ratios of the dinosaurs, as low as or lower than those of the Cenozoic (and modern) mammals.



LONGISQUAMA, a small animal whose fossil was discovered in middle Triassic lake beds in Turkestan by the Russian paleontologist A. Sharov, was a thecodont. Its body was covered by long overlapping scales that were keeled, suggesting that they constituted a structural stage in the evolution of feathers. The long devices along the back were V-shaped in cross section; they may have served as parachutes and also as threat devices, as shown here.



SORDUS PILOSUS, also found by Sharov, was a pterosaur: a flying reptile of the Jurassic period that was a descendant of thecodonts or of very early dinosaurs. Superbly preserved fossils show that the animal was insulated with a dense growth of hair or hairlike feathers; hence the name, which means "hairy devil." Insulation strongly suggests endothermy.

elycosaur *Ophiacodon*. As the climate became more arid in Europe and America these water-linked forms decreased in numbers, and the fully terrestrial herbivore *Diadectes* became the chief prey genus. In all zones from all environments the calculated biomass ratio of predator to prey in finback communities is very high: from 35 to 60 percent, the same range seen in living ectothermic spiders and lizards.

All three of the paleobioenergetic indicators agree: the finback pelycosaur and their contemporaries were ectotherms with low heat production and a lizardlike physiology that confined their distribution to the Tropics.

Therapsid Communities

The mammal-like reptiles (order Therapsida), descendants of the finbacks, made their debut at the transition from the early to the late Permian and immediately became the dominant large land vertebrates all over the world. The three metabolism-measuring techniques show that they were endotherms.

The earliest therapsids retained many finback characteristics but had acquired limb adaptations that made possible a trotting gait and much higher running speeds. From early late Permian to the middle Triassic one line of therapsids became increasingly like primitive mammals in all details of the skull, the teeth and the limbs, so that some of the very advanced mammal-like therapsids (cynodonts) are difficult to separate from the first true mammals. The change in physiology, however, was not so gradual. Detailed studies of bone histology conducted by Armand Riqules of the University of Paris indicate that the bioenergetic transition was sudden and early: all the finbacks had fully ectothermic bone; all the early therapsids—and there is an extraordinary variety of them—had fully endothermic bone, with no growth rings and with closely packed blood vessels and Haversian canals.

The late Permian world still had a severe latitudinal temperature gradient; some glaciation continued in Tasmania, and the southern end of Gondwanaland retained its cold-adapted *Glossopteris* flora. If the earliest therapsids were equipped with endothermy, they would presumably have been able to invade southern Africa, South America and the other parts of the southern cold-temperature realm. They did exactly that. A rich diversity of early therapsid families has been found in the southern Cape District of South Africa, in Rhodesia, in Brazil

and in India—regions reaching to 65 degrees south Permian latitude [see illustration on page 63]. Early therapsids as large as rhinoceroses were common there, and many species grew to an adult weight greater than 10 kilograms, too large for true hibernation. These early therapsids must have had physiological adaptations that enabled them to feed in and move through the snows of the cold Gondwanaland winters. There were also some ectothermic holdovers from the early Permian that survived into the late Permian, notably the immense herbivorous caseid pelycosaurs and the big-headed, seed-eating captorhinids. As one might predict, large species of these two ectothermic families were confined to areas near the late Permian Equator; big caseids and captorhinids are not found with the therapsids in cold Gondwanaland. In the late Permian, then, there was a “modern” faunal zonation of large vertebrates, with endothermic therapsids and some big ectotherms in the Tropics giving way to an all-endothermic therapsid fauna in the cold south.

In the earliest therapsid communities of southern Africa, superbly represented in collections built up by Lieuwe Boonstra of the South African Museum and by James Kitching of the University of the Witwatersrand, the predator-prey ratios are between 9 and 16 percent. That is much lower than in early Per-

mian finback communities. Equally low ratios are found for tropical therapsids from the U.S.S.R. even though the prey species there were totally different from those of Africa. The sudden decrease in predator-prey ratios from finbacks to early therapsids coincides exactly with the sudden change in bone histology from ectothermic to endothermic reported by Riqules and also with the sudden invasion of the southern cold-temperate zone by a rich therapsid fauna. The conclusion is unavoidable that even early therapsids were endotherms with high heat production.

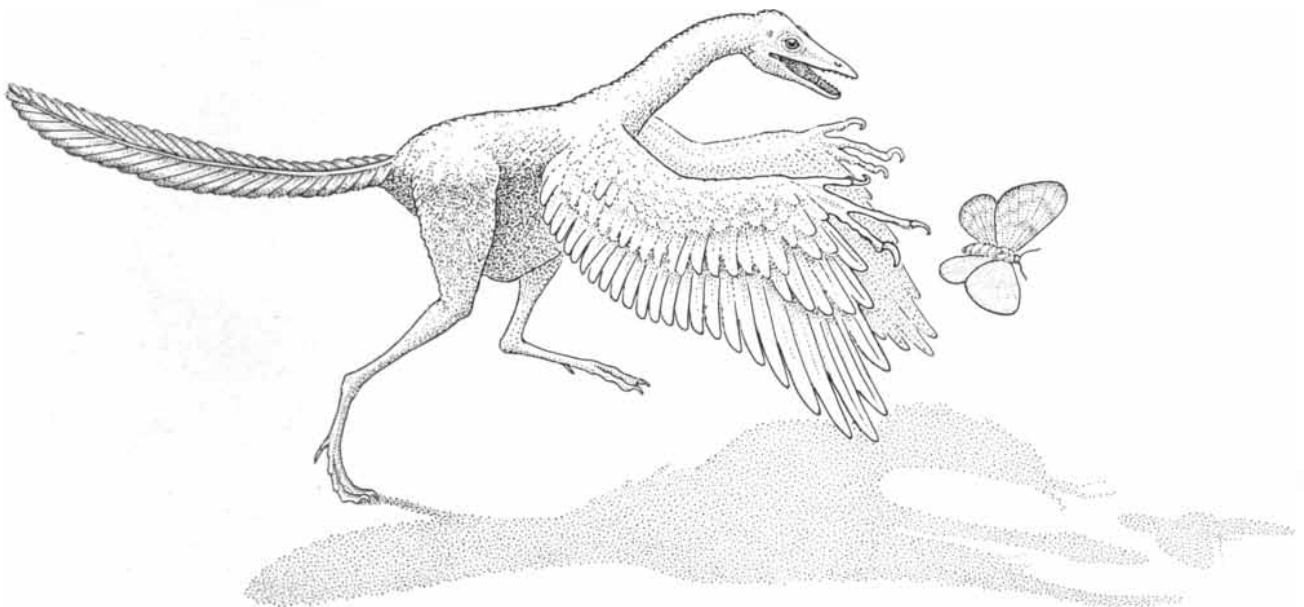
It seems certain, moreover, that in the cold Gondwanaland winters the therapsids would have required surface insulation. Hair is usually thought of as a late development that first appeared in the advanced therapsids, but it must have been present in the southern African endotherms of the early late Permian. How did hair originate? Possibly the ancestors of therapsids had touch-sensitive hairs scattered over the body as adaptations for night foraging; natural selection could then have favored increased density of hair as the animals' heat production increased and they moved into colder climates.

The therapsid predator-prey ratios, although much lower than those of ectotherms, are still about three times higher than those of advanced mammals today.

Such ratios indicate that the therapsids achieved endothermy with a moderately high heat production, far higher than in typical reptiles but still lower than in most modern mammals. Predator-prey ratios of early Cenozoic communities seem to be lower than those of therapsids, and so one might conclude that a further increase in metabolism occurred somewhere between the advanced therapsids of the Triassic and the mammals of the post-Cretaceous era. Therapsids may have operated at a lower body temperature than most living mammals do, and thus they may have saved energy with a lower thermostat setting. This suggestion is reinforced by the low body temperature of the most primitive living mammals: monotremes (such as the spiny anteater) and the insectivorous tenrecs of Madagascar; they maintain a temperature of about 30 degrees Celsius instead of the 36 to 39 degrees of most modern mammals.

Thecodont Transition

The vigorous and successful therapsid dynasty ruled until the middle of the Triassic. Then their fortunes waned and a new group, which was later to include the dinosaurs, began to take over the roles of large predators and herbivores. These were the Archosauria, and the first wave of archosaurs were the the-



ARCHAEOPTERYX, generally considered the first bird, is known from late Jurassic fossils that show its feather covering clearly. In spite of its very birdlike appearance, *Archaeopteryx* was closely related to certain small dinosaurs (see illustration on next page)

and could not fly. The presence of insulation in the thecodont *Longisquama* and in *Sordus* and *Archaeopteryx*, which were descendants of thecodonts, indicates that insulation and endothermy were acquired very early, probably in early Triassic thecodonts.

codonts. The earliest thecodonts, small and medium-sized animals found in the rapsid communities during the Permian-Triassic transition, had an ectothermic bone histology. In modern ecosystems the role played by large freshwater predators seems to be one in which ectothermy is competitively superior to endothermy; the low metabolic rate of ectotherms may be a key advantage because it allows much longer dives. Two groups of thecodonts became large freshwater fish-eaters: the phytosaurs, which were confined to the Triassic, and the crocodylians, which remain successful today. Both groups have ectothermic bone. (The crocodylian endothermy was either inherited directly from the first thecodonts or derived secondarily from endothermic intermediate ancestors.) In most of the later, fully terrestrial advanced thecodonts, on the other hand, Riquelme discovered a typical endothermic bone histology; the later thecodonts were apparently endothermic.

The predator-prey evidence for thecodonts is scanty. The ratios are hard to compute because big carnivorous cynodonts and even early dinosaurs usually shared the predatory role with thecodonts. One sample from China that has only one large predator genus, a big-headed erythrosuchid thecodont, does give a ratio of about 10 percent, which is in the endothermic range. The zonal evi-

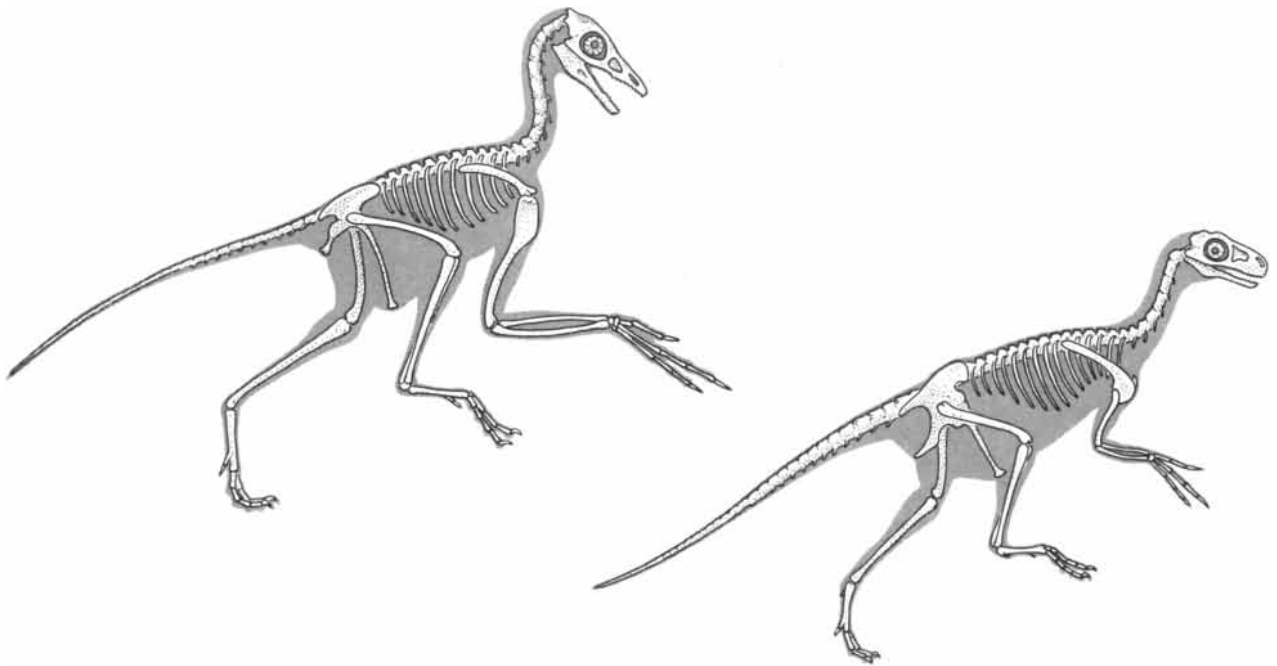
dence is clearer. World climate was moderating in the Triassic (the glaciers were gone), but a distinctive flora and some wood growth rings suggest that southern Gondwanaland was not yet warm all year. What is significant in this regard is the distribution of phytosaurs, the big ectothermic fish-eating thecodonts. Their fossils are common in North America and Europe (in the Triassic Tropics) and in India, which was warmed by the equatorial Tethys Ocean, but they have not been found in southern Gondwanaland, in southern Africa or in Argentina, even though a rich endothermic thecodont fauna did exist there.

Did some of the thecodonts have thermal insulation? Direct evidence comes from the discoveries of A. Sharov of the Academy of Sciences of the U.S.S.R. Sharov found a partial skeleton of a small thecodont and named it *Longisquama* for its long scales: strange parachutelike devices along the back that may have served to break the animal's fall when it leaped from trees. More important is the covering of long, overlapping, keeled scales that trapped an insulating layer of air next to its body [see top illustration on page 68]. These scales lacked the complex anatomy of real feathers, but they are a perfect ancestral stage for the insulation of birds. Feathers are usually assumed to have appeared only late in

the Jurassic with the first bird, *Archaeopteryx*. The likelihood that some thecodonts had insulation is supported, however, by another of Sharov's discoveries: a pterosaur, or flying reptile, whose fossils in Jurassic lake beds still show the epidermal covering. This beast (appropriately named *Sordus pilosus*, the "hairy devil") had a dense growth of hair or hairlike feathers all over its body and limbs. Pterosaurs are descendants of Triassic thecodonts or perhaps of very primitive dinosaurs. The insulation in both *Sordus* and *Longisquama*, and the presence of big erythrosuchid thecodonts at the southern limits of Gondwanaland, strongly suggest that some endothermic thecodonts had acquired insulation by the early Triassic.

The Dinosaurs

Dinosaurs, descendants of early thecodonts, appeared first in the middle Triassic and by the end of the period had replaced thecodonts and the remaining therapsids as the dominant terrestrial vertebrates. Zonal evidence for endothermy in dinosaurs is somewhat equivocal. The Jurassic was a time of climatic optimum, when the poleward temperature gradient was the gentlest that has prevailed from the Permian until the present day. In the succeeding Cretaceous period latitudinal zoning of ocean-



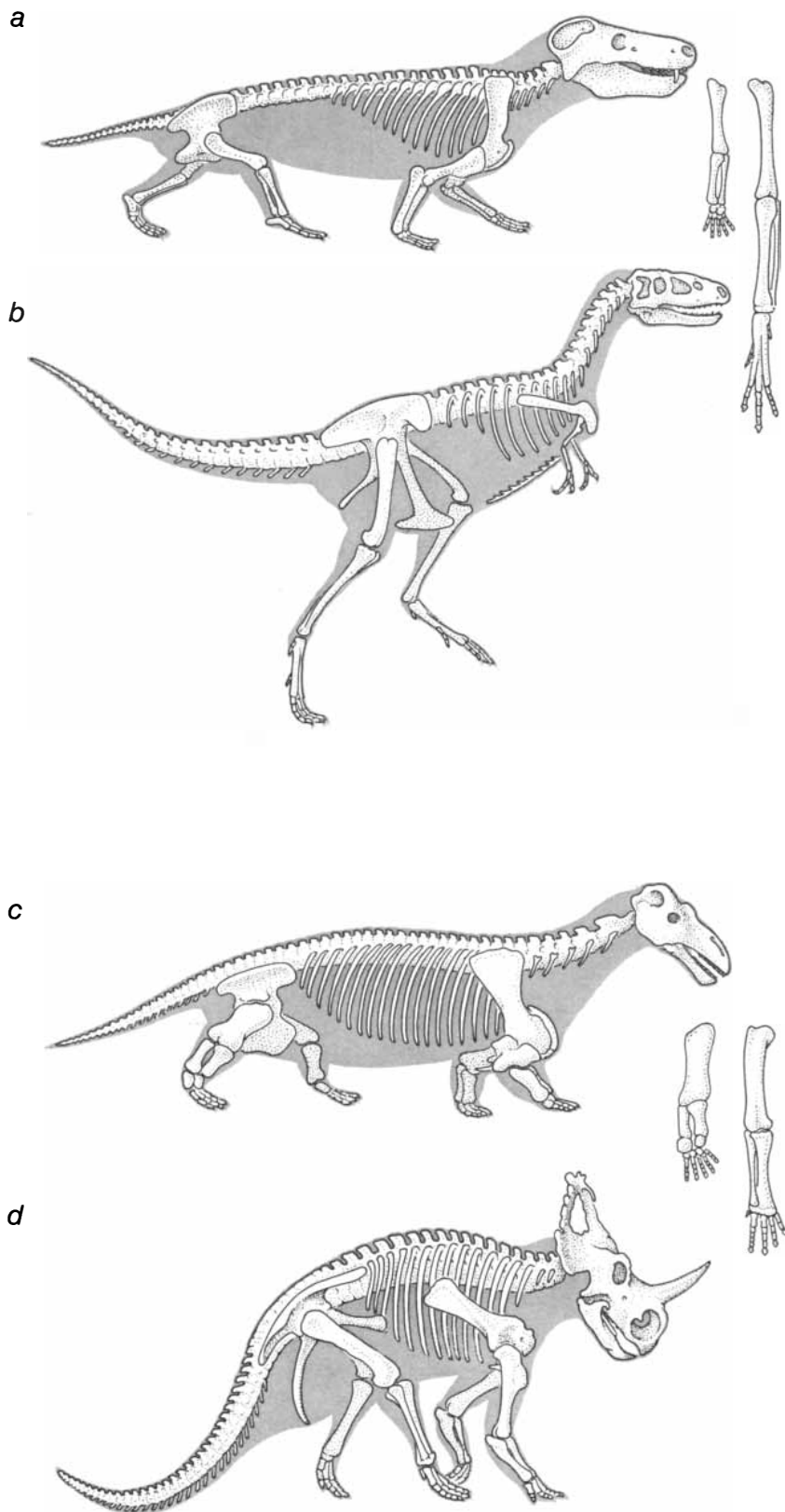
DINOSAURIAN ANCESTRY of *Archaeopteryx* (left), and thus of birds, is indicated by its close anatomical relation to such small dinosaurs as *Microvenator* (right) and *Deinonychus*; John H.

Ostrom of Yale University demonstrated that they were virtually identical in all details of joint anatomy. The long forelimbs of *Archaeopteryx* were probably used for capturing prey, not for flight.

ic plankton and land plants seems, however, to have been a bit sharper. Rhinoceros-sized Cretaceous dinosaurs and big marine lizards are found in the rocks of the Canadian far north, within the Cretaceous Arctic Circle. Dale A. Russell of the National Museums of Canada points out that at these latitudes the sun would have been below the horizon for months at a time. The environment of the dinosaurs would have been far severer than the environment of the marine reptiles because of the lack of a wind-chill factor in the water and because of the ocean's temperature-buffering effect. Moreover, locomotion costs far less energy per kilometer in water than on land, so that the marine reptiles could have migrated away from the arctic winter. These considerations suggest, but do not prove, that arctic dinosaurs must have been able to cope with cold stress.

Dinosaur bone histology is less equivocal. All dinosaur species that have been investigated show fully endothermic bone, some with a blood-vessel density higher than that in living mammals. Since bone histology separates endotherms from ectotherms in the Permian and the Triassic, this evidence alone should be a strong argument for the endothermy of dinosaurs. Yet the predator-prey ratios are even more compelling. Dinosaur carnivore fossils are exceedingly rare. The predator-prey ratios for dinosaur communities in the Triassic, Jurassic and Cretaceous are usually from 1 to 3 percent, far lower even than those of therapsids and fully as low as those in large samples of fossils from advanced mammal communities in the Cenozoic. I am persuaded that all the available quantitative evidence is in favor of high heat production and a large annual energy budget in dinosaurs.

Were dinosaurs insulated? Explicit evidence comes from a surprising source: *Archaeopteryx*. As an undergraduate a decade ago I was a member of a paleontological field party led by John H. Ostrom of Yale University. Near Bridger, Mont., Ostrom found a remarkably preserved little dinosaurian carnivore, *Deinonychus*, that shed a great deal of light on carnivorous dinosaurs in general. A few years later, while looking for pterosaur fossils in European museums, Ostrom came on a specimen of *Archaeopteryx* that had been mislabeled for years as a flying reptile, and he noticed extraordinary points of resemblance between *Archaeopteryx* and carnivorous dinosaurs. After a detailed anatomical analysis Ostrom has now established beyond any reasonable doubt that the



LIMB LENGTHS of dinosaurs are compared with those of two ecologically equivalent therapsids. The limbs were relatively longer in the dinosaurs and the appended muscles were larger, indicating that the dinosaurs had a larger capacity for high levels of exercise metabolism. The two top drawings represent the animals as if they were the same weight; the adult carnivorous therapsid *Cynognathus* (a) actually weighed 100 kilograms and the juvenile dinosaur *Albertosaurus* (b) 600 kilograms. Two herbivores, therapsid *Struthiocephalus* (c) and horned dinosaur *Centrosaurus* (d), weighed about 1,500 kilograms.

immediate ancestor of *Archaeopteryx* must have been a small dinosaur, perhaps one related to *Deinonychus*. Previously it had been thought that the ancestor of *Archaeopteryx*, and thus of birds, was a thecodont rather far removed from dinosaurs themselves.

Archaeopteryx was quite thoroughly feathered, and yet it probably could not fly: the shoulder joints were identical with those of carnivorous dinosaurs and were adapted for grasping prey, not for the peculiar arc of movement needed for wing-flapping. The feathers were probably adaptations not for powered flight or gliding but primarily for insulation. *Archaeopteryx* is so nearly identical in all known features with small carnivorous dinosaurs that it is hard to believe feathers were not present in such dinosaurs. Birds inherited their high metabolic rate and most probably their feathered insulation from dinosaurs; powered flight probably did not evolve until the first birds with flight-adapted shoulder

joints appeared during the Cretaceous, long after *Archaeopteryx*.

It has been suggested a number of times that dinosaurs could have achieved a fairly constant body temperature in a warm environment by sheer bulk alone; large alligators approach this condition in the swamps of the U.S. Gulf states. This proposed thermal mechanism would not give rise to endothermic bone histology or low predator-prey ratios, however, nor would it explain arctic dinosaurs or the success of many small dinosaur species with an adult weight of between five and 50 kilograms.

Dinosaur Brains and Limbs

Large brain size and endothermy seem to be linked; most birds and mammals have a ratio of brain size to body size much larger than that of living reptiles and amphibians. The acquisition of endothermy is probably a prerequisite for the enlargement of the brain because

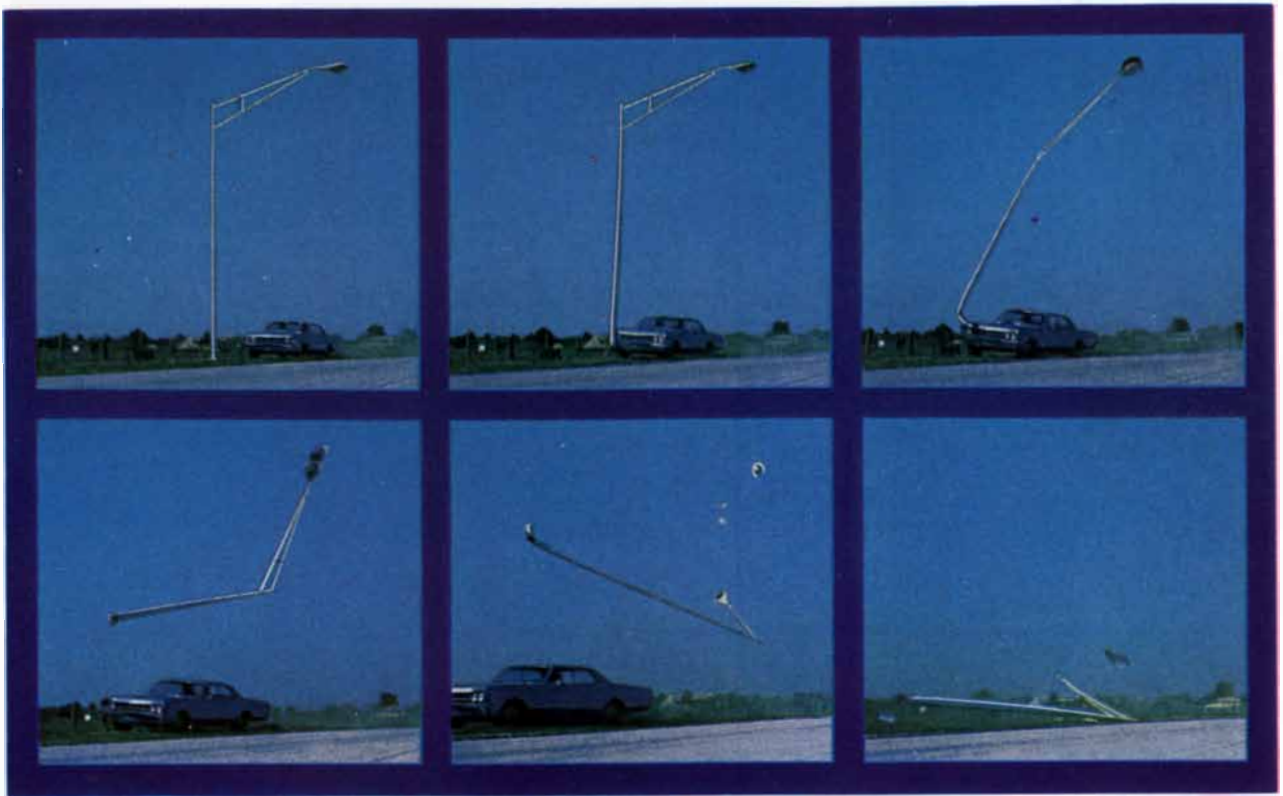
the proper functioning of a complex central nervous system calls for the guarantee of a constant body temperature. It is not surprising that endothermy appeared before brain enlargement in the evolutionary line leading to mammals. Therapsids had small brains with reptilian organization; not until the Cenozoic did mammals attain the large brain size characteristic of most modern species. A large brain is certainly not necessary for endothermy, since the physiological feedback mechanisms responsible for thermoregulation are deep within the "old" region of the brain, not in the higher learning centers. Most large dinosaurs did have relatively small brains. Russell has shown, however, that some small and medium-sized carnivorous dinosaurs had brains as large as or larger than modern birds of the same body size.

Up to this point I have concentrated on thermoregulatory heat production. Metabolism during exercise can also be read from fossils. Short bursts of intense exercise are powered by anaerobic metabolism within muscles, and the oxygen debt incurred is paid back afterward by the heart-lung system. Most modern birds and mammals have much higher levels of maximum aerobic metabolism than living reptiles and can repay an oxygen debt much faster. Apparently this difference does not keep small ectothermic animals from moving fast: the top running speeds of small lizards equal or exceed those of small mammals. The difficulty of repaying oxygen debt increases with increasing body size, however, and the living large reptiles (crocodilians, giant lizards and turtles) have noticeably shorter limbs, less limb musculature and lower top speeds than many large mammals, such as the big cats and the hoofed herbivores.

The early Permian ectothermic dynasty was also strikingly short-limbed; evidently the physiological capacity for high sprinting speeds in large animals had not yet evolved. Even the late therapsids, including the most advanced cynodonts, had very short limbs compared with the modern-looking running mammals that appeared early in the Cenozoic. Large dinosaurs, on the other hand, resembled modern running mammals, not therapsids, in locomotor anatomy and limb proportions. Modern, fast-running mammals utilize an anatomical trick that adds an extra limb segment to the forelimb stroke. The scapula, or shoulder blade, which is relatively immobile in most primitive vertebrates, is free to swing backward and forward and thus increase the stride length. Jane A. Peterson of Harvard has shown that

	BONE HISTOLOGY	PRESENT IN TEMPERATE ZONE	PREDATOR-PREY RATIO	LIMB LENGTH
FINBACKS, OTHER EARLY PERMIAN LAND VERTEBRATES		NO	50 PERCENT	SHORT
LATE PERMIAN CASEIDS AND BIG CAPTORHINIDS		NO	NOT APPLICABLE	SHORT
LATE PERMIAN-EARLY TRIASSIC THERAPSIDES		YES	10 PERCENT	SHORT
EARLIEST THECODONTS		?	?	SHORT
MOST LAND THECODONTS		YES UP TO 600 KILOGRAMS	10 PERCENT	SHORT
FRESHWATER THECODONTS		NO UP TO 500 KILOGRAMS	?	SHORT
DINOSAURS		YES	1-3 PERCENT	LONG
CENOZOIC MAMMALS		YES	1-5 PERCENT	LONG

PALEOBIOENERGETIC EVIDENCE is summed up here. The appropriate blocks are shaded to show whether the available data constitute evidence for ectothermy (gray) or endothermy (color) according to criteria discussed in the text of this article. Caseids and captorhinids are herbivores, so that there is no predator-prey ratio. There are early thecodonts in temperate-zone deposits, but they are small and so the evidence is not significant.



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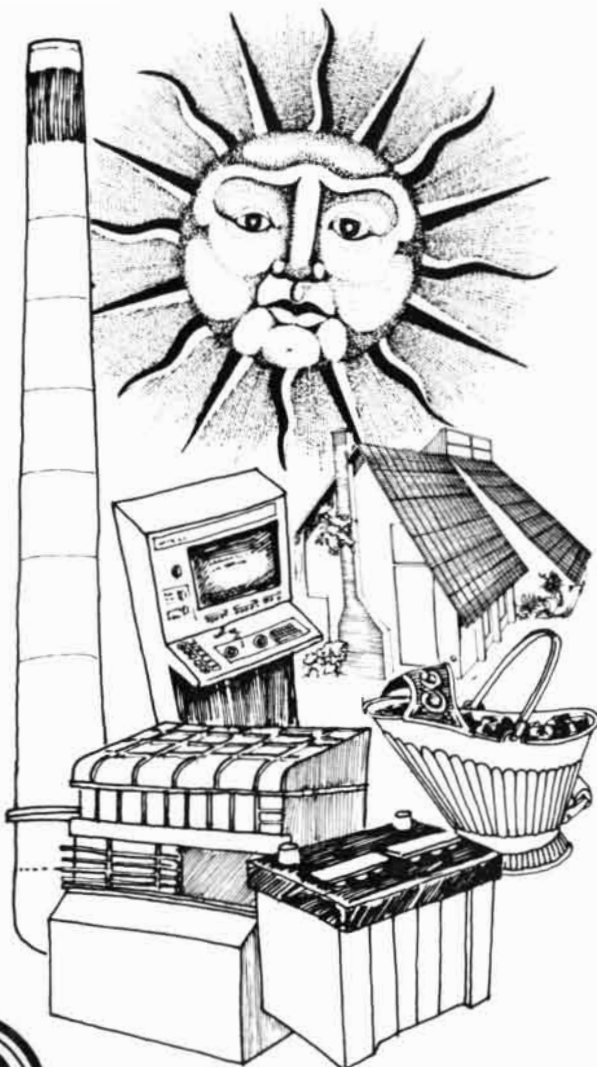
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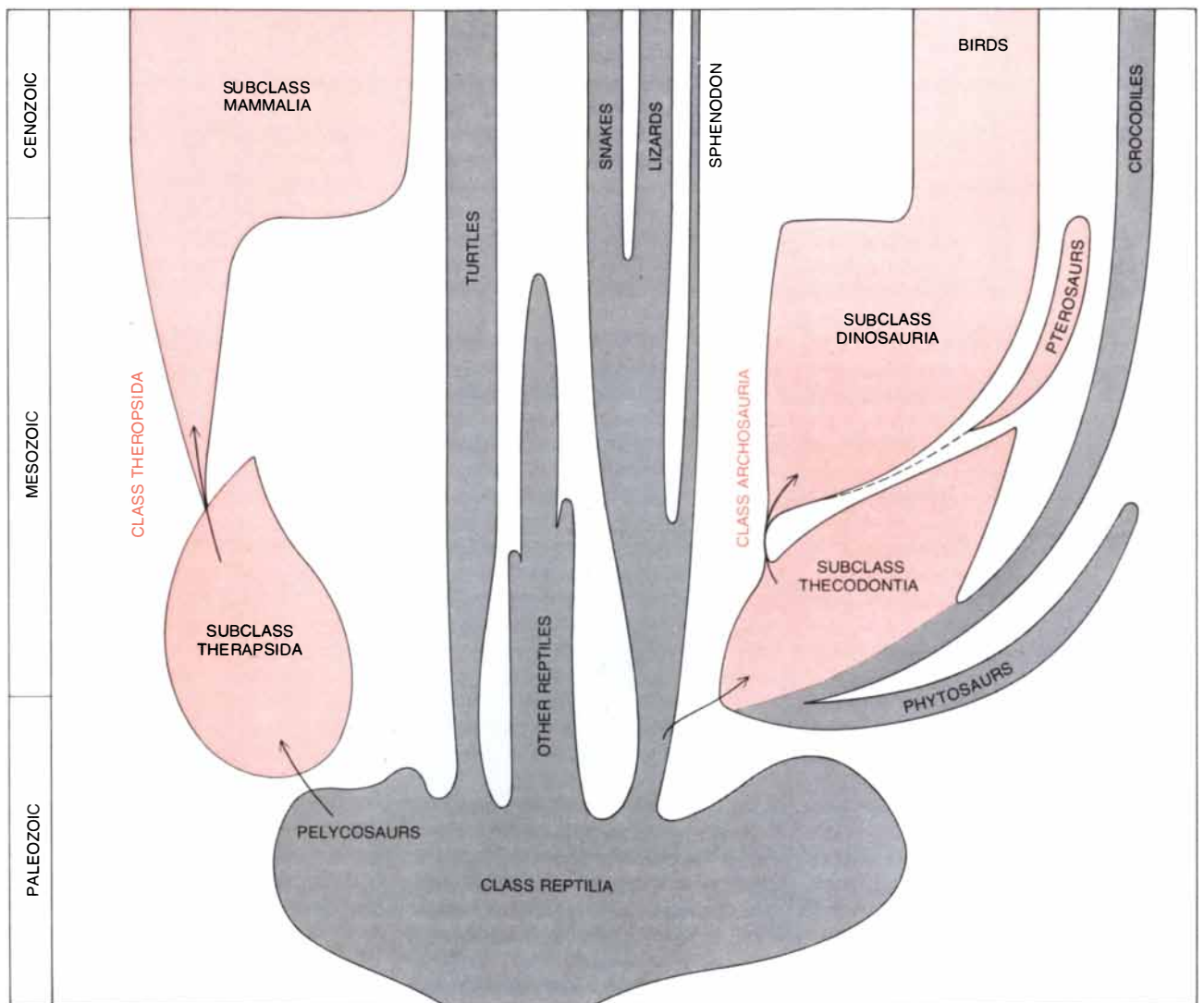
living chameleonid lizards have also evolved scapular swinging, although its details are different from those in mammals. Quadrupedal dinosaurs evolved a chameleon-type scapula, and they must have had long strides and running speeds comparable to those of big savanna mammals today.

When the dinosaurs fell at the end of the Cretaceous, they were not a senile, moribund group that had played out its evolutionary options. Rather they were vigorous, still diversifying into new orders and producing a variety of big-brained carnivores with the highest grade of intelligence yet present on land. What caused their fall? It was not competition, because mammals did not begin

to diversify until after all the dinosaur groups (except birds!) had disappeared. Some geochemical and microfossil evidence suggests a moderate drop in ocean temperature at the transition from the Cretaceous to the Cenozoic, and so cold has been suggested as the reason. But the very groups that would have been most sensitive to cold, the large crocodilians, are found as far north as Saskatchewan and as far south as Argentina before and immediately after the end of the Cretaceous. A more likely reason is the draining of shallow seas on the continents and a lull in mountain-building activity in most parts of the world, which would have produced vast stretches of monotonous topography. Such geologi-

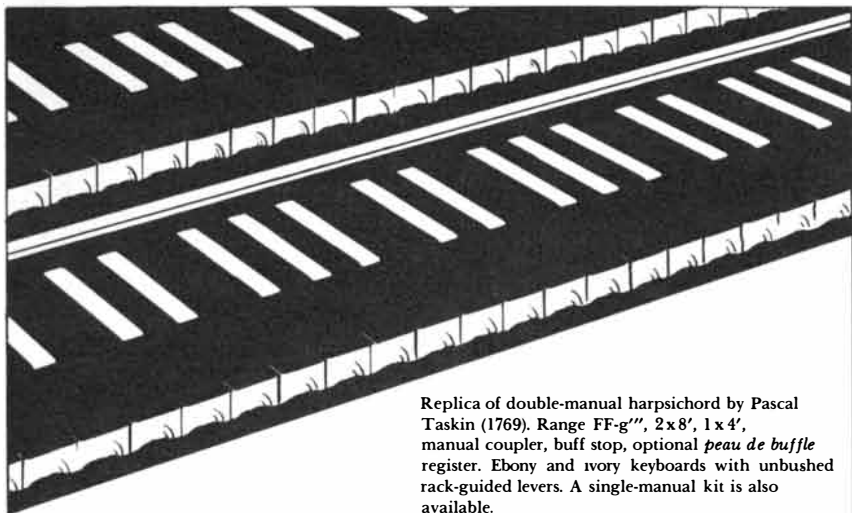
cal events decrease the variety of habitats that are available to land animals, and thus increase competition. They can also cause the collapse of intricate, highly evolved ecosystems; the larger animals seem to be the more affected. At the end of the Permian similar changes had been accompanied by catastrophic extinctions among therapsids and other land groups. Now, at the end of the Cretaceous, it was the dinosaurs that suffered a catastrophe; the mammals and birds, perhaps because they were so much smaller, found places for themselves in the changing landscape and survived.

The success of the dinosaurs, an enigma as long as they were considered



RECLASSIFICATION of land vertebrates (excluding the Amphibia) is suggested by the author on the basis of bioenergetic and anatomical evidence. The critical break comes with the development of endothermy (color), which is competitively superior to ectothermy (gray) for large land vertebrates. Therapsids were endothermic, closer in physiology to mammals than to today's rep-

tiles. Birds almost certainly inherited their bioenergetics (as well as their joint anatomy) from dinosaurs. The new classes presented here, the Theropsida and the Archosauria, reflect energetic evolution more faithfully than the traditional groupings (see illustration on page 61). The width of the pathways representing the various groups is proportional to the biomass represented by their fossils.



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"cold-blooded," can now be seen as the predictable result of the superiority of their high heat production, high aerobic exercise metabolism and insulation. They were endotherms. Yet the concept of dinosaurs as ectotherms is deeply entrenched in a century of paleontological literature. Being a reptile connotes being an ectotherm, and the dinosaurs have always been classified in the subclass Archosauria of the class Reptilia; the other land-vertebrate classes were the Mammalia and the Aves. Perhaps, then, it is time to reclassify.

Taxonomic Conclusion

What better dividing line than the invention of endothermy? There has been no more far-reaching adaptive breakthrough, and so the transition from ectothermy to endothermy can serve to separate the land vertebrates into higher taxonomic categories. For some time it has been suggested that the therapsids should be removed from the Reptilia and joined with the Mammalia; in the light of the sudden increase in heat production and the probable presence of hair in early Therapsids, I fully agree. The term Therapsida has been applied to mammals and their therapsid ancestors. Let us establish a new class Theropsida, with therapsids and true mammals as two subclasses [see illustration on preceding page].

How about the class Aves? All the quantitative data from bone histology and predator-prey ratios, as well as the dinosaurian nature of *Archaeopteryx*, show that all the essentials of avian biology—very high heat production, very high aerobic exercise metabolism and feathery insulation—were present in the dinosaur ancestors of birds. I do not believe birds deserve to be put in a taxonomic class separate from dinosaurs. Peter Galton of the University of Bridgeport and I have suggested a more reasonable classification: putting the birds into the Dinosauria. Since bone histology suggests that most thecodonts were endothermic, the thecodonts could then be joined with the Dinosauria in a great endothermic class Archosauria, comparable to the Theropsida. The classification may seem radical at first, but it is actually a good deal neater bioenergetically than the traditional Reptilia, Aves and Mammalia. And for those of us who are fond of dinosaurs the new classification has a particularly happy implication: The dinosaurs are not extinct. The colorful and successful diversity of the living birds is a continuing expression of basic dinosaur biology.

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