

The evolutionary consequences of possible physiological adaptations of the therapsids, so-called mammal-like reptiles, and the dinosaurs are further assessed by Baur and Friedl and by Hotton. They seek to explain contrasting patterns of evolutionary size change and the timing of adaptive radiations in herbivorous and carnivorous therapsids, as well as in dinosaurs. Many variables and inferences are involved, relating such characteristics of the animals as their mobility, foraging capacities, mechanisms for temperature regulation and water conservation, and so on, with the availability of food resources and environmental conditions of temperature, rainfall and perhaps even the partial pressure of atmospheric oxygen. In our present state of knowledge, such studies are ambitious, even speculative, but they are intellectually stimulating and truly reflect the general problems of identifying causal factors in evolution.

The studies in this book give some indication of the variety of kinds of data and inference that can be brought to bear on the problems of dinosaur bioenergetics. By the same token, it is clear that a full understanding of dinosaur population structures, ecology, behavior, biogeography and evolution is critically dependent upon a resolution of the complex problems of dinosaur thermal physiology. No such resolution of the controversy over whether dinosaurs were rescaled-up, cold-blooded reptiles or warm-blooded surrogate "mammals" is reached here, although the weight of current opinion lies between these extremes. This book will have served its purpose if it helps to clarify the issues and points the way to new lines of research in this active and exciting field.

1

The Evidence for Endothermy in Dinosaurs

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Abstract

Several different and seemingly independent lines of evidence have been represented, by various authors, as indicative of internal temperature regulation and high exercise metabolism in dinosaurs. These convergent conclusions are based on evidence of posture and gait, inferred haemodynamics and activity levels, feeding adaptations, bone histology, inferred trophic dynamics of dinosaurian communities, and the geographic and latitudinal distribution of dinosaurs. These arguments are reviewed and evaluated. Critics of the hypothesis that dinosaurs were endothermic have correctly pointed out that much of the supposed evidence can be explained in other ways. However, these other explanations do not disprove the hypothesis of warm-bloodedness and/or endothermy; they are simply alternative, also viable explanations of the several lines of evidence. The range of anatomical varieties among the animals called dinosaurs is very great. It follows that they may have differed just as much in their modes of temperature regulation and metabolism. It is rarely mentioned that not all of the evidence for endothermy applies to all kinds of dinosaurs. In fact, only one dinosaurian group - the Theropoda - is susceptible to all the kinds of evidence that have been marshalled by advocates of endothermy. The probability that birds are direct descendants of theropods adds an intriguing dimension to the subject. At the moment, the collective evidence is highly suggestive, but as yet still inconclusive.

Introduction

The abundance of dinosaurian remains in Mesozoic strata around the world is clear evidence that these animals dominated the lands of the earth for a period of close to 140 million years. There is no general consensus as to why that was so - especially in view of the fact that primitive

mammals co-existed with them throughout their reign and also were widespread, but never important until the demise of the dinosaurs approximately 65 million years ago.

It is evident from the fossil record that the dinosaurs were very diverse, with many different kinds occupying a wide range of ecological niches. From their first appearance in the last half of the Triassic some 200 million years ago, they quickly diversified into a wide variety of anatomical types that clearly reflect great differences in life styles and habitat preferences. Included were carnivores and herbivores, bipeds and quadrupeds, terrestrial and possibly amphibious forms, ranging from 2 to 3 kg chicken-sized animals up to 60 and 80 ton monsters. Most dinosaurs were large, weighing in excess of 500 kg, while many weighed more than 5 tons!

The undeniable success of the dinosaurs, both in terms of their long-term dominance of the land areas of the world, and of their great diversity and apparently large population numbers, has been compared to the success of the mammals during the Cenozoic (Bakker 1968, 1971, 1972). This, together with certain anatomical evidence, has led to the hypothesis that dinosaurs were competitively superior to their mammalian contemporaries, being physiologically more like modern mammals and birds than like living reptiles. That is to say that they were possibly endothermic and capable of mammal-like or bird-like levels of high exercise metabolism (Wieland 1942; Bakker 1968, 1971, 1972; Dodson 1974; Ostrom 1970, 1974; Ricqlès 1974). Not surprisingly, these speculations precipitated a rash of contrary interpretations (Feduccia 1973, 1974; Bennett and Dalzell 1973; Bennett 1974; Thulborn 1973) and still further counter arguments (Bakker 1974, 1975b; Halstead 1976).

The purpose of this paper is to review and evaluate the various kinds of evidence that have been cited as being indicative of endothermy or mammal-like thermoregulatory physiology in dinosaurs.

Terminology

Before reviewing the evidence, it is necessary to define a few terms that are critical for any further discussion of the problem. The definitions that follow are those given by Bligh and Johnson (1973), unless otherwise noted (" - ") or emended.

Bradymetabolism. The low levels of basal metabolism of reptiles and other nonavian, nonmammalian animals relative

to those of birds and mammals of the same body size and at the same tissue temperature.

Cold-blooded. The thermal state of an animal in which core temperature remains close to ambient temperature "as it rises and falls". (The existence of only a small temperature gradient between the organism and its environment results from the low rate of metabolic heat production (bradymetabolism) of cold-blooded animals relative to the high rate of heat production (tachymetabolism) of warm-blooded animals.) Synonym: Poikilothermic.

Core temperature. The mean temperature of the tissues at a depth below that which is affected directly by a change in the temperature gradient through peripheral tissues. Synonym: Deep body temperature.

Ectothermy. The pattern of thermoregulation in which the body temperature depends on the behaviorally and autonomically regulated uptake of heat from the environment.

Endothermy. The pattern of thermoregulation in which the body temperature depends on a high (tachymetabolic) and controlled rate of heat production.

Heliothermy. The regulation of the core temperature of an ectothermic animal by behavioral variation in exposure to solar radiation.

Heterothermy. The pattern of temperature regulation in a tachymetabolic species in which the variation in core temperature, either "daily" or seasonally, exceeds that which defines homeothermy.

Homeothermy. The pattern of temperature regulation in a tachymetabolic species in which the cyclic variation in core temperature, either "daily" or seasonally, is maintained within arbitrarily defined limits ($\pm 2^{\circ}$ C) despite much larger variations in ambient temperature.

Poikilothermy. "The wide variation of body temperature of a species such that core temperature varies as a proportional function of ambient temperature."

Tachymetabolism. The high level of basal metabolism of birds and mammals relative to those of reptiles and other nonavian, nonmammalian animals of the same body weight and at the same tissue temperature. (This relatively high level of basal metabolism in mammals and birds is a precondition for the relative stability of core temperature during

Body Temperature — Ambient Temperature Relationships

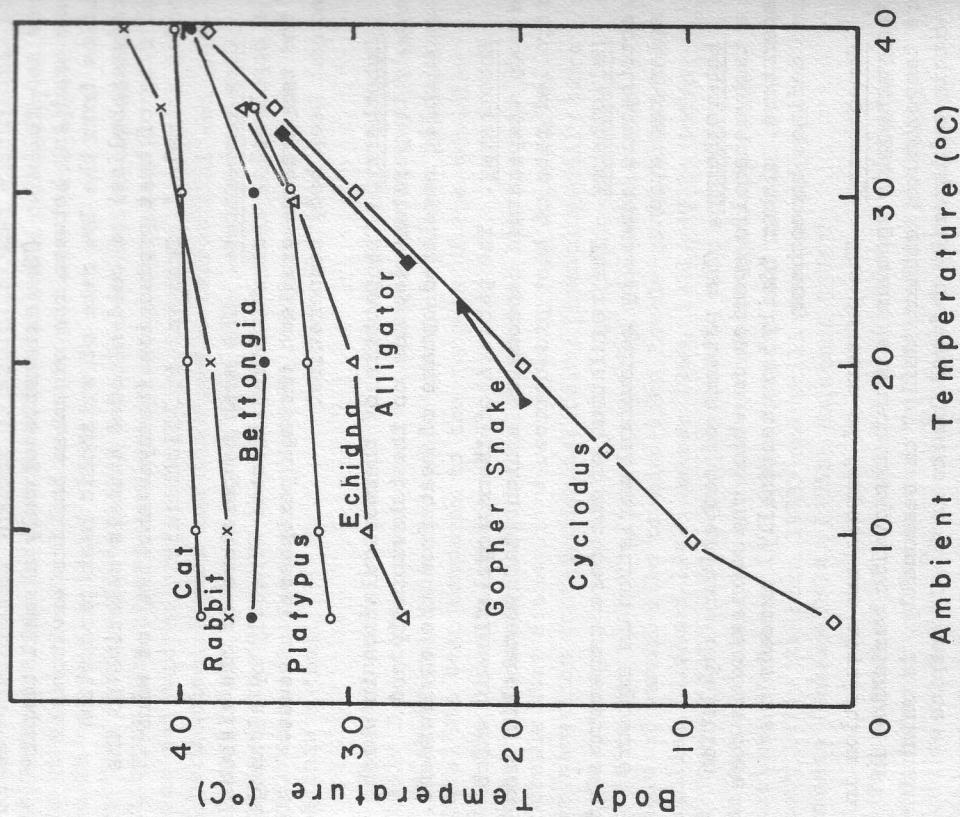


Figure 1. Comparison of the impact of environmental temperatures on the body temperatures of ectotherms (the lizard *Cyclodius*, the gopher snake and the alligator), vs. endotherms (the near-homeothermic monotremes, *Echidna* and the duck-billed platypus *Ornithorhynchus*; the marsupial *Bettongia*; and the placentals *Lupus* and *Felis*). Data from Johansen (1962), Benedict (1932), and Colbert, Cowles and Bogert (1946).

exposure to cold and of endothermic homeothermy and heterothermy.

Temperature conformer. An organism, the core temperature of which varies as a proportional function of ambient temperature; an animal without effective temperature regulation by autonomic or behavioral means. Synonym: Poikilotherm.

Temperature regulator. An organism, the core temperature of which is regulated to some extent by autonomic and/or behavioral processes. (Both homeothermic and heterothermic animals are classified as temperature regulators, having different degrees of thermostability which are defined arbitrarily.)

Warm-blooded. The thermal state of an animal which maintains its core temperature considerably higher than that of the environment when subjected to a low ambient temperature. Synonym: Tachymetabolic.

The Question

Traditionally all dinosaurs have been classified as reptiles; for that reason they have generally been assumed to have been reptile-like in their physiology and mode of temperature regulation (Colbert 1958, 1961; Swinton 1970). Living reptiles are "cold-blooded" and dependent on external heat sources — the sun, atmosphere or substrate — to elevate their body temperatures to optimum levels for activity. They lack internal temperature regulating mechanisms, in contrast with "warm-blooded" mammals and birds that are capable of adjusting their body temperatures by internal metabolic processes independent of external environmental temperatures. Body temperatures of ectotherms vary directly with the environmental temperature, whereas those of endotherms are maintained at nearly uniform high levels even at cold ambient temperatures (see Figure 1). The higher and more uniform body temperatures of mammals and birds are related to their higher metabolic rates. This is in contrast with the generally lower and more variable operating temperatures of reptiles and other lower vertebrates with their lower metabolic rates (see Figure 2). In general, until ectotherms have warmed up to optimum operating levels, they are relatively inactive or torpid, in contrast to non-hibernating endotherms that are always at optimum temperature and metabolic levels for maximum activity.

Quite incorrectly, there has been a chauvinistic tendency in some quarters to view "cold-blooded" reptiles as

inferior to "warm-blooded" mammals and birds. Ectothermy, however, is a highly successful strategy among modern reptiles and amphibians; it is not evident that the more expensive tachymetabolic regime of endotherms is a better one. Despite the "higher" and more complex organization of endotherms, they are vastly outnumbered by ectotherms and poikilotherms. Nevertheless, it has been suggested that some or all dinosaurs - even though classified as reptiles - may not have been either poikilothermic or ectothermic, but rather that they were endotherms. That, according to some, is the reason for their success.

In the absence of direct means of measuring dinosaurian body temperatures and their fluctuations, metabolic rates and scope, O₂ consumption, and exercise levels, we are forced to rely on indirect evidence that may pertain to these matters, combined with judiciously drawn analogies with modern species. Obviously, dinosaur analogues among modern animals must be viewed with extreme caution. The question is this: can we determine anything about physiological thermoregulation in any of the dinosaurs?

Dramatis Personae

Although dinosaurs probably need no introduction to most readers, it seems appropriate to include at least a brief summary of the principals in this drama. Everyone has his own favored classification; most of those published in recent years conform to the one below on most major points, although they may differ in minor details. The age and provenance of each taxon is given, together with the common name or a brief description of the animals. The formal roster of dinosaurs is as follows:

- Class REPTILIA
- Subclass ARCHOSAURIA
- Order SAURISCHIA - Mid-Triassic to Late Cretaceous.
 - (All continents except Antarctica)
 - Suborder THEROPODA - (Bipedal carnivores) - Mid-Triassic to Late Cretaceous. (Same distribution)
 - Infraorder COELOSAURIA - (Small, lightly built carnivores) - Mid-Triassic to Late Cretaceous. (Same distribution)
 - Family COELURIDAE - Early Jurassic to Early Cretaceous. (Same distribution)
 - Family COMPSOGNATHIDAE - Late Jurassic (Europe)
 - Family DROMAEOSAURIDAE - Early to Late Cretaceous. (North America and Asia)
 - Family ORNITHOMIMIDAE - Early to Late Cretaceous. (Europe, Asia and North America). Ostrich mimics.

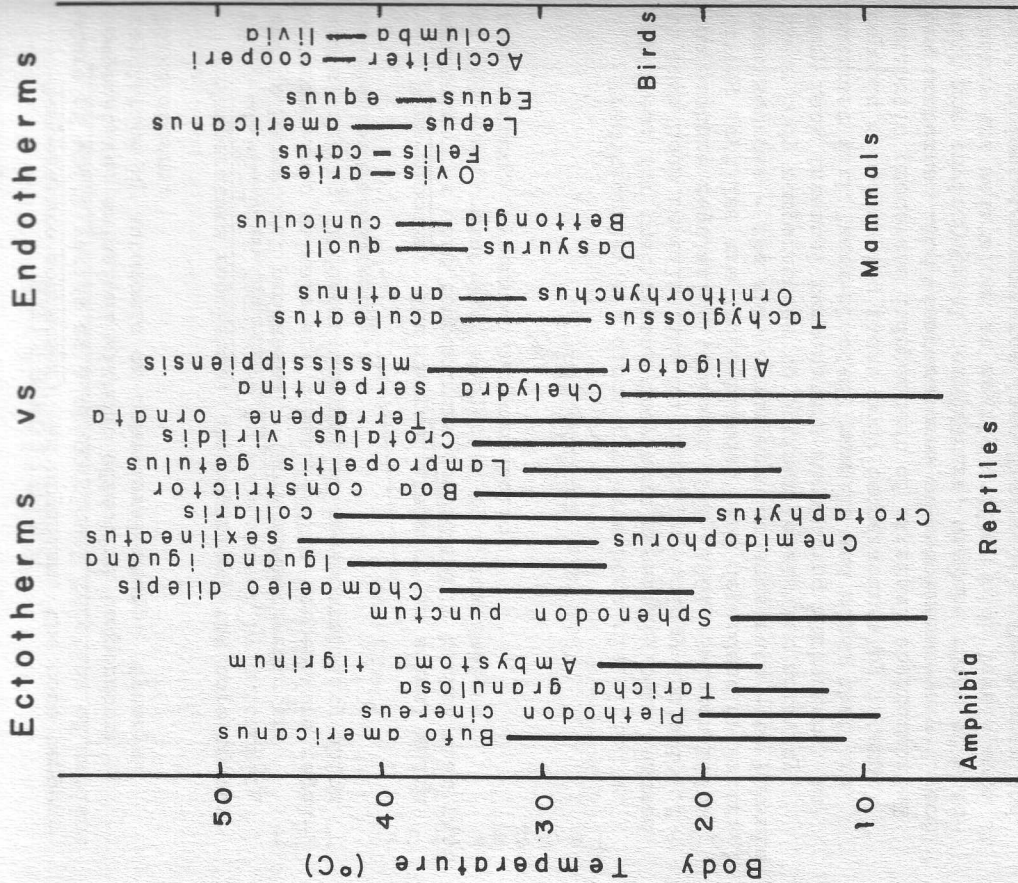


Figure 2. Comparison of active body temperature variation ranges between ectotherms (amphibians and reptiles) and endotherms (mammals and birds). Note that some ectotherms experience temperatures as high, or higher than those of some endotherms, but their body temperatures fluctuate more widely. Data from Brattstrom (1963, 1965), Prosser and Brown (1962), and Welty (1962).

- Family OVIRAPTORIDAE - Late Cretaceous. (Asia)
 Family PODOKESAUROIDAE - Mid- to Late Triassic.
 (All continents except Antarctica and Australia)
 Family SEGISAURIDAE - Late Triassic. (North America)
 Infraorder CARNOSAURIA (Large, heavily-built carnivores)
 Early Jurassic to Late Cretaceous.
 (All continents except Antarctica and Australia)
 Family MEGALOSAURIDAE - Early Jurassic to Early
 Cretaceous. (Same distribution)
 Family THEREZINOSAURIDAE - Late Cretaceous. (Asia)
 Family TYRANNOSAURIDAE - Late Cretaceous. (All
 continents except Europe, Antarctica and Australia)
 Suborder SAUROPODOMORPHA (Medium to extremely large
 herbivores) - Mid-Triassic to Late Cretaceous.
 (All continents except Antarctica and Australia)
 Infraorder PROSAUROPODA (Semi-bipedal herbivores)
 Mid- to Late Triassic. (Same distribution)
 Family ANCHISAURIDAE - Mid- to Late Triassic.
 (Same distribution)
 Family MELANOROSAURIDAE - Mid- to Late Triassic.
 (Africa, Asia and Europe)
 Family PLATOSAURIDAE - Mid- to Late Triassic.
 (South America, Asia and Europe)
 Infraorder SAUROPODA (Gigantic, quadrupedal,
 Brontosaurus-like herbivores) - Mid-Jurassic to
 Late Cretaceous. (All continents except
 Antarctica and Australia).
 Family BRACHIOSAUROIDAE - Mid-Jurassic to Late
 Cretaceous. (Same distribution)
 Family TITANOSAURIDAE - Mid-Jurassic to Late
 Cretaceous. (Same distribution)
- Order ORNITHISCHIA - Mid-Triassic to Late Cretaceous.
 (All continents except Antarctica and Australia)
 (All herbivores)
 Suborder ORNITHOPODA (Small to large, bipedal herbivores)
 Mid-Triassic to Late Cretaceous.
 (Same distribution)
 Family HADROSAURIDAE - Late Cretaceous. (Asia, North
 America and Europe) (The duck-bills)
 Family HETERODONTOSAURIDAE - Mid- to Late Triassic.
 (Africa and South America)
 Family HYPsilOPHONTIDAE - Late Triassic to Late
 Cretaceous. (Africa, Asia, North America, Europe)
 Family IGUANODONTIDAE - Late Jurassic to Late
 Cretaceous. (All continents except Australia,
 Antarctica and South America)
 Family PACHYCEPHALOSAURIDAE - Late Cretaceous.
 (North America and Asia) (The "bone-heads")
 Family PSITTACOSAURIDAE - Late Cretaceous. (Asia)

- Suborder STEGOSAURIA - Late Jurassic to Early Cretaceous.
 (Europe, Asia, Africa and North America)
 (The plated dinosaurs)
 Family SCOLIDOSAURIDAE - Early Jurassic to Early
 Cretaceous. (Europe)
 Family STEGOSAURIDAE - Late Jurassic to Early
 Cretaceous. (Europe, Asia, Africa, North America)
 Suborder ANKYLOSAURIA - Early to Late Cretaceous.
 (Europe, Asia, Africa, North and South America)
 (The armored dinosaurs)
 Family ANKYLOSAURIDAE - Late Cretaceous.
 (Asia and North America)
 Family NODOSAURIDAE - Early and Late Cretaceous.
 (Europe, North America, Africa? and South America?)
 Suborder CERATOPSIA - Late Cretaceous. (Asia and North
 America) (The horned or frilled dinosaurs)
 Family CERATOPSIDAE - Late Cretaceous. (North America)
 Family PROTOCERATOPSIDAE - Late Cretaceous. (Asia)

These are the 'players' - not in their order of appearance,
 or importance.

The two orders of dinosaurs are considered by most to
 have had separate and independent origins among primitive
 Early Triassic archosaurs, the pseudosuchian thecodonts.

The Evidence

Several different and seemingly unrelated kinds of
 evidence have been cited as indicative of warm-bloodedness,
 and even endothermy in dinosaurs (Bakker 1971, 1972;
 Currey 1962; Enlow and Brown 1957; Ostrom 1970, 1974;
 Ricqlès 1969, 1974). The evidence can be categorized as
 anatomical, histological, ecological, zoogeographic and
 phylogenetic. The variety of these different lines of
 evidence may be as significant as the individual items
 themselves.

Posture and Gait

The majority, but not all, of the dinosaurs were char-
 acterized by upright or erect posture. The limbs were held
 in nearly vertical, parasagittal positions beneath the
 shoulder and hip sockets, rather than projecting out to the
 sides in a sprawling posture, as in virtually all living
 ectotherms. Limb-movement in a fore-and-aft, nearly
 vertical plane is clearly established for both the fore and
 hind limbs of most dinosaurs by the shapes of the humeri and
 femora and by the design of the glenoid and acetabular
 sockets. Where the head of the femur projects nearly at

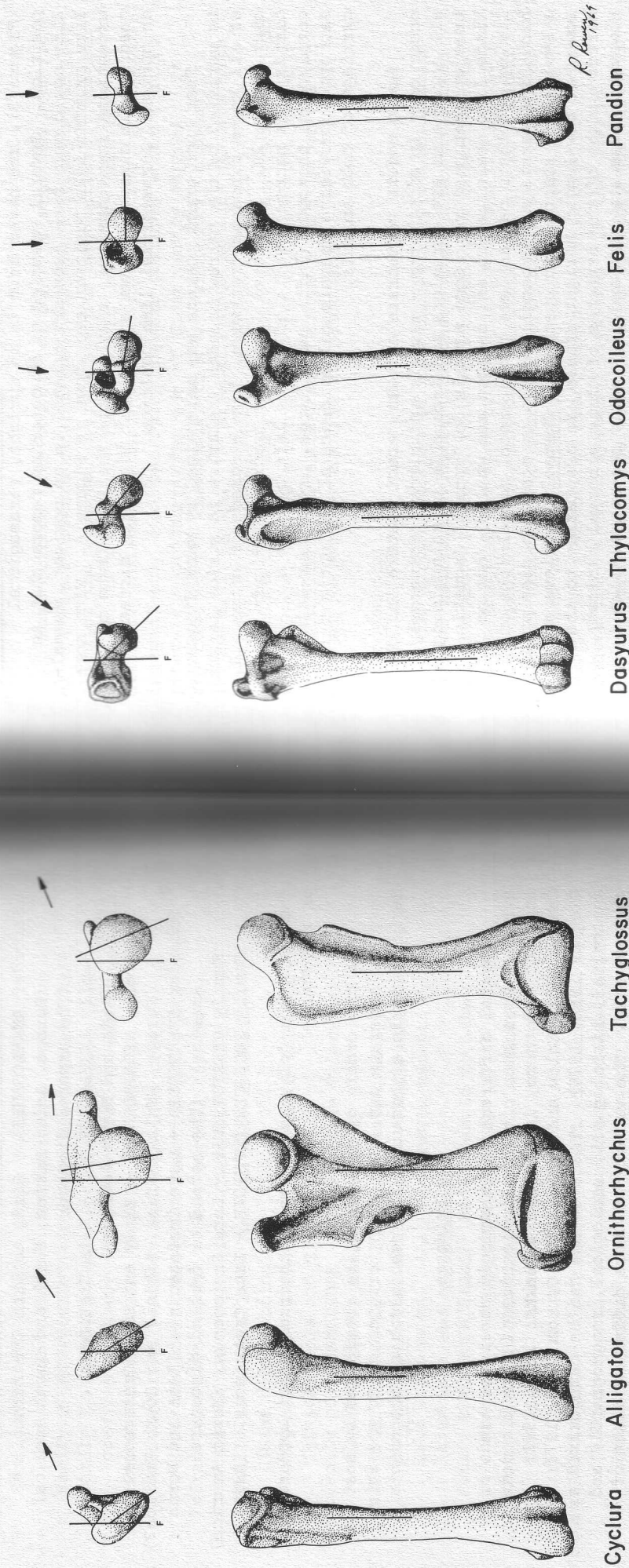


Figure 3. Right femora of selected recent higher vertebrates viewed proximally (above) and in the plane of flexion-extension (below). In the latter, flexion of the distal limb elements is away from the viewer. All are drawn to unit length; the vertical lines equal 2 cm. The proximal views are drawn so that the plane of flexion-extension at the knee

has a vertical trace (line F). The additional line extending to the right in each proximal view indicates the approximate axis of the femoral head, relative to the plane of flexion. The arrows point forward. From Ostrom (1970). Reprinted with permission from the Proceedings of the North American Paleontological Convention, Volume 1.

right angles to the shaft and in the plane formed by the distal condyles, as in the deer, cat or osprey (Figure 3), we know from direct observation that leg excursion is in a near-vertical, parasagittal plane. Similarly, we know from observation of living animals that femora with heads only slightly offset and at a distinct angle to the plane of the distal condyles, as in the lizard *Cyclura* and the Alligator (Figure 3), are never held in an upright, parasagittal position. Several examples of dinosaurian femora that in life could only have been articulated in an upright, mammal-like or bird-like position are shown in Figure 4. With some exceptions (ceratopsians, ankylosaurs) the fore limbs of quadrupedal dinosaurs have a form that similarly dictates an upright, parasagittal limb position.

That such erect posture was maintained by many dinosaurs is verified by the narrow breadth (relative to stride length) of all known dinosaur trackways, from hundreds of sites all over the world. The famed Glen Rose trackways (Figure 5) display the narrow breadth of tracks left by both a carnivorous theropod (left) and a large, brontosaurus-like sauropod, providing unequivocal evidence of the upright carriage of both animals.

Among modern vertebrate animals, erect posture and gait occur only in endotherms - mammals and birds. Conversely, all ectotherms are sprawlers and incapable of maintaining a true upright posture. Some mammals do "sprawl" (aquatic kinds like seals, walruses, dugongs and whales), but no living ectotherm can achieve truly erect, mammal-like or bird-like carriage. Crocodilians do on occasion rise up in a semi-erect stance, and species of *Chamaeleo* achieve a somewhat bow-legged upright stance (an adaptation to the narrow widths of the branches of their arboreal habitat). However, these are rare and distinctly non-mammal-like exceptions among reptilian locomotory adaptations.

The correlation of upright posture and endothermy, as against sprawling posture and ectothermy, among living tetrapods suggests that upright dinosaurs may have been endothermic. But, as some critics have correctly pointed out, no cause-and-effect relationship between posture and physiology has been established. However, the correlation between posture and endothermy or ectothermy is virtually absolute and surely is not merely coincidental. It may be that a metabolic regime subject to ectothermic temperature regulation imposes a major physiological obstacle that makes erect posture and locomotion impossible. It is true that many mammals and birds are able to stand erect at rest at very low metabolic expense, but erect posture has been

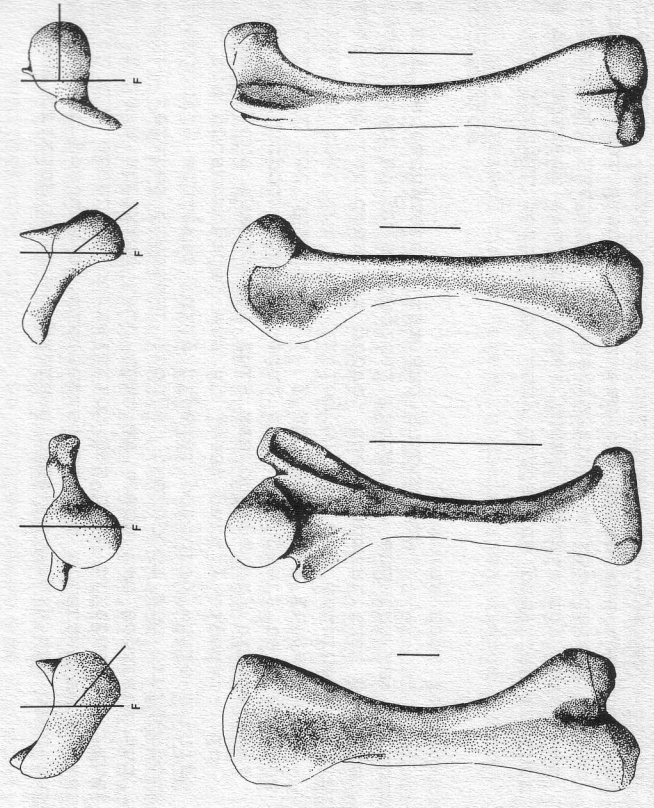
perfected in these forms and is well beyond any possible "threshold" that might exist between semi-erect and fully erect carriage. We do not know whether erect posture could be achieved by an ectotherm, or whether the externally affected physiology of an ectotherm is so unstable that evolution from the primitive sprawling condition to an erect carriage simply could not take place.

Some critics have complained that too much has been made of the erect posture of dinosaurs, but no alternative explanation of the observed correlation has been offered. Furthermore, it is a striking fact that at least two separate and distantly related dinosaur groups, theropods and ornithomorphs, independently achieved fully bipedal posture, while a third group, the prosauropods, was at least partly bipedal. In the case of the theropods, this was obligatory bipedality; in the ornithomorphs, the bipedal stance appears to have been habitual, if not obligatory. I suggest that it is no coincidence that the only living bipeds are endotherms. This strengthens, but does not prove, the argument that posture is controlled by physiological factors - and the key factors here may be tachymetabolism and endothermy.

Haemodynamics

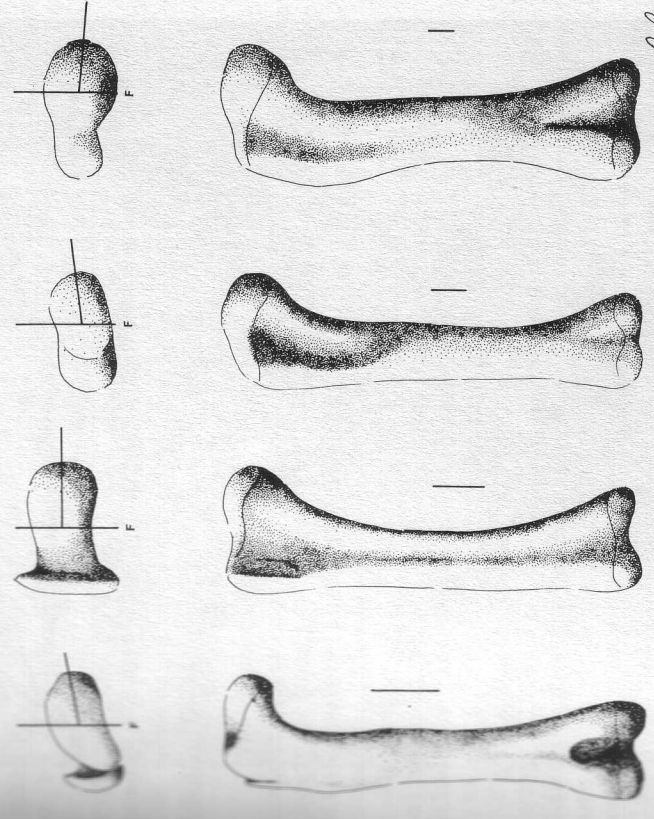
The upright posture of many dinosaurs provides another line of indirect evidence that these animals may have been endothermic. Skeletal reconstructions allow determination of the vertical distance between the brain and the position of the heart. Hence, one can calculate the systemic blood pressure necessary to overcome the hydrostatic pressure of that fluid column and perfuse the elevated brain (Hohnke 1973). The greater the heart-brain vertical distance, the greater the required systemic pressure. In the case of *Brachiosaurus*, with the head and neck upright, the vertical heart-brain distance approximated 6 m, thus requiring a systemic systolic pressure of more than 500 mm of Hg, assuming a minimum cerebral perfusion pressure of 60 mm Hg (Hohnke 1973; Seymour 1976) (see Figure 6).

High tissue metabolism requires high blood pressure and rapid circulation in the systemic circuit to provide adequate exchange of metabolites. This is especially true of tachymetabolic species. Rapid circulation within the pulmonary circuit is required for the same reason, but systolic pressure here must be comparatively low, in order to prevent fluid loss (edema) or hemorrhaging across the gas exchange membranes of the lungs. Seymour (1976) notes these requirements, assumes that the same was probably true for dinosaurs, and concludes that at least the large forms must have had



Dimetrodon Oligokyphus Diademodon Thescelosaurus

Figure 4. Right femora of selected Paleozoic and Mesozoic tetrapods, including a primitive (Dimetrodon) and advanced (Oligokyphus and Diademodon) mammal-like reptiles and various dinosaurs. Views and symbols as in Figure 3, except that the vertical lines adjacent to the dinosaurian femora equal



Allosaurus Triceratops Stegosaurus Apatosaurus

10 cm here. Notice the sharply offset femoral heads, especially in the ornithomimid Thescelosaurus and the theropod Allosaurus. From Ostrom (1970). Reprinted with permission from the Proceedings of the North American Paleontological Convention, Volume 1.

*R. Bayliss
1967*



Figure 5. Trackways left by a large four-legged Brontosaurus-like dinosaur (on the right) and a large bipedal Tyrannosaurus-like carnivore (on the left). Notice the narrow breadth of both trackways, compared with the lengths of the strides - proof of upright carriage in both animals. The locality is at the Paluxy River near Glen Rose, Texas, 60 miles southwest of Fort Worth. By permission of the American Museum of Natural History, New York.

fully divided four-chambered hearts, capable of producing large pressure differentials between the pulmonary and systemic tracts.

Several authors (Russell 1965; Bakker 1968; Swinton 1970) have theorized that dinosaurs might have had four-chambered hearts, like crocodilians, but without any evidence other than the fact that crocodiles (and birds) are believed to be the closest living relatives of the dinosaurs. It is true that crocodilians have a four-chambered heart, but the systemic and pulmonary circuits develop only moderate pressure differentials of 15 to 20 mm Hg (White 1969), about the same or slightly less than the systolic differential in Iguana (White 1968), which has a three-chambered heart!

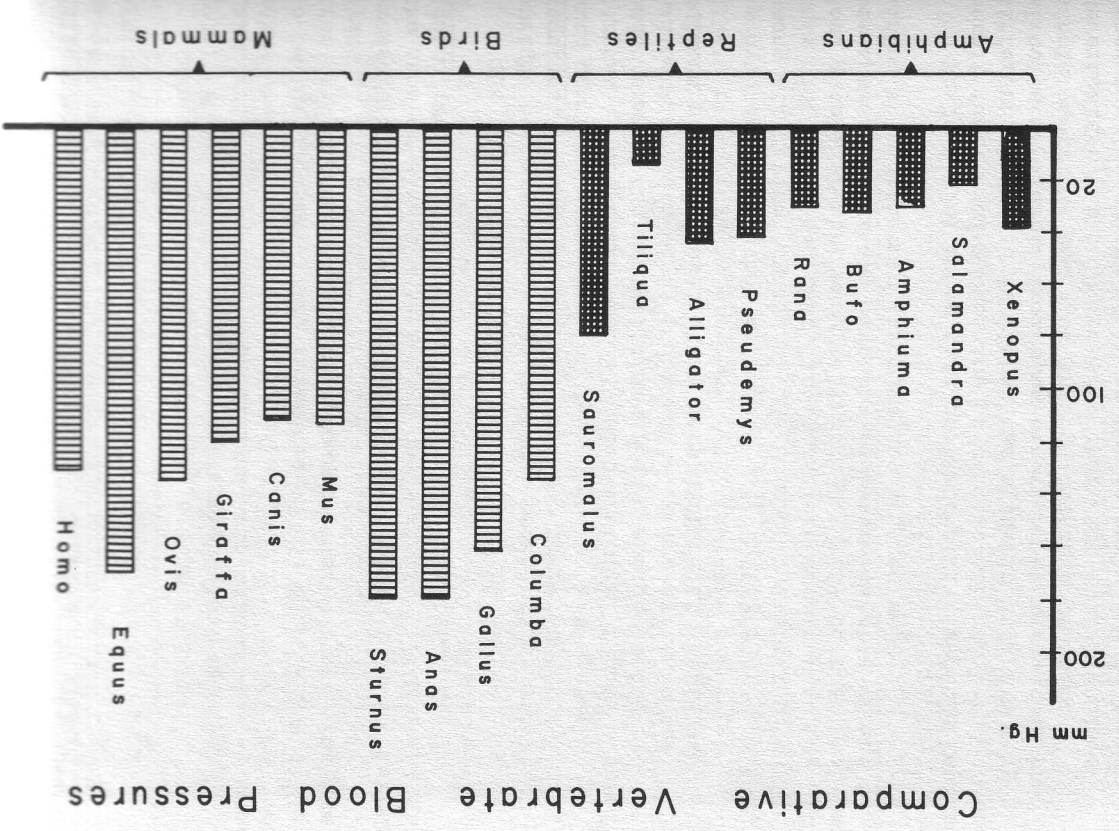
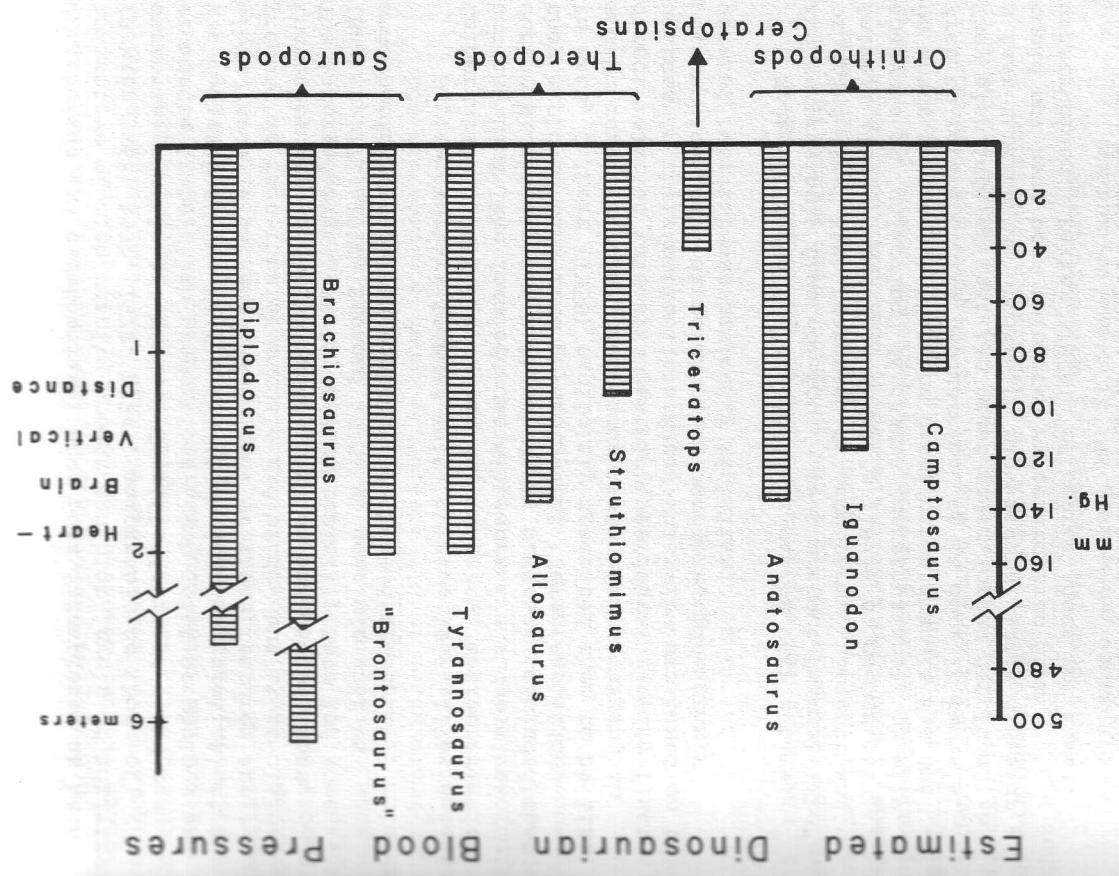
The importance of all this lies in the certainty that upright posture with large vertical heart-brain separation requires a double pump, fully divided four-chambered heart, with complete separation of the pulmonary and systemic circuits. These are probably also essential requirements for endothermy. The fully divided four-chambered heart is a hallmark of both birds and mammals, where systemic and pulmonary blood pressure are very different. It is very likely that it is this common trait that has permitted tachymetabolic regimes to evolve only in birds and mammals, among all living organisms. As Seymour correctly notes, this does not prove that dinosaurs were endothermic, but it does establish that many (although not all) of them must have possessed a heart and circulatory system capable of maintaining an endothermic (tachymetabolic) regime.

White (1976) notes that non-crocodilian reptile hearts permit functional separation of cardiac sub-chambers, so that differential pressures within the systemic and pulmonary circuits may result from time-sequenced events within the single ventricle and flow through discrete channels. Nevertheless, it is impressive that high systemic blood pressures (in excess of 80 mm Hg) do not occur in living ectotherms, while all ectotherms have a very short heart-brain vertical separation, as well as sprawling posture. Conceivably, the low systemic pressure imposed by the required low pressure of the confluent pulmonary circulation may be the critical factor that limits living ectotherms to low sprawling posture and low head-heart vertical distances, as well as being ectothermic and bradymetabolic.

Activity Levels

Certain features of the skeletal anatomy of the legs, shoulders, and pelvis in some dinosaurs (theropods,

Figure 6. Comparison of systemic blood pressures in various living ectotherms and endotherms, with estimated blood pressures for some well-known kinds of dinosaurs. Dinosaur blood pressures were estimated as equivalent (at least) to the hydrostatic pressure of fluid columns equal in length to the vertical distances between the heart and the brain, as measured in the various mounted skeletons. Data from Prosser and Brown (1962), Welty (1962), and White (1976).



ornithopods and ceratopsians) have been interpreted as being indicative of high running speeds and high levels of activity (Bakker 1968, 1971, 1972, 1974), comparable to those of cursorial mammals and birds. Specific features cited are elongated limbs, limb proportions, limb joint morphology and the capacity for acute flexion (limb joint angulation) at the elbow, knee, wrist and ankle. All of these features are present in fast-running mammals and birds, but it is claimed that they are absent in modern lizards and crocodylians. The inferred high activity and cursoriality have led some (Bakker 1971, 1972; Desmond 1975) to conclude that an endothermic regime was employed by these dinosaurs.

Earlier workers (Osborn 1917; Swinton 1936, 1970; Colbert 1958, 1961) noted that some of these characteristics and the bird-like form of some dinosaurs are suggestive of cursorial ability and high activity, but none concluded that they employed bird-like physiological thermoregulation. In fact, Colbert (1958) explicitly described them to be like modern reptiles, with their body temperatures varying in direct relation to environmental temperature, causing fluctuations in their metabolic rates. This view was based on the presumption that, since dinosaurs were reptiles, their general behavior was basically reptilian.

Modern lizards and crocodylians can be very active, and surprisingly fleet-of-foot - even without "mammal-like" or "bird-like" limb features, or endothermy. Bennett and Dalzell (1973) criticized Bakker's (1971) biomechanical analysis of "galloping" dinosaurs (ceratopsians), chiefly on their assessment that the dinosaurian scapula was not free to rotate during protraction, as it does in mammals. They also implied that the great shear forces developed in a fast-running (as opposed to slow-moving) large dinosaur could not have been tolerated by ceratopsian limb construction. Bakker (1974), of course, does not agree.

From my own analysis of the ceratopsian shoulder girdle and forelimb, I agree with Bennett and Dalzell that the scapula could not possibly have swung in the same fashion that it does in present day cursorial mammals. Thus, ceratopsians could not have galloped in the same way that horses, gazelles, or even rhinos gallop. As for the significance of limb joint morphology in bipedal and ornithopods, this is clearly correlated with bipedal (and therefore, erect) posture, which required near-vertical parasagittal excursion of the hindlimbs. Obviously, this could also have facilitated high speed, but it does not prove long-term high levels of activity, or endothermy.

On a very different tangent, high activity levels require greater motor and sensory control, and, as Feduccia (1973, 1974) observed, this should be reflected in increased brain size and complexity. But dinosaurs are notorious for their puny brains. Drawing on Jerison's (1969) work, which described dinosaur brains as typically reptilian in size (relative to body size) and conservatively evolved, Feduccia concludes that the required motor and sensory controls cannot be deduced from dinosaur endocasts. Russell (1969, 1972), however, reported that brain size in some of the small theropods was much larger relatively than is true of Alligator, and Hopson (1977) has concluded that brain sizes in all adequately known coelurosaurs and carnosaurs, as well as in most ornithopods, were greater than those of living crocodylians. Thus, those dinosaurian kinds at least, may have possessed the motor and sensory control centers necessary for high and complex activity. Hopson concludes that

"except for coelurosaurs, the range of behaviors that existed in dinosaurs, as inferred from trackways and skeletal morphology, may not have lain much outside the range observed in living ectotherms".

Although not explicitly aimed at the claims of high running speeds as evidence for an endothermic metabolic regime in dinosaurs, Alexander's (1976) estimate of dinosaur speeds, based upon fossil trackways, does challenge these hypothesized activity levels. Russell and Beland (1976) have properly responded that inferences from fossil "trackway evidence so far obtained are not yet adequate for generalization on dinosaurian metabolism". The admirable analysis by Alexander deserves a much more realistic conclusion than his

"This does not necessarily mean that large dinosaurs never ran, but it seems to conform better with the traditional image of lumbering dinosaurs than with that of the lively runners shown in some recent restorations." The restorations referred to are those of Protoceatorops (Bakker 1968) and medium-sized ornithopods (Galton 1970), all of which are much smaller than an average-sized race horse.

Alexander's analysis of four trackway sites should be viewed as interesting, but of little or no relevance to the question of dinosaurian running velocities (or activity levels), for the simple reason that running, or even fast walking, is not the usual mode of tetrapod (or bipedal)

locomotion. Animals walk most of the time, walk briskly or trot some of the time, and run or gallop only under unusual circumstances. From the point of view of energetics alone, it is doubtful if the cumulative traverses of any individual animal include more than 5 to 10% at velocities above that of a walking pace. Therefore, the statistically insignificant number of trackway sites of Alexander's study tells us only that these particular dinosaurs walked at human-like speeds, or slightly better (1.0 to 3.6 m/sec). Man is capable of a four-minute mile (6.9 m/sec) or four miles an hour (1.6 m/sec) on a brisk walk. We can come to no firm conclusion about maximum running speeds of dinosaurs from the limited data used by Alexander.

Group Activity

If dinosaurs were mammal-like or bird-like in their physiology, we might suppose that they had mammal or bird-like behavioral patterns as well. There is some evidence that this may have been so. In addition to the anatomical evidence cited above, further insight into dinosaur behavior comes from fossil footprint sites that preserve evidence of group activity, such as multiple trackways. Bird (1944) was the first to suggest that such multiple trackways indicated herding behavior in dinosaurs, although von Huene (1928) had previously suggested migratory herding behavior to explain the many skeletons of the prosauropod *Plateosaurus* found at Trossingen, in West Germany. The footprints reported by Bird, in Bandera County, Texas, west of San Antonio, clearly record the passage of at least 23 sauropod like animals, walking together in a group. Bakker (1968) later pointed out that Bird's "herd" apparently was structured - the young individuals had been at the center of the herd, surrounded by the adults. In 1972, I reported on another impressive footprint site at Holyoke, Massachusetts, where a surprisingly high percentage (70%) of the trackways are preserved with near-parallel bearings. These and other similar occurrences are strong evidence of group behavior.

While we normally associate herding or group behavior with various mammals and birds, rather than with reptiles, recent studies by Rand (1968), Brattstrom (1974) and Burghardt (1977) document relatively complex social behavior in a variety of ectotherms. The parallel trackways mentioned above could be the result of truly gregarious animals aware of the presence and behavior of others of their own kind - and whose passage was stimulated by the actions of the group. All this suggests a relatively high degree of neural organization, which in turn, by analogy with modern birds and mammals, suggests but does not prove that these dinosaurs

may have been endothermic.

Feeding Adaptations

If some dinosaurs were tachymetabolic and capable of high, long-term exercise metabolism, then we must presume that, like modern mammals and birds, they required large volumes of food, at a much higher intake rate per unit of body weight than is required by comparably-sized ectotherms. We might expect to find some evidence of this in dinosaurian anatomy. In fact, some such evidence does exist.

The bipedal herbivores, the ornithomids - and especially the hadrosaurs or duck-bills - featured specialized grinding dentitions, composed of hundreds of teeth arranged in large batteries with extensive and continuous grinding surfaces. These grinding surfaces are comparable to those of modern elephants, although not as large. They were maintained by a never-ending supply of replacement teeth that erupted in such a way that no gaps ever developed in the grinding surfaces. There can be no doubt that this dental system was ideally adapted for processing large volumes of tough vegetation (Ostrom 1961, 1964) (see Figure 7).

The horned dinosaurs or ceratopsians (with the exception of the most primitive kind, *Protoceratops*) had similar dental batteries, also composed of hundreds of teeth and with a comparable replacement mechanism that insured uninterrupted integrity of the occlusal surfaces. Here, however, the batteries formed continuous shearing blades for slicing large quantities of fibrous plant matter (Ostrom 1966).

The largest of all dinosaurs, the sauropods, might be expected to show the most extensive specializations for processing large volumes of food, but this is not so. Their mouths are very small relative to the size of the animals, and the teeth seem poorly designed for chewing or preparing large amounts of food. Similarly, the miniscule teeth of stegosaurs and ankylosaurs provide no evidence of any capacity for enhanced food preparation in the mouth. The absence of grinding dentitions, however, cannot be taken as proof that these forms did not ingest large volumes of food (Bakker 1971), although there is no positive evidence that they did so. Their large sizes might alone be construed as evidence of the intake of a large food volume, but these animals might have been very long-lived and slow-growing, as compared with living reptiles.

Another peculiarity of some dinosaurs is the evidence that the nasal passages by-passed the mouth cavity. In

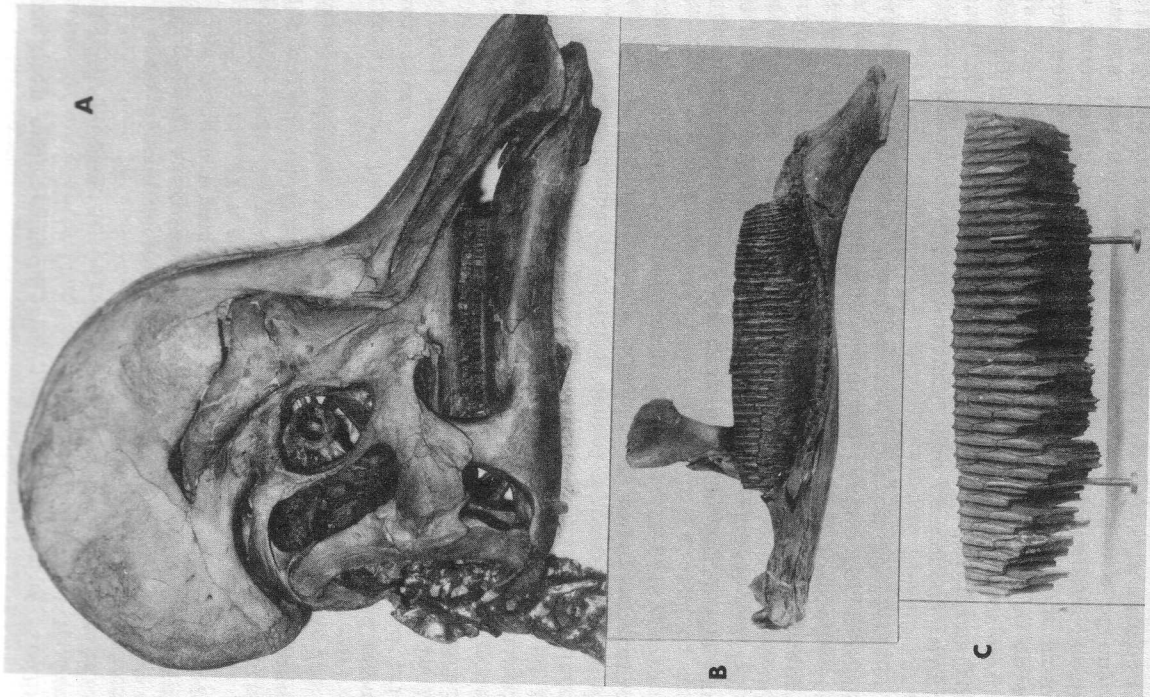


Figure 7. Skull, lower jaw and dental battery of a duck-billed dinosaur (*Corythosaurus casuarius*) to illustrate the highly specialized food-processing equipment of these ornithomimid dinosaurs. As can be seen in C, the dental battery is composed of dozens of tightly compacted teeth forming one continuous grinding surface (upper edge). B and C, lingual or medial views, by the author. A, by permission of the American Museum of Natural History, New York.

living non-crocodilian reptiles, the mouth constitutes a major part of the respiratory tract, channeling air between the internal nares in the front of the mouth and the trachea at the rear. In many sauropods, the nostrils were placed high on the head above the eyes, indicating that the nasal passages descended straight down to the trachea at the back of the mouth cavity. In many duck-billed dinosaurs, the nasal passages ascended into a hollow crest on top of the skull (see Figure 7A) and then descended to the trachea, by-passing the mouth. The armored dinosaurs (ankylosaurs) featured a secondary bony palate, with the internal nares positioned far to the back of the mouth, as in mammals. These conditions appear to have separated the mouth cavity from the breathing passages, much as the secondary palate of mammals does, completely separating breathing and feeding activities. This may mean that food preparation could have been carried on in the mouth without interruption for breathing - or vice versa. High food intake and high respiratory rates are both important to endotherms.

It is reasonable to infer that these dental specializations and modifications of the nasal tracts are evidence of large food-volume intake. Whether this large volume of food was a requisite of endothermy and high metabolic rates, or simply a consequence of the large body sizes of the animals involved, cannot be determined. We simply do not know.

Predator-Prey Ratios

A continuation of this line of reasoning - that endothermic animals require greater food intake than comparably sized ectotherms - has led to the examination of the relative abundance of remains of predaceous and potential prey dinosaurs in several richly fossiliferous Late Cretaceous strata (Bakker 1972, 1974, 1975a, 1975b). Since direct observation of food intake by any dinosaur is now obviously impossible, Bakker reasoned that the ratio of predaceous dinosaurs to co-existing potential prey animals should reflect the food requirements of the predators. From observations of modern animal communities, it is evident that a given number of prey animals can support a much smaller number of endothermic predators than ectothermic predators of similar size. Or as Bakker (1972, p. 82) has expressed it:

"Because endothermic carnivores require prey at a rate an order of magnitude higher than that of ectotherms, the predator standing crop [total predator biomass] to prey standing crop ratio in an ectothermic predator/prey complex should be an order of magnitude higher than in an endothermic complex."

Census data of modern mammalian communities (Dasmann and Mossman 1962; Schaller 1967) indicate that mammalian predator/prey standing crop ratios range from less than 1% to something more than 6%. Comparable census data for modern reptilian communities are not available, but observations of an ectothermic predator, *Varanus komodoensis* (Auffenberg 1971), have led Bakker (1972) to infer a consumption rate equal to the predator's own body weight every 60 days, as contrasted with mammalian predator consumption rates equal to their own body weights every 6.6 days for wild dogs (*Lycan pictis*), 7.7 to 9.1 days for the lion (*Panthera leo*), and 10 days for the cheetah (*Acionyx jubatus*) (Wright 1960; Schaller 1968). Ignoring the size differences between the Komodo dragon (50 kg), cheetah (50 to 60 kg) and lion (180 to 227 kg), these data translate into a consumption rate for mammalian predators approximately ten times that for *Varanus komodoensis*. This suggests that ectothermic predator/prey standing crop ratios may range as high as 60%.

A census (Russell 1967) of all the dinosaur specimens that have been collected from Late Cretaceous rocks in Alberta reveal low predator/prey standing crop ratios from 3 to 5% (Bakker 1972, 1974, 1975a, 1975b). These low values have been interpreted by Bakker as proof of endothermy in dinosaurs. Of course, that conclusion is dependent on the assumption that the predator populations were resource-limited, and that the prey populations were limited by predation, rather than by resources. Even if these two assumptions held true, which cannot be established, the predator/prey ratios of fossil communities are subject to substantial indeterminate errors (Charig 1976). As every geologist and paleontologist knows, all fossil collections are the residual end-products of several kinds of destructive filtering processes, including destruction before burial, non-random preservation, differential representation of habitats, and discovery and collecting biases. There is no way to correct, with any degree of confidence, for the effects of these errors on the collected samples. It is impossible to know what is missing.

Bakker (1972, 1975a) is aware of some of these sources of error and has attempted to correct for collecting bias. Thulborn (1973), Farlow (1976) and Tracy (1976) have pointed out certain weaknesses in Bakker's assumptions about ingestion rates, and Halstead (1976) notes that the low predator/prey ratios of dinosaurs might be the direct result of their large size. However, it is well-documented that the food requirements per unit weight decrease with increasing body size, which would result in a higher predator/prey ratio, rather than the low ratio obtained by Bakker.

It is clear that the unknowns, and the unverifiable correction factors, render this approach to dinosaur trophic dynamics imprecise at the very best. The low predator/prey ratios of the Oldman Formation and other formations may reflect the original compositions of these dinosaur communities, and these ratios may be the result of high metabolic regimes and endothermy - in the predators. It must be emphasized that these ratios provide no information at all about the physiology of any of the prey animals - the other 95% of the Oldman dinosaur fauna. This point, more than any other, underscores the impropriety of viewing the dinosaurs as though they were all characterized by identical physiological parameters. As noted above, they were extremely diverse anatomically, and they were possibly just as diverse in their physiological regimes. The vast majority of dinosaurs were herbivores and the predator/prey ratios are of no value in assessing the likelihood that any of them were endothermic.

Bone Histology

A completely different line of evidence that may be related to dinosaurian physiology is found in the microscopic structure of bone. Compact bone in many living ectotherms contains few primary vascular channels - the sites of blood vessels. Such bone is termed primary vascular bone. In contrast, the compact bone of many mammals and birds commonly contains large numbers of vascular channels that are secondary (reconstructed) in origin. These are termed Haversian canals. The occurrence of such densely vascularized secondary Haversian bone in mammals and birds has been attributed to their high metabolic, endothermic physiologies, with their consequent demands for calcium and phosphorus flux from bone mineral reservoirs (Enlow and Brown 1957; Enlow 1962; Bakker 1972; Ricqlès 1974, 1976).

Dinosaurian bone has been shown to exhibit very similar densely vascularized secondary Haversian construction (Enlow and Brown 1957, 1958; Currey 1962). This was interpreted by Currey as evidence of possible physiological specialization ("homeothermy") in dinosaurs. Others (Ricqlès 1972, 1974, 1976; Bakker 1972, 1974, 1975a) see this condition as strong evidence of endothermy in dinosaurs. That interpretation may be correct, but the evidence is not conclusive. Enlow and Brown, Ricqlès, Currey, and most recently Bouvier (1977) have pointed out that the presence or absence of secondary Haversian bone is not consistent among living endotherms and ectotherms. Secondary Haversian bone is present in some ectotherms (turtles and crocodilians), but absent in many small endotherms (both mammals and birds). Since the

correlation between endothermy and secondary Haversian bone is not absolute, we must conclude that rather than being an index of endothermy, Haversian bone must be related to some other factor, such as growth rates, body size, or increased mechanical strength (Ricqlès 1974, 1976; Halstead 1976; Bouvier 1977).

Dinosaur Zoogeography

Occasionally, the geographic distribution of dinosaur specimens is mentioned as evidence that they were probably not ectothermic (Bakker 1975a). The reasoning here is that their distribution apparently extended to much higher latitudes than we might expect of cold-blooded (or heliothermic) animals. Emphasis has been given to those discovery sites that are now located at high latitudes, such as the Early Cretaceous dinosaur foot print locality in Spitzbergen (Lapparent 1962; Heintz 1963) and that where dinosaur bones were discovered in northern Yukon Territory, Canada (Rouse and Srivastava 1972; Russell 1973). The latter site is practically on the Arctic Circle and Spitzbergen is within a dozen degrees of the North Pole - environs now totally hostile to terrestrial ectotherms.

Geophysical and tectonic evidence (Cox, Doell and Dalrymple 1963, 1964; Vine and Matthews 1963; Vine 1966; Isacks, Oliver and Sykes 1968) has firmly established that the continents are not fixed but have drifted over the earth's surface throughout geologic time (Dietz 1961; Hess 1962), in consequence of relative movements by sea-floor spreading and subduction of rigid crustal plates. In many cases, past positions of continent-bearing plates can be reconstructed from paleomagnetic, tectonic and paleontologic data; in most instances the land masses occupied very different latitudes in past times. Precise reconstruction of the Cretaceous geography of the tectonically complex Arctic Ocean - North Atlantic Ocean area is uncertain, but it appears that Spitzbergen was then situated further from the North Pole than it is today. The Yukon site, however, now at 66° north latitude, was much closer to the Late Cretaceous North Pole - perhaps as far as 80° north paleolatitude. At present, this represents the most extreme northerly occurrence (in terms of paleolatitude) of dinosaur remains yet found. I will come back to these two sites later. The above paleogeographic interpretations are based on the reconstructions by Briden *et al* (1974) and Smith *et al* (1973).

It is clear that the present latitudinal distribution of dinosaur sites does not record the actual paleolatitudinal spread of dinosaurs during the Mesozoic. In fact, as

Figures 8 and 9 show, almost all known dinosaur localities were originally situated within 40 to 50 degrees of the paleo-equator, corresponding to today's tropical to low temperate zones - the region now inhabited by the vast majority of terrestrial ectotherms. Addition of the paleo-positions of the Spitzbergen and Yukon localities increases the dinosaurian paleolatitudinal spread by approximately 25°, from about 110° to perhaps 135°. That compares with a composite latitudinal spread of 120° for modern reptiles. This might be considered important evidence for endothermy in dinosaurs (Ostrom 1970) except for the fact that Mesozoic climates were significantly warmer and more equable than those of today (Dorf 1970; Axelrod and Bailey 1968), as determined from paleobotanical evidence.

Oxygen isotope determinations (Urey *et al* 1951; Epstein *et al* 1951) provide other indications that paleotemperatures of shallow marine water, as determined from the calcareous shells of various organisms, were approximately 15°C warmer than at present (Lowenstam and Epstein 1959), apparently at nearly all middle and high latitudes. It was estimated that the Cretaceous north polar water was no colder than 10° to 15°C. Work by Spaeth *et al* (1971) showed that oxygen isotope paleotemperature determinations based on belemnites are not as reliable as had been supposed, but other studies of oxygen and carbon isotopes in the tests of both benthonic and planktonic foraminifera (Emiliani 1954; Douglas and Savin 1973; Shackleton and Kennett 1975) have confirmed the earlier conclusions. Early Cenozoic and Late Mesozoic sea water temperatures, both at the surface and on the bottom, were some 10 to 15°C warmer than at present.

Further confirmation of this general picture is found in fossil plant remains from the Yukon dinosaur site and from other Late Cretaceous strata much closer to the Cretaceous North Pole (Russell 1973). These data, which indicate climatic conditions like those of today at latitudes 40° to 50°, clearly belie any suggestion that cold polar climatic conditions existed at high latitudes in Mesozoic times. Whatever the cause, greater solar radiation, increased heat absorption by more extensive oceanic areas, greenhouse effect, or more efficient heat distribution by ocean currents to ice-free polar regions, it is evident that high latitude climates were much warmer and less seasonal than now, especially during the Jurassic and the Cretaceous.

As the latitude-temperature graph (Figure 10) shows, given a mean annual temperature 15°C higher than that of today, Mesozoic ectotherms should have been dispersed over 160° of latitudinal spread, as compared with 120° for today's

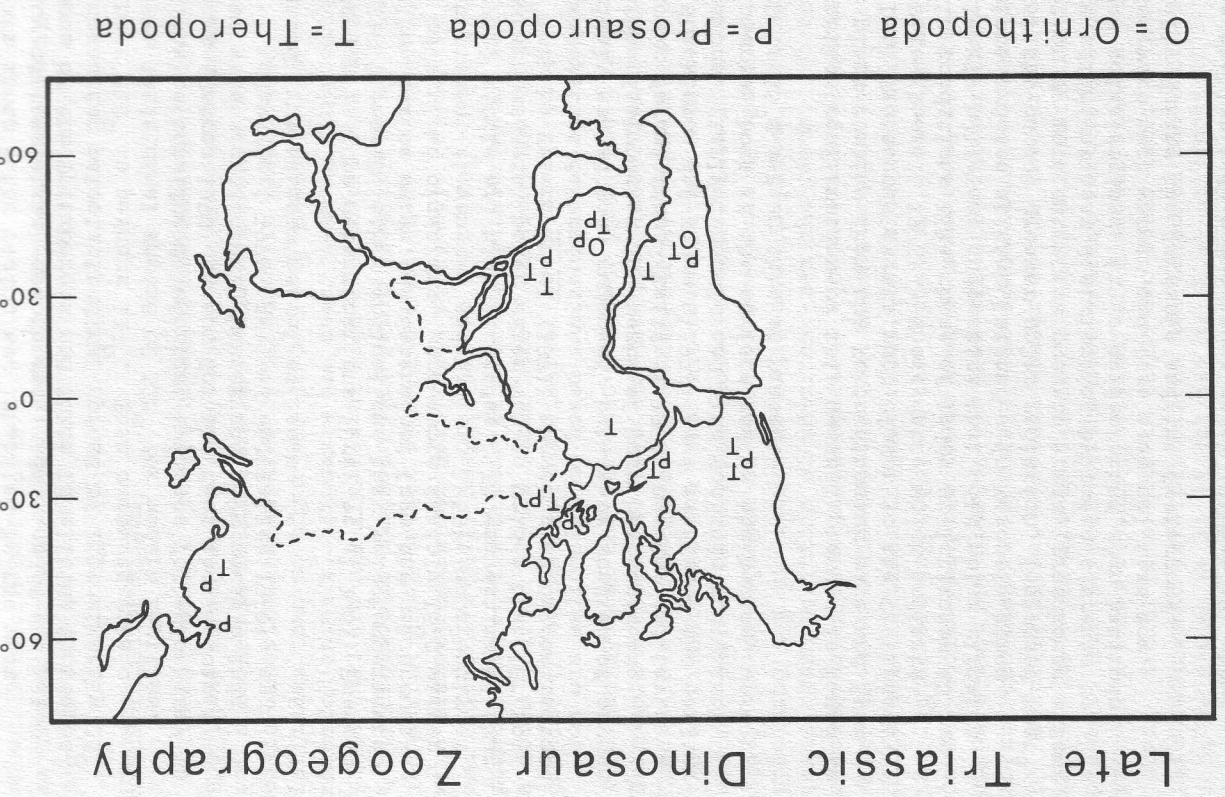
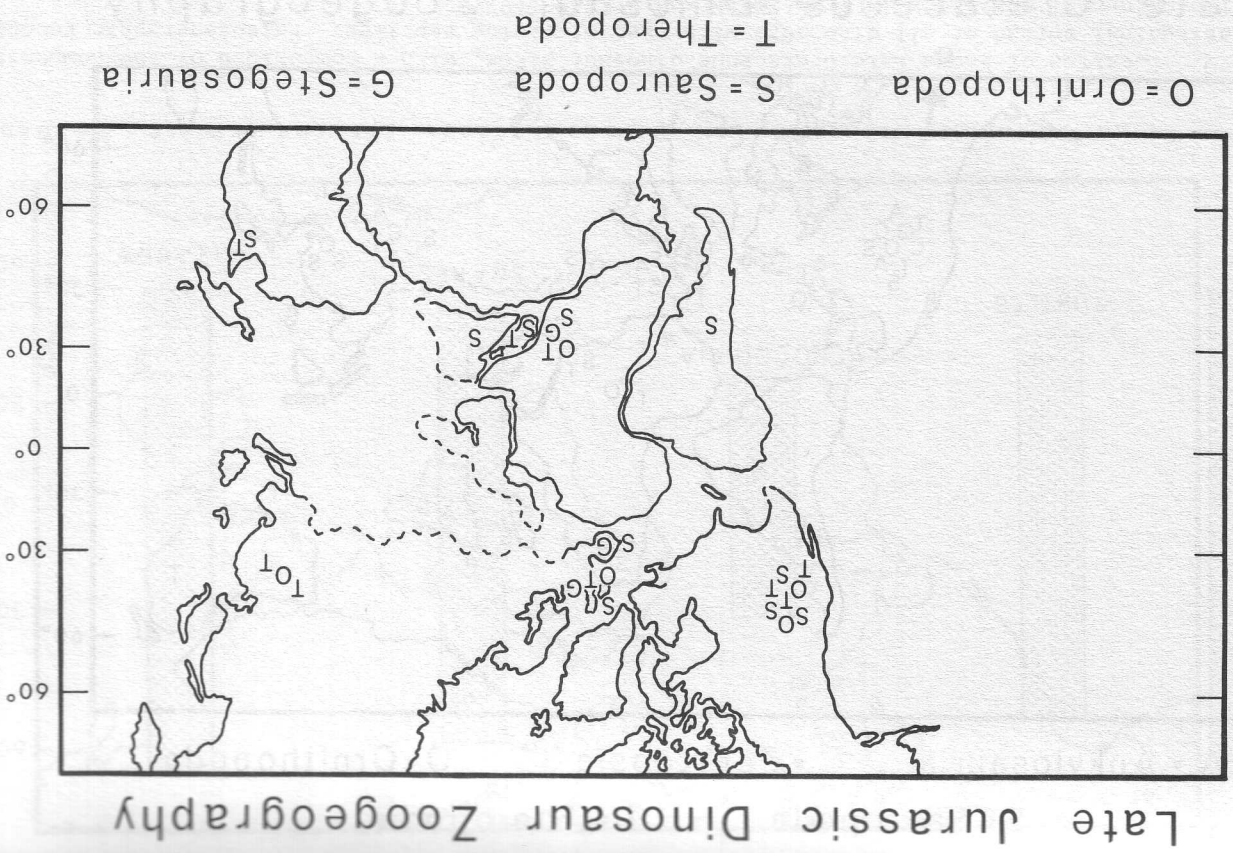
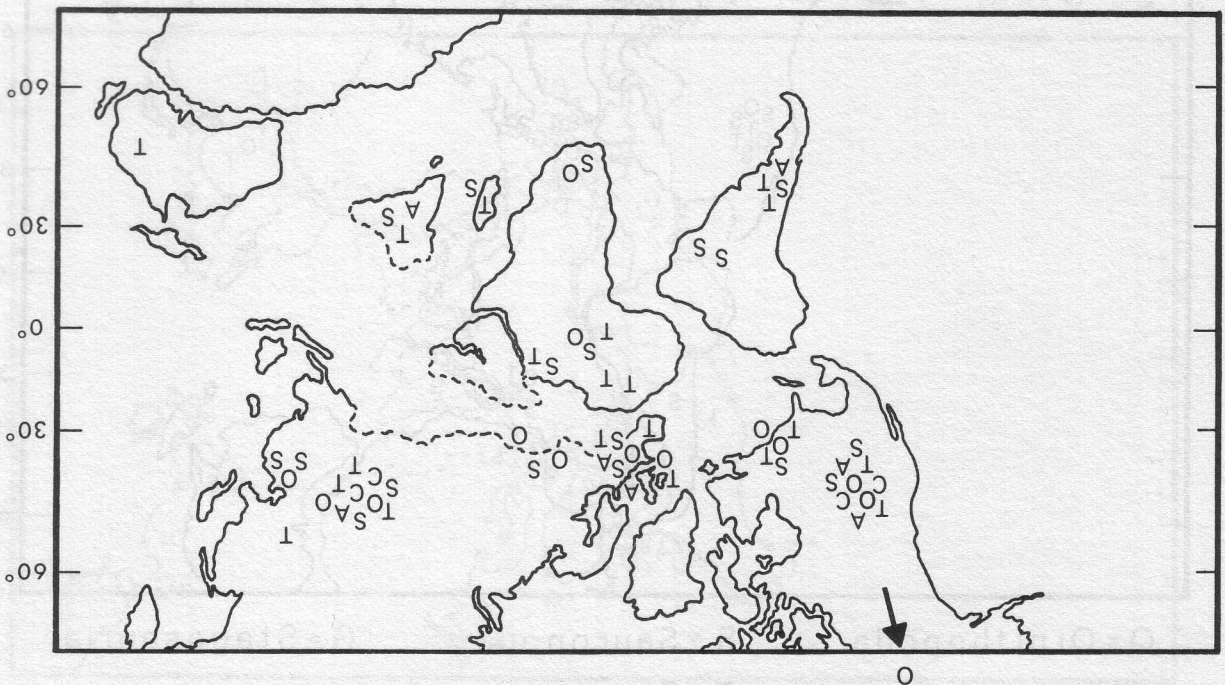


Figure 8. Location of known Late Triassic (above) and Late Jurassic (below) dinosaur sites, to show paleolatitudinal spread. Paleogeographic reconstruction of continental positions is from Smith and Breden (1977).



Late Cretaceous Dinosaur Zoogeography



Latitudinal Ranges of Dinosaurs and Living Reptiles

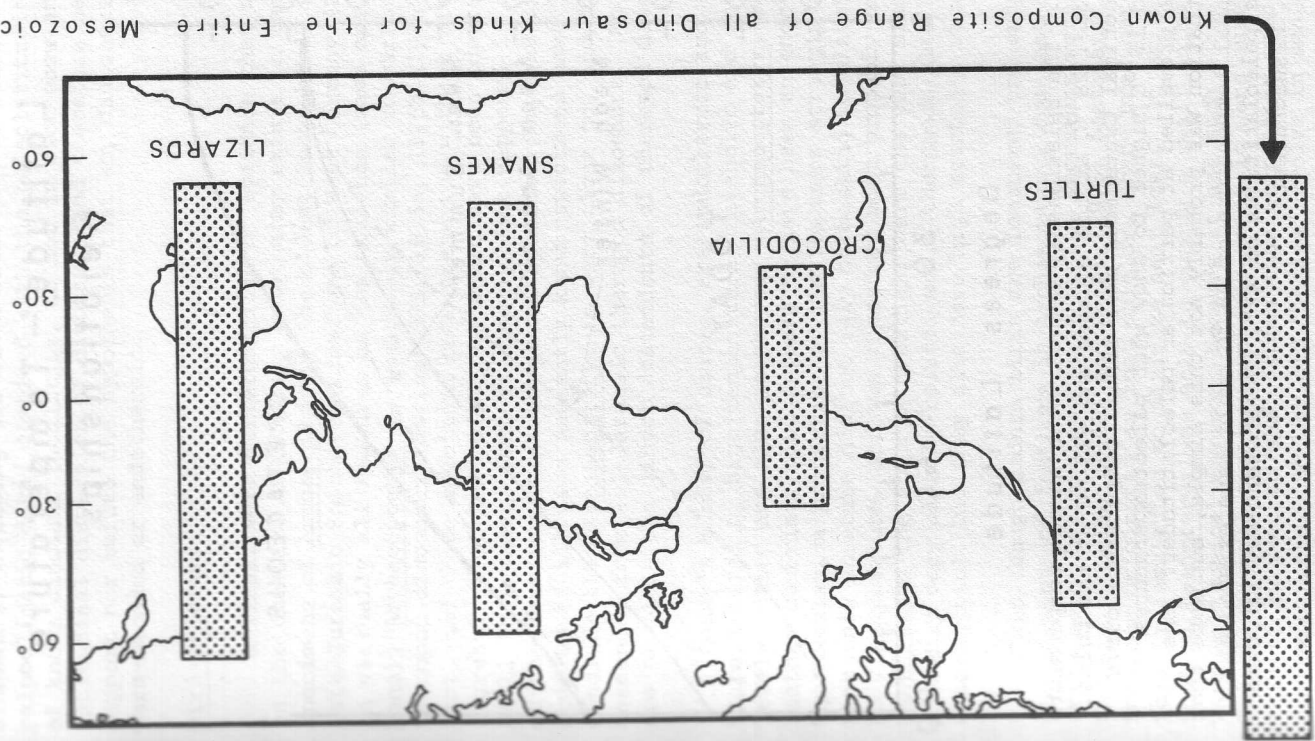


Figure 9. Location of known Late Cretaceous dinosaur sites, with a comparison of the composite paleolatitudinal spread of all dinosaurs with that of living reptiles. Paleogeographic reconstruction of continental positions is from Smith and Briden (1977).

Latitude - Temperature Relationships

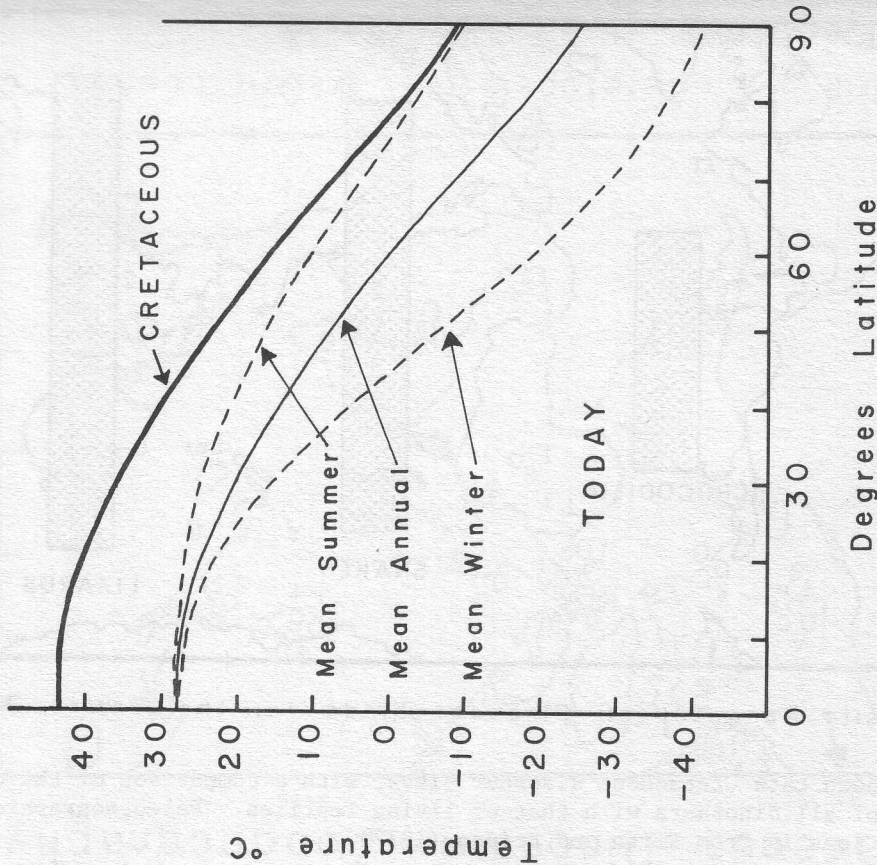


Figure 10. The relationship between mean annual temperature and latitude: 28 °C at the equator and -25 °C at the poles. The hypothetical Cretaceous mean annual temperature curve is plotted 15 °C higher to show what paleotemperatures might have prevailed at particular paleolatitudes. The actual situation was probably not this simple, but note that a mean annual temperature of 28 °C could have existed at Cretaceous paleolatitudes of 42°, the present-day latitude of Boston, Massachusetts.

reptiles. That exceeds the known paleolatitudinal spread of dinosaurs, including the Yukon site. My conclusion is that paleoclimatic data, combined with the paleolatitudinal spread of known dinosaur localities, do not in fact show an unusual latitudinal dispersion of dinosaurs and therefore neither support nor refute the hypothesis that any dinosaurs were warm-blooded or endothermic.

Bird Origins

A final, very different line of evidence that may bear on the question of dinosaur endothermy exists in the rare specimens of *Archaeopteryx*, the oldest known bird, from the Late Jurassic Solnhofen Limestone of West Germany (Figure 11). In virtually all features of the skeleton (save one, a wish-bone), *Archaeopteryx* is remarkably similar to various small theropod dinosaurs (Ostrom 1973, 1975a, 1975b, 1976). In fact, had these specimens been preserved without clear impressions of feathers, they would have been identified as small theropods. That is exactly what happened in the case of the most recently recognized specimen (Mayr 1973). My studies of all five presently known specimens have led me to conclude that *Archaeopteryx* is very close to, and directly descended from Mid-Jurassic theropod dinosaurs. Modern birds are probably the direct descendants of theropod dinosaurs.

Today's birds, of course, are endothermic and are characterized by high temperature, metabolic and activity levels. They are also feathered. *Archaeopteryx*, with its feather covering, also appears to have been an endotherm. The insulative properties of its feathers strongly suggest that this creature did not rely on basking to elevate its body temperature, and was therefore most probably endothermic. That raises the obvious question: were the very similar and probably very closely-related small theropods also endothermic? Did they also have high metabolic rates?

Even though modern birds are feathered and endothermic, the presence of feathers in *Archaeopteryx* does not necessarily mean that *Archaeopteryx* or its ancestors were endothermic. Cowles (1946) and Regal (1975) postulated that the feathers originated as heat shields, shade producers, rather than as insulation to minimize heat loss. It could well be that *Archaeopteryx* was able to occupy a small animal niche in warm or tropical environs because it had such a heat shield. But then, small creatures of the Mesozoic were surely better able to retreat to shady spots than were their ponderous contemporaries. So why did "shades" evolve in small animals rather than in giants?

Once again, the evidence is not conclusive, but I see it as being strongly suggestive that Archaeopteryx was endothermic and that at least some of the theropods approached the birds in their physiology and thermoregulation.

Reflections

In pondering the pros and cons of endothermy among the dinosaurs, it is important to keep several other questions in mind. Why adopt endothermy at all? Despite the fact that endothermy has evolved independently at least twice (mammals and birds), the adaptive value of thermoregulation at a body temperature significantly higher than that of the environment is not clear, because it is achieved at great expense. The usual explanation offered, that it permits higher levels of sustained activity, is not necessarily correct. Heinrich (1977) and many others have noted that numerous poikilotherms are capable of sustained high levels of activity.

Most air-breathing animals, including both ectotherms and endotherms, generate enough heat to reach body temperatures that may exceed ambient temperatures by several degrees centigrade when they are active. Their enzyme systems have evolved to tolerate and even capitalize upon these elevated temperatures during such critical activities; this almost certainly is the key factor behind the evolution of the high optimum body temperatures of all endotherms. But, ectotherms return to ambient temperature levels during periods of inactivity, whereas nearly all endotherms cool only to normal body temperatures that may still be well above ambient levels. What is the selective advantage of maintaining an expensive high body temperature during periods of relative inactivity? The advantages of heterothermy, characteristic of a variety of mammals and birds, are obvious, but the advantages of endothermy as maintained by most mammals and birds are not. The most frequently cited explanation is that it permits the animal to be instantly ready for activity at all times. However, this does not answer the related question: does that return fully compensate for the added costs? Under what circumstances is continuous alertness so essential? Were the huge dinosaurs able to pay this bill?

A final question to keep in mind is: how valid are the analogies we have used? The single most important fact that applies to the interpretation of all fossil evidence is that direct observation of the habits and activities of the organisms under study is not possible. We are forced to reconstruct the possible natures of extinct organisms by means of analogy with living species. Analogy

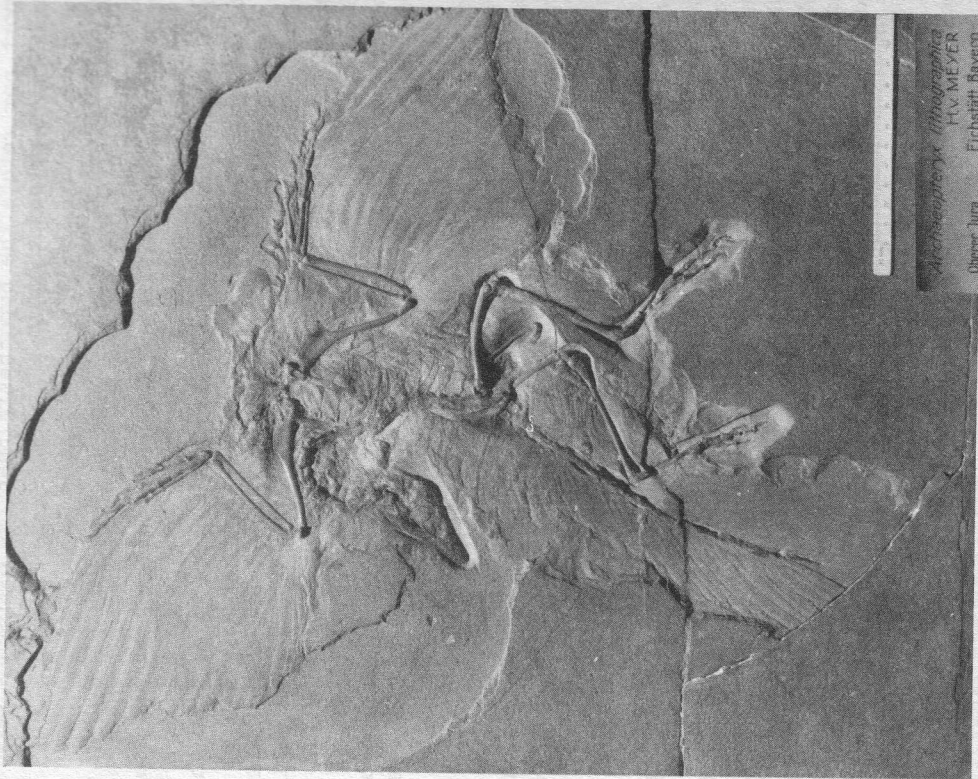


Figure 11. The Berlin specimen of Archaeopteryx. By author.

means: similarity without identity - resemblance only. Nevertheless, analogy is the most important tool we have, and carefully applied, it permits us to make general inferences about the probable nature of extinct organisms. It goes without saying, though, that any inferences drawn are only as valid as the analogue chosen. With these matters in mind, what can we conclude about the nature of dinosaurian physiology and thermoregulation?

Conclusions

All of the several lines of evidence reviewed above are susceptible to alternative explanations. Of course, these alternatives do not disprove the hypothesis of dinosaur endothermy. Erect posture and gait may well be required to support large size, rather than a locomotory advance made possible by a tachymetabolic regime. That some small forms were also erect, or that other large and presumed ectotherms (therapsids) were sprawlers, does not invalidate this alternative explanation. Similarly, the fact that some mammals "sprawl" does not eliminate the possibility that sprawling is imposed by ectothermy. Upright posture and gait may still be products of endothermy.

The inferred high activity levels of some dinosaurs seem to provide particularly attractive evidence in favor of dinosaurian endothermy, but high and sustained activity levels do not require endothermy. The relatively small brain size of most dinosaurs is seen as evidence against mammal-like or bird-like levels of activity (Feduccia 1973; Hopson 1977), but larger brains in theropods and ornithopods (Russell 1969, 1972; Hopson 1977) might support other skeletal evidence of high activity in these forms. Again, endothermy may be involved, but the evidence does not prove it.

The specialized feeding adaptations of some dinosaurs (ornithopods, ceratopsians and perhaps sauropods) may have been responses to the great absolute volumes of food required by animals of very large size, but this argument is weakened by the absence of similar feeding specializations in other comparably-sized dinosaurs (stegosaurs, ankylosaurs and prosauropods). Could the former have been endothermic and the latter ectothermic? The presumed huge volumes of food that would be required by the largest varieties is strong evidence against endothermy. Predator/prey ratios hold significance only for the carnivores - and the data available may not provide reliable evidence even for them.

Until the functional significance of secondary Haversian bone is understood in modern vertebrates, its presence in most dinosaurs cannot be evaluated. The fact that it apparently occurs most commonly in large animals (reptiles as well as mammals and birds) suggests that secondary Haversian bone is correlated with large size, rather than being directly related to warm-bloodedness or tachymetabolism.

Considering the 10° to 15°C warmer and less seasonal climates of the later Mesozoic, and the redistribution of dinosaur carcasses by plate movements since their heyday, the present zoogeographic distribution of dinosaurs remains does not weigh on either side of this question.

The evolutionary relationship between Archaeopteryx and the theropods seems reasonably secure, but we cannot be certain of the physiological state of Archaeopteryx. In modern birds, feathers serve as insulation to minimize heat loss in endotherms. But, feathers in Archaeopteryx and its ancestors might have functioned to keep heat out in ectothermic animals. The evidence is ambiguous and susceptible to alternative explanations.

The most promising evidence for endothermy may lie in the combination of erect posture and large heart-brain vertical distances. These indicate the almost certain existence of a double-pump, four-chambered heart, with fully separated systemic and pulmonary circulation in dinosaurs. This seems to be a primary requisite of a tachymetabolic thermoregulating animal, explicable only in such a setting. Such circulation obviously is not required in brady-metabolic or ectothermic animals. No other explanation for its development in dinosaurs (and elsewhere) comes to mind.

In summary, notice that only three of the above lines of evidence (posture and gait, dental specializations, and bone histology) are factual, based on direct observation; three others are inferences, interpretations only (high blood pressure and a double-pump heart, high activity-levels, and the theropod origin of birds); and two are ambiguous or of unverified accuracy (predator/prey ratios and geographic distribution). The significance (relative to endothermy) of the first three is uncertain; interpretations of the remainder are untestable and therefore of doubtful value.

These several lines of evidence are extremely interesting and highly suggestive, but they are far from conclusive, even when taken collectively. Endothermy in any kind of dinosaur has not yet been proved. But, neither has it been

disproved. Personally, I believe that some dinosaurs - especially the theropods, to which all lines of evidence seem to apply, were probably endothermic. By this, I mean tachymetabolic. The vast majority, however, I suspect were ectothermic "homeotherms", as first suggested by Colbert, Cowles and Bogert (1946, 1947). That is, they were "warm-blooded" by virtue of their ectothermic response to a warm and equable environment, and "homeothermic" by virtue of the thermal inertia imposed by their uncommonly large body sizes (Spotila et al 1973; McNab and Auffenberg 1976). That conclusion is supported by the intriguing hypothesis (Farlow, Thompson and Rosner 1976) that the staggered and highly vascularized bony plates along the back of Stegosaurus were "forced convection heat-loss fins" designed for shedding excess heat.

Predator/Prey Biomass Ratios, Community Food Webs and Dinosaur Physiology

James O. Farlow

Abstract

Recent studies have suggested that reconstructed predator/prey biomass ratios can be used to interpret the physiology of fossil vertebrates. On the basis of such arguments, dinosaurs have been interpreted as endotherms. However, several complicating factors suggest that this conclusion may be premature.

It is difficult to satisfactorily characterize the predator/prey ratios of ectothermic as opposed to endothermic predator/prey systems, even for living animals. In particular, we do not know how low this ratio can get for large ectothermic predators and their prey. Furthermore, it is possible that there is some convergence of ectothermic and endothermic metabolic rates at large sizes. If so, predator/prey ratios might not provide sufficient resolution to distinguish ectotherms from endotherms for dinosaur-sized animals, particularly for fossil faunas, where biases of preservation and collecting, and errors in weight estimates, might distort predator/prey ratios from their true values.

Differences in community structure and function between dinosaurs (or other fossil reptiles) and mammals, or between dinosaurs and other groups of fossil reptiles (sphenacodonts, therapsids, and thecodonts), could also complicate interpretation of predator/prey biomass ratios. If large carnivorous dinosaurs preyed upon a relatively narrower range of large-vertebrate prey species than mammalian or other reptilian carnivores, or if competition from other predators significantly reduced the amount of large-vertebrate prey available to these large theropods, a large carnivorous dinosaur / large-vertebrate biomass ratio as reconstructed for a fossil community might be