# THE MANY MYTHS, SOME OLD, SOME NEW, OF DINOSAUROLOGY

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The study of dinosaurs has always been hindered by a body of unsubstantiated or false beliefs about their biology, and about the biology of other animals that can be applied to dinosaurs. Some of these myths, such as the supposedly horizontal femora of birds, or the importance of heat radiators, are relatively minor. Other myths have greatly distorted our understanding of dinosaur biology. These myths include the persistent selective advantage of energy efficient bradymetabolic physiologies, the impossibility of high speed in large animals, the danger of overheating of large animals, the supposed correlation between brain size and energetics, the great difficulty of flying, especially in large forms, and the inherent vulnerability of the big dinosaurs to extinction.

KEY WORDS: Dinosaurs, pterosaurs, archosaurs, anatomy, locomotion, brains, physiology, extinction, myths.

#### INTRODUCTION

As soon as dinosaurs were discovered, myths started gathering around them and their archosaur relatives. Among the earliest was the belief that they were overgrown lizards, a myth that continues in modified form today in their classification as reptiles. Some old myths have recently been discredited, such as the theropods' fear of entering the water, and the sauropods' and hadrosaurs' water-loving habits. The polyphyletic split of the Dinosauria into Saurischia and Ornithischia has been displaced by widespread agreement upon the group's monophyly. The great myth that only big brained mammals and birds can exhibit complex social and parental behaviour has been demolished by a new appreciation of the many parallel dinosaur trackways, the finding of dinosaurian nesting colonies, and so on-although the implications of these facts have yet to be fully appreciated. Yet many myths remain, and new ones are being generated. Many of these beliefs are directly contrary to the knowledge gathered by biologists on living animals. Others have not been substantiated by detailed studies. Most of them share the characteristic of being repeated ad nauseum, without adequate support for their reality. Others look like they are about to join this unhappy mythology. It is beyond the scope of this paper to thoroughly examine and disprove each of the myths found in the professional literature. Instead, the intent is to point out and challenge some of these beliefs, in the hope that the below comments will give pause to those who might repeat them, and inspire a more rigorous attitude towards dinosaurology. After all, the many popular misconceptions about dinosaurs can be corrected by better education, but this is hard to do when myths are perpetuated by the professionals who study the beasts.

## DINOSAURS DRAGGED THEIR TAILS ON THE GROUND AND OTHER SUCH MATTERS

Myth: I mention this old belief because many dinosaur skeletons continue to be mounted with drooping tails and other anatomical errors.

Reality: It is now widely agreed that the world's many trackways prove that all types of dinosaurs usually carried their tails well clear of the ground, in accord with the upwards arch seen in the base of many, but not all, dinosaurs. With rare exceptions, there is no reason except inertia for restoring tail dragging dinosaurs.

Other anatomical points that have been recognized, either recently or well in the past, include the posterior sweep of the anterior dorsal ribs, the placement of the coracoids close to the body midline, and the digitigrade foot posture true of all dinosaurs (Paul, 1987a; Carpenter, 1989). Yet many dinosaurs are restored with vertical chest ribs, overly broad shoulder girdles, and sauropod hindfeet and even forefeet are often mounted as being plantigrade (the astragalus of sauropods has rotated posteriorly from the prosauropod condition, rather than anteriorly as argued by Cooper, 1984).

# MODERATELY SHORT ARMS, SUPPLE HANDS AND HINDPRINT ONLY TRACKWAYS SHOW THAT MANY DINOSAURS WERE BIPEDAL, OR SLOW

Myth: Ornithopod trackways made up only of hindprints are usually taken as proof of bipedalism. The arms of large ornithopods, and the supple hands of heterodontosaurs, have been viewed as unsuitable for a fast quadrupedal gait. Because the arms of large ornithopods and ceratopsids supposedly lagged behind the longer legs, they would have caused the subjects to either nose dive, or to spin around at high speeds (Thulborn, 1989; and in part Bakker, 1986).

Reality: Quadrupedal elephants usually leave only their hindprints behind, the foreprints are wiped out by the forefeet. The arms of large ornithopods, especially hadrosaurs, were ungulate-like and suitable for progression at all speeds, and it is possible that many seemingly bipedal trackways were made by individuals on all fours (Figure 1). Some terrestrial primates, such as baboons and patas monkeys, trot and gallop on supple fingered hands, so it is possible that long fingered heterodontosaurs did the same. As long as all the limbs are long enough to easily reach the ground when the body is horizontal, then the stride lengths of limbs of differing length are equalized by increasing the recovery/step phase ratio of the shorter limb—this occurs in quadrupedally running long armed giraffe, gnu and hyenas, and short armed dik-diks, cats, crocs and lizards. In addition, scapular rotation probably increased the functional length of dinosaur forelimbs (Paul, 1987a).

## THE FORELIMBS OF QUADRUPEDAL DINOSAURS WERE NOT FULLY ERECT

Myth: New skeletal mounts continue to be equipped with wide space forelimbs, and a few workers continue to favor such a limb posture, especially in ceratopsids and ankylosaurs (Coombs, 1978b; Johnson, 1990; Lehman, 1989).

Reality: Almost all quadrupedal dinosaur trackways, including those of ceratopsids and ankylosaurs, show the forefeet following a narrow gauge that is either the same or a little broader than that of the hindlimbs. The orientation of quadrupedal handprints shows that the elbow was tucked in. The design and orientation of the shoulder glenoids of quadrupedal dinosaurs is very different from those of reptiles with sprawling limbs, and clearly favors a more vertical action. Stress analyses of dinosaur humeri and detailed joint articulation diagrams indicate a vertical arm

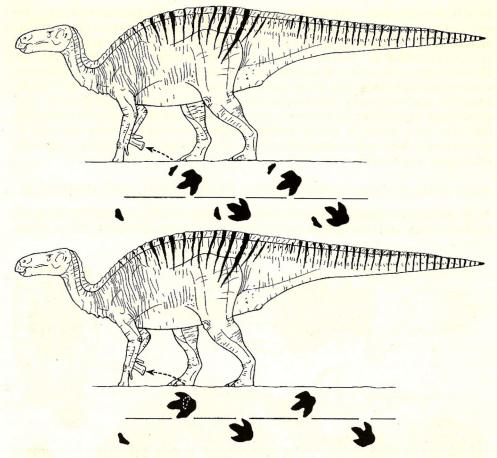


Figure 1 How quadrupedal dinosaurs could leave only their hindprints behind. At top a generalized iguanodont walks slowly and waddles so the hindfeet fall behind and inside the foreprints (based on preserved trackways, Currie, 1983; Lockley and Gillette, 1989). In the bottom figure the subject increases step length a little while decreasing waddling so that the hindfeet step onto and obliterate the foreprints.

posture. This has led to a general consensus that dinosaur forelimb action was usually fully erect (Carpenter, 1982; Currie, 1983; Bakker, 1986, 1987; Paul, 1987a; Lockley and Gillette, 1989; Adams, 1990). A partial exception is found in ornithopods, whose more laterally open shoulder glenoids, plus some trackways, are compatible with their occasionally having adopted a less erect arm posture when moving slowly (alternatively, they were waddling about their hips when making the wide gauged forefoot trackways). For further details on ceratopsids, see Figure 2.

## THE FEMORA AND HINDLIMBS OF FULLY ERECT ANIMALS WORK IN A VERTICAL FORE AND AFT PLANE

Myth: Most fore-and-aft view figures of mammal and bird legs show the femora in a simple vertical posture.

Reality: This is correct only for cats and a few other animals. It is common for knees

to be bowed outwards, with the femur substantially everted (this can be seen in the rear views of ungulates and ostriches in Muybridge, 1887). Femoral eversion may increase as the femur is protracted to clear the belly, or it may be constant. Typical eversions are 10 to 25°. It is as high as 45° in swans, which must run fast to take off. However, the trackway is still narrow, so the gait is effectively erect. Elbows also are often bowed outwards, and wrists and knees are bowed a little inwards, in birds, ungulates and carnivores. Most dinosaurs follow this pattern (see Figure 2). Elephant limbs slope down and inwards, and sauropods and stegosaurs are rather like this. The false belief in strictly vertical mammal and bird femora can lead to misinterpretations and misunderstandings of archosaur limb action, especially pterosaurs (see below).

#### BIRD FEMORA ARE ALWAYS HELD HORIZONTAL AND IMMOBILE

Myth: Birds have unusually short femora, and it is generally assumed that these are held horizontal and relatively immobile during locomotion (Cracraft, 1971; Galton,

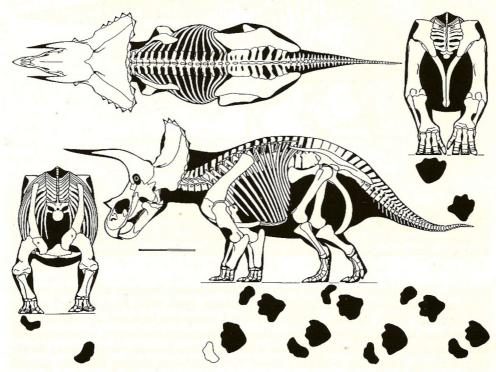


Figure 2 A multiview skeletal restoration based primarily on large USNM 4842, which is either *Triceratops* or *Torosaurus* (here fitted with the scaled up head and presacrals of *T. horridus* USNM 4928). It is shown walking out a large Laramie Formation trackway (from Lockley and Gillette, 1989; calculated speed 2.4 km/h) that probably belongs to one of the two taxa. Especially note that the right and left manus prints, which are somewhat lateral to the pes prints, are separated by only one and a half times their own breadth, and that they are directly beneath the ceratopsid's shoulder joints. The partial outwards turning of the manus prints shows that the elbows were not strongly bowed outwards (although they, and the knees also, are somewhat bowed outwards). These points confirm that big ceratopsid forelimbs were normally fully erect. The gauge of the forefeet may have decreased as speed increased and the substrate became firmer, while the arms may have become less erect during intraspecific head–head contests. USNM 4842 and trackway are to same scale, bar equals 1 m.

1970; Coombs, 1978a; Bakker, 1980; Gatesy, 1988; Padian and Olsen, 1988; Campbell and Marcus, 1990). This has led to reconstructions of small theropod and ornithischian dinosaurs with horizontal femora (Padian and Olsen, 1988; Campbell and Marcus, 1990).

Reality: The above is true when birds walk and run slowly, but still and motion photos show that avian femoral action is much more extensive at the highest speeds (Paul, 1987a, 1988a)—animals do not waste limb segments when moving fast! Avian femoral mobility is important because most ornithischians, including some of the largest examples, have hip joints very similar to those of birds, with a large, true antitrochanter on the posterior rim of the acetabulem articulating with the outer femoral head. If birds really did have fixed, horizontal femora, this would indicate that ornithischians did too. This would be unsatisfactory for dinosaurs because the resulting limb action would be very awkward and limited, due to their having shorter distal leg segments than birds. It would also cause the long tailed dinosaurs to be tail heavy. Instead, as in birds, the antitrochanter and femoral head remain in proper articulation as the long ornithischian femur swings in a long arc that ends at about vertical. Manipulation of uncrushed theropod hip joints show that femoral action was extensive in that group also.

## LIMB RATIOS AND FOOT MASSES ARE GOOD INDICATORS OF DINOSAUR SPEED

Myth: There is a close correlation between the elongation of the distal limb segments and speed, and this can be used as a measure of animal locomotory performance (see Hildebrand and Hurley, 1985; McGowan, 1984, notes that dead mass added to human feet degraded running performance). Dinosaurs tend to have longer proximal limb segments and heavier feet than fast mammals and birds, so they were slower than the latter (as per Coombs, 1978a).

Reality: The relationship between limb ratios, limb gracility and speed is not as close as often believed. Speed has been observed to be constant in ungulates of varying limb ratios (Alexander, 1977). Some canids and hyaenids appear to achieve chase speeds comparable to those of their more gracile limbed ungulate prey (Kruuk, 1972). Even plantigrade, short lower limbed bears have been observed to chase down ungulate prey over modest distances. Limb energy efficiency is similar in animals with gracile and big pawed feet (Taylor et al., 1974). Adding mass to feet may improve performance, as per running shoes. Likewise, distal bones, muscles and connective tissues are power producing and storing masses that can enhance running speed if properly designed. The femur may be a particularly important limb segment in the large tailed dinosaurs because the caudo-femoralis remained an important limb retractor. This would favor a longer femur in dinosaurs than in birds and mammals, whose tail based femoral retractors are very reduced. It is probable that the speed of the gracile ornithomimids and tyrannosaurs was comparable to that of the shorter femured ratites, and that ceratopsids charged at speeds comparable to longer footed rhinos.

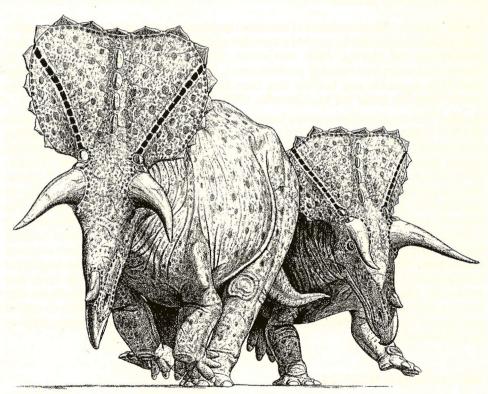
#### **BIG ANIMALS MUST BE SLOW**

Myth: It is not possible for animals the size of elephants and larger to move more rapidly than a fast amble. All large adult dinosaurs were therefore equally slow

(Coombs, 1978a; Halstead and Halstead, 1981; Ostrom, 1987; Padian, 1989; and Thulborn, 1989, who asserts that shire horses are the biggest gallopers).

Reality: This is a very extensive, complex subject. Here it will be pointed out that a number of extinct tetrapods of two to 20 plus tonnes have limbs that are more gracile, more powerfully muscled, and less derived than the highly modified, slow action legs of elephants. These include large theropods, iguanodonts-hadrosaurs, ceratopsids, ankylosaurids, titanotheres, giant extinct rhinos, and the indricotheres. In particular, all of these retain highly mobile ankles and long feet that allow a push off into a long suspended phase. This suggests that these animals were much faster than elephants, being capable of a true run with an airborne phase. In the modern fauna, rhinos are the biggest high speed gallopers.

A number of biomechanic and scaling studies support the possibility that speed can remain high in large animals if they retain the proper body design, and if they properly scale limb and body proportions as size increases (Heglund *et al.*, 1982; McMahon, 1984; Lindstedt *et al.*, 1985; Alexander, 1989). The retention of legs that are both virtually identical in morphology and increasingly strong and powerful in ornithomimids and tyrannosaurs of increasing size is one of the best examples of this phenomenon (Paul, 1988a). In addition, adults are usually as fast or faster than their young, even when their limbs are stouter and distally shorter, so tyrannosaurs should not have lost speed as they grew up from their gracile young. Bald assertions that big animals cannot be fast are therefore obsolete (Figure 3).



**Figure 3** The elephantine bulk of 6 tonne *Triceratops horridus* was not a barrier to galloping because, unlike elephants, it had the strong boned, powerfully muscled, and flexed jointed limbs needed to propel it at high speeds.

Note that increasing the speed of very large animals simply by increasing the stride length during fast walking is not the equivalent of maintaining a true running performance.

#### SMALL DINOSAURS HAD SCALY SKIN UNLESS PROVEN OTHERWISE

Myth: Since scales are known to have been present on large dinosarus, and feathers or fur are not known on smaller dinosaurs such as *Compsognathus*, it is usually argued that the burden of proof is upon those who argue that dinosaurs were insulated (as per Ostrom, 1978).

Reality: I believe this view exposes how an unsubstantiated prejudice in favor of a traditional view can remain in force despite the lack of confirming or denying evidence. The scaly integument of large dinosaurs does not establish that of smaller species, just as elephants are a poor model for the integument of small ungulates. As for smaller species, it is just as true that scales—which should be fossilized more readily than softer insulation—have never been found on any examples, including Compsognathus. The fossil record and objective thought do not, therefore, favor scales over insulation in small dinosaurs. Insulation has evolved in mammals, birds, pterosaurs, a number of insects, and even some plants, so its presence in dinosaurs would not be extraordinary. It is widely agreed that at least some small dinosaurs were endothermic, and hatchling hadrosaurs lived for months in nests exposed to the elements. In both cases either feather or fur insulation would be important thermoregulatory devices. Restorations of scaly small dinosaurs are just as speculative as those showing them adorned with feathers. Eventually fossil remains will solve the problem (Figure 4).

#### TACHYMETABOLISMS BAD, BRADYMETABOLISMS GOOD

Myth: Because bradymetabolic animals are far more energy efficient than those with mammalian-avian metabolic rates, it is widely thought that the former is inherently the superior system to have, especially among big animals which are homeothermic regardless of internal heat production. Only special circumstances, such as big brains, flight, very cold habitats, or an inability to abandon an ancestral endothermic system, justify the retention of high heat production. Since large dinosaurs fit none of this criteria, they should have achieved homeothermy without tachymetabolism (Feduccia, 1973; Baur and Friedl, 1980; Regal and Gans, 1980; Spotila, 1980; McNab, 1983).

Reality: Preide (1985) explains that there has been a strong evolutionary trend that favors higher energetics over energy efficiency, and that tachymetabolic endothermy is the logical outgrowth of this trend. This is because higher energy systems process and utilize information more rapidly than slower acting ones, an important advantage in an energy rich universe (so powerful is this trend that it promises the evolution of a super high energy information processing system via computers and robotics, Barrow and Tipler, 1986; Moravec, 1988). This view is confirmed by the high degree of success enjoyed by mammals, birds, leatherback sea turtles, tuna, and lamnid sharks (all these appear to have metabolic rates elevated above the reptilian level), and which range in size from 2 g to 200 tonnes, and live in places and climates ranging from polar to tropical, from oceans to land. In comparison, big land reptiles have been relatively rare, and have never exceeded much more than one tonne, thereby

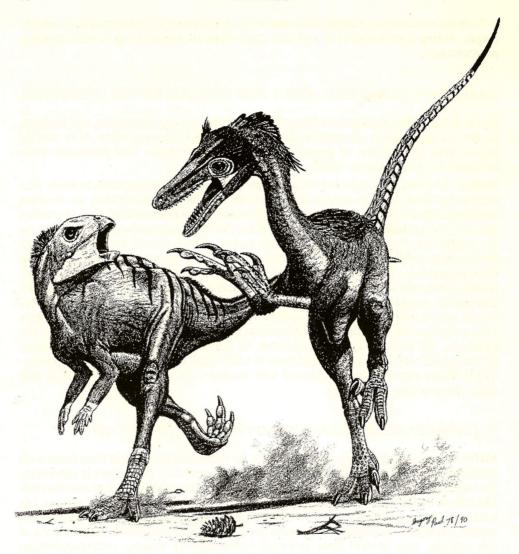


Figure 4 Until either preserved scaly or insulative integuments are found adorning small dinosaurs, restorations such as this portraying *Troodon formosus* chasing *Orodromeus makelai* are just as legitimate as those that show small taxa without a plumage.

demonstrating the apparent inferiority of this system for large land tetrapods even in the tropics.

# TACHYMETABOLIC ENDOTHERMY IS A RADICAL MODEL WHEN APPLIED TO DINOSAURS

Myth: A model that postulates all dinosaurs as tachymetabolic endotherms is more "extreme" and "hardline" (Hotton, 1980; Prothero, 1990) than is a more traditional model that incorporates reptilian energetics.

Reality: In historical terms dinosaur endothermy is a radical concept, but traditional consensus that favored reptilian dinosaur metabolics was never subjected to rigorous scientific scrutiny, so it has limited bearing on the current scientific debate. Models that blend reptilian with avian-mammalian characters are not superior just because they attempt to reach a compromise or a consensus, they may be just as false as other models. Following the basic engineering principle that machines that are built much the same way operate much the same way, it is a straightforward and entirely logical matter to apply to dinosaurs, that were so like birds and mammals, a nonreptilian physiology that is patterned after those of birds and mammals.

# IF YOU BELIEVE DINOSAURS WERE TACHYMETABOLIC ENDOTHERMS, PROVE IT, BUT IT'S OK TO THINK THAT DINOSAURS HAD INSECT-LIKE PHYSIOLOGIES

Myth: The burden of proof lies upon those who wish to show that dinosaurs had avian-mammalian like energetics. It is more prudent to believe that, although dinosaurs had sustained activity levels approaching those of mammals and birds, their standard metabolic rates were closer to those of reptiles.

Reality: While it is known that tachymetabolic endothermy works in large tropical animals similar in design, size and activity levels to dinosaurs, not one example of a living or extinct tropical animal similar in design to dinosaurs, or much over one tonne, that combines a double pump heart with reptilian SMR (as per Regal and Gans, 1980; Reid, 1987) has been positively identified. In addition, Bennett and Ruben (1979) stress that in all vertebrates the SMR is a high percentage of sustained active metabolic rates, so all active vertebrates *must have high SMR's!* Only insects can achieve high active metabolic rates with reptilian level SMR's. It is therefore much more speculative to apply unproven reptile- and insect-like physiologies to dinosaurs than it is to apply vertebrate based avian-mammalian systems of proven performance. The burden of proof, then, lies upon those who wish to argue that the big, continuously active dinosaurs had a physiology that combined features found in reptiles and insects.

# DINOSAUR ANATOMY WAS INTERMEDIATE TO REPTILES AND BIRDS-MAMMALS, SO THEIR PHYSIOLOGY SHOULD HAVE BEEN INTERMEDIATE AS WELL

Myth: Since dinosaurs were intermediate in general anatomical grade to reptiles on the one hand, and to birds and mammals on the other, their energetics should have fallen between the two groups (as per Ricqles, 1980; Reid, 1987).

Reality: Dinosaurs were not intermediate in design. Not only did they match birds and placentals in most of their anatomy (erect, digitigrade limbs, high held heads, high power feeding systems, etc.), but in growth and social patterns as well. There was little of the reptile left in them. The ways in which they remained, or may have remained, reptilian were either not important (brain size, see below), or are not certain (scaly skin in small examples). In all the ways that count, dinosaurs were most similar to birds and mammals, and should be expected to have a broadly similar

physiology. It is the thecodonts that had an intermediate design and should be expected to have had intermediate physiologies.

#### DINOSAUR PHYSIOLOGY DIFFERED FROM GROUP TO GROUP

Myth: Since the Dinosauria represented a diverse group, from little theropods to great sauropods, they should have shown a diverse array of physiologies, as per the Mammalia (Ostrom, 1980; Ricqles, 1980; Spotila, 1980; Reid, 1987; Russell, 1989).

Reality: Non-passerine birds and elephants share the same mass specific metabolic rate despite the differences in their anatomy and ancestry. This is true because they share a basically similar circulatory system and limb design. Within the Mammalia, there is substantial physiological diversity because there is equally substantial anatomical diversity. This is especially true in limb design, lower metabolic rate insectivores and edentates have short, slow action limbs for instance. The Dinosauria was not as diverse as the Mammalia, instead dinosaurs show about as much anatomical diversity as seen in large birds, carnivores, ungulates and proboscideans. This uniformity in basic design suggests that dinosaurian physiology was equally uniform.

## THE BIG SIZE OF DINOSAURS SHOWS THAT THEY DID NOT EVOLVE TACHYMETABOLIC ENDOTHERMY

Myth: The persistent tendency of dinosaur groups to evolve large size indicates that great bulk rather than high internal heat production was the key aspect of their system of thermoregulation. This differs from birds and mammals, which underwent an initial size squeeze that promoted the development of tachymetabolic endothermy (See Crompton *et al.*, 1978; Baur and Friedl, 1980; Hotton, 1980; Spotila, 1980; McNab, 1983; Reid, 1984).

Reality: One reason the above scenario is not convincing is because it depends upon an unproven hypothesis which discounts the evidence that therapsids and the codonts, which did not experience an initial size squeeze, may already have been low order endotherms. It also ignores the great success of large tropical endotherms, compared to the comparatively dismal record of large, known ectotherms. This strongly suggests that tachymetabolisms are inherently advantageous for such animals, in which case it is probable that elevated metabolisms can evolve in large animals.

The hypothesis also ignores the fact that the ornithosuchid thecodonts and protodinosaurs that appear to form the base of the dinosaur radiation were very small. Lagosuchus in particular was only a third as large as Archaeopteryx. This shows that the first dinosaurs did experience a size squeeze compatible with the development of high internal heat production (Carroll, 1988; Paul, 1988a). Since this size squeeze was among diurnal forms, it is compatible with an energy boost to the placental-marsupial level.

The size increase common to many, but not all, dinosaur groups is no more indicative of lowered metabolic rates than is the same pattern observed in many mammal groups.

# THE METABOLIC RATES AND OR THERMOREGULATORY PERFORMANCE OF BIG ANIMALS CONVERGE, RESULTING IN GIGANTOTHERMY

Myth: The metabolic rates of reptiles scale to a higher exponent than the 3/4's value seen in birds and mammals, and large size confers a degree of homeothermy regardless of internal heat production. This means that the physiological performance of all large animals is similar, blurring the distinctions seen between smaller forms, and resulting in a universal "gigantothermy" (term coined by Paladino et al., 1990; also see Hotton, 1980; Ricqles, 1980; Spotila, 1980; Dunham et al., 1989).

Reality: Large reptiles do enjoy much more stable body temperatures than smaller ones, but otherwise the concept of convergent gigantothermy is greatly overstated. The various exponents for the scaling of reptilian metabolic rates range from 0.62 to 0.82, with some near 0.75. This means there is no clear evidence supporting the metabolic convergence. Instead, the metabolic rates, food consumption and biomass densities of large crocodilians, monitors, snakes, and giant tortoises differ by a factor of six to ten or more times from those of mammals of similar size and trophic habits, supporting a continued separation in line with a 3/4's scaling. Leatherback sea turtles do not support a convergence between the metabolics of reptiles and mammals, because according to the data presented in Paladino *et al.* (1990) their metabolic rates may be elevated above those of other reptiles, and match those of some mammals.

The models by Spotila et al. (1973), Spotila (1980), Dunham et al. (1989) and Paladino et al. (1990) differ on whether large, bradymetabolic dinosaurs would have been as seasonally homeothermic as mammals and birds, or would have experienced

widely fluctuating seasonal body temperatures.

Much the same metabolic gradation seen in reptiles, insectivores, marsupials, and placentals of 10 g to 1 kg can be seen in big animals as well, showing that there is no such thing as gigantothermy. Giant tortoises and pareisaurs with SMR's of 4–8 kcal/kg 0.75/day have short sprawling or semi-erect limbs, relatively simple food gathering apparatus, and low held heads. Giant edentates had dental batteries and double pump hearts that allowed them to carry their heads high, and limbs were erect, but the heavy, awkward legs and feet show that foraging ranges were limited, and mass specific SMR's were probably only 20–40 kcal. Big marsupials either had heavy, awkward footed limbs that indicate short foraging ranges, or highly efficient hopping legs, and SMR's are from 40–60 kcal. Elephants, ungulates and ratites with SMR's of 55–85 kcal have long legs with feet well designed for walking at high cruising speeds in search of forage, and their necks are sometimes very tall. Energetics do make a *lot* of difference in body design, and vice versa, whether one masses 10 grams or 10 tonnes.

# BIG TACHYMETABOLIC DINOSAURS WOULD HAVE COOKED IN THE HEAT

Myth: Because tachymetabolic rates scale to W0.75, while surface area scales to W0.67, it is almost universally believed that big endotherms suffer serious heat stress in tropical climes. Big dinosaurs, sauropods especially, should have had low metabolic rates to avoid this dire fate (Martin, 1979; Regal and Gans, 1980; Spotila, 1980; Reid, 1984; Schmidt-Nielsen, 1984; Carroll, 1988; Alexander, 1989; Prothero, 1989; Russell, 1989). Alternately, tachymetabolic sauropods needed well developed cooling systems (Bakker, 1980, 1986).

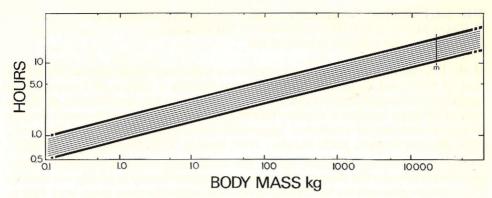


Figure 5 This plot shows the time it takes high level endotherms to overheat if they store all internal heat production and exclude external heat by allowing their body temperature to rise to maximum tolerable levels. The mass range approximates that of adult dinosaurs (including lagosuchians), with the highest masses of mammals also indicated: note that giant endothermic dinosaurs would have been more resistant to overheating than giant mammals! Energy storage capacity is in kcal assuming a 6–8°C rise in body temperature (up to 46.5°C), with 0.83 kcal/kg stored for each 1°C rise in body temperature; total active metabolic rates are either 2.0 times endothermic standard energy production/hour, or only 1.3 times normal standard metabolic rates due to suppressed levels of activity and/or standard metabolic rates. The results are in good agreement with thermal tolerances observed among large tropical endotherms.

Reality: This is a major misconception (Costanzo and Paul, 1978; Paul, 1988a, 1990a). Many tropical mammals have reached from 1 to 20 tonnes, but no classic reptiles have done so, exactly opposite the predicted pattern. Elephants lack well developed evaporative cooling systems. Elephants living in treeless habitats do not drop dead from heat stroke, even in the most dangerous conditions of an extremely hot drought when it is not possible to dump excess heat by radiation or evaporative cooling in the first place, and shade is not available. Instead, large bull elephants have the highest survival rates under such circumstances, again opposite the predicted pattern (Owen-Smith, 1988). Field biologists have long known that endotherms from 100 kg on up use a classic thermal strategy in which their great mass is used to store a relatively low rate of internal heat production for most or all of the day, body temperatures are allowed to rise 3-10°C, and water loss is kept to a minimum (Schmidt-Nielsen et al., 1957; Taylor, 1969, 1970, 1972; Gordon, 1972; Finch and Robertshaw, 1979; Schmidt-Nielsen, 1984). The built up heat is then unloaded into the cool night sky. This makes large endotherms practically invulnerable to overheating under the harshest conditions, small endotherms must seek refuge or quickly die from heat stroke or dehydration. The large size of dinosaurs may have been an adaptation for better coping with high heat loads with a tachymetabolic level of heat production (Figure 5).

## HEAT RADIATORS WERE IMPORTANT FOR KEEPING DINOSAURS COOL

Myth: Because big dinosaurs had low surface areas and lived in hot climates, they needed large surface area organs (long necks, tails, horns, head frills, dorsal frills, dorsal plates, etc.) in order to successfully unload excess heat (Desmond, 1976; Farlow *et al.*, 1976; Ostrom, 1980; Bakker, 1986; Rigby, 1989).

Reality: As shown above, low surface areas were an advantage, not a problem, for dinosaurs in extremely hot conditions, so radiators were not critical. Indeed, as environmental heat loads rise, it becomes increasingly difficult and eventually impossible to radiate heat out from a body, so radiators become ineffective when they are needed the most (Hiley, 1975, notes that the use of ears for cooling in elephants is limited to moderate temperatures). The importance of heat radiators to dinosaurs has been overstated.

## SAUROPODS WERE NOT BIG-MOUTHED ENOUGH TO BE TACHYMETABOLIC

Myth: Ever since their skulls have been found, people have wondered how sauropods fed themselves. Currently, it is generally held that sauropod heads were too small and weak toothed for them to sustain a high rate of food consumption, so they are portrayed as relatively weak herbivores unable to sustain a high metabolic rate (McGowan, 1979; Ostrom, 1980, 1987; Regal and Gans, 1980; Halstead and Halstead, 1981; Weaver, 1983; Reid, 1984, 1987; Farlow, 1987; Coe *et al.*, 1987; Russell, 1989).

Reality: Complete nonsense. The heads of the biggest 40-80 tonners were as big as those of albertosaurs, massed 100 kg or more, could swallow a 70 kg body whole, and had cropping teeth much larger than those of giraffe's (Weaver's 1983 characterization of the head of *Brachiosaurus* as comparable to a giraffe's is therefore wholly false). Even the smallest adult diplodocid skulls were as big as those of large alligators, and were much broader than and had many more teeth than those of giraffes. Over all, sauropods could browse at great heights, could rear up to use clawed hands and very strong dorsal columns to bring down trees that even they were too short to browse, had powerful necks, and could break down fodder in large multi-chamber fermenting digestive tracts that probably began with a stone rolling gizzard mill. Sauropods were the most powerful herbivores in Earth history, and could easily consume the 1-2% of their body mass needed to sustain a mammalian level of heat production. Just how true this is is obvious when it is considered that a sauropod would need to consume only two to four ounces (50-100 g) per bite (assuming six bites per minute, as per elephants, giraffes and tortoises) in order to be tachymetabolic.

#### BIG BRAINED ANIMALS ARE ALWAYS TACHYMETABOLIC AND VICE VERSA, AND SMALL BRAINED ANIMALS ARE ALWAYS BRADYMETABOLIC AND VICE VERSA

Myth: Vertebrates are usually segregated into "lower" bradymetabolic vertebrates with small simple brains (fishes, amphibians and reptiles), and "higher" tachymetabolic vertebrates with large, complex brains (birds and mammals; Jerison, 1973). Those dinosaurs with small, simple brains are therefore considered to be bradymetabolic, those with larger, more complex brains supposedly have higher metabolic rates (Feduccia, 1973; McGowan, 1979; Hopson, 1980; Ostrom, 1980; Regal and Gans, 1980; Farlow, 1987; Coe et al., 1987; Desmond, 1976; Bakker, 1980, 1986; Paul, 1988a and other supporters of endothermic dinosaurs have also tended to accept that modern ectotherms and endotherms have large and small brains respectively).

Reality: As usual, life is not so simple (Figure 6; Paul, 1990a). Tuna and leatherbacks are very active, fast swimmers with metabolic rates in the lower mammal range, and very high rates of food consumption. Yet their brains are small and simple. Pterosaurs were highly active, insulated fliers that must have had elevated metabolic rates, and although their brains were fairly complex, their EQ's fall entirely within the reptile range (Figure 7). At the other extreme, some advanced rays are inactive and bradymetabolic bottom dwellers with brains as large as those of felids, canids, and ungulates of similar size (Northcutt, 1977). Reef and hammerhead sharks are bradytherms whose brains are as large as those of ground birds of similar size, and that have enlarged, complex forebrains.

The overlap between vertebrates with differing brain sizes and physiologies is so extensive that their traditional segregation into "lower" and "higher" vertebrates must be considered obsolete. Brain size and complexity does not have any consistent correlation with metabolic rates or activity levels, and cannot be used to determine dinosaur physiology at even the gross or detailed levels. It is widely acknowledged that small brained dinosaur species were often social and parental (Horner and Gorman, 1988; Coombs, 1989), if so, then they were intelligent enough to have maintained a high level of energy consumption and production. Note that small brains in highly energetic dinosaurs does not violate the evolutionary trend towards increased information processing (see above). In addition to the higher rate of generational inspired genetic turnover, the higher feeding rates of endotherms require an order of magnitude increase in the frequency of brain activity in order to achieve the levels of activity needed to search for and consume the food. Small brained ants, bees and termites have also achieved a similar boost in information processing, in their case via intense socialization.

#### BRADYMETABOLIC DINOSAURS COULD GROW UP FAST

Myth: It is now widely acknowledged that many or all dinosaurs grew as fast as tachymetabolic mammals and birds, which grow 10 to 30 times faster than wild bradymetabolic reptiles. Since many of these workers also believe that dinosaurs combined double pump hearts with reptilian energetics, they argue that non-tachymetabolic animals can also grow rapidly (Ricqles, 1980; Regal and Gans, 1980; Reid, 1984, 1987; Dunham *et al.*, 1989).

Reality: This emerging myth badly needs nipping in the bud. For a free living, self feeding juvenile to grow fast, it must have very high sustained activity levels in order to find the abundant amounts of food needed to grow so rapidly, and the little creature must remain warm around the clock in order to maintain continuous growth. Both of these needs require the hyper-elevated energy levels (one third over the mass specific adult level) seen in juvenile mammals and birds (Case, 1978). That captive reptiles can grow much faster than their free-living counterparts only reinforces the fact that they must have food brought to them in order to do so; they cannot acquire enough food on their own. Excellent confirmation of the correlation linking metabolisms and maximum potential growth rates is found in the fact that land animals with intermediate metabolic rates, marsupials and monotremes, grow at rates intermediate to placentals and reptiles. Note that the only fast growing reptile, the leatherback, is a highly energetic swimmer with low locomotary energy costs. It is hardly likely that fossil animals somehow broke these barriers. Equally unlikely is that, if it is possible for low energy land animals to grow fast, not a

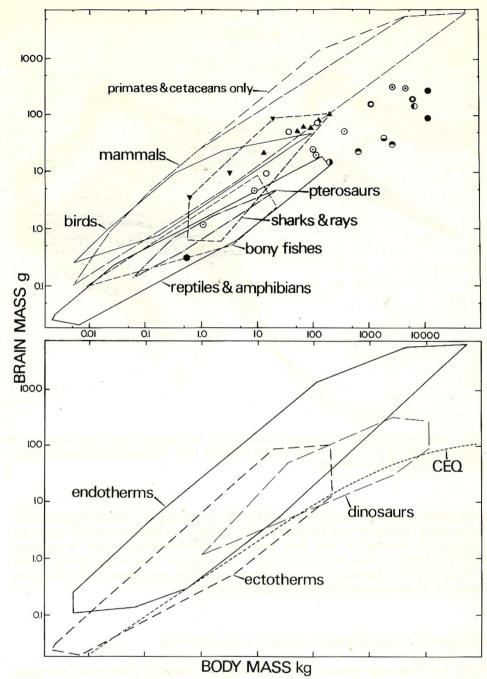


Figure 6 The upper plot shows the relationship of brain and body mass in major vertebrate groups, including small (open) and large (partly filled) theropod, sauropod (solid), small ornithopod (small dotted), hadrosaur (large dotted), stegosaur (upper solid), ankylosaur (lower solid), and small (right solid) and large (left solid) ceratopsid juvenile and adult dinosaurs (circles). Data in part from Jerison (1973), Northcutt (1977), Hopson (1980), Galton (1989), Rich & Rich (1989). Body and brain masses of some dinosaurs have been corrected (in particular, *Brachiosaurus* is downgraded from an 87 tonner to an 11 tonne juvenile), body masses for some other dinosaurs and pterosaurs are approximate. Note that bradymetabolic myliobatiform rays (inverted triangles) and reef sharks (triangles) enter well into the avian-mammalian range, while highly energetic pterosaurs and tuna (hexagon) have reptilian-sized brains. The extensive overlap observed in the brain/body mass relationships of tachymetabolic and bradymetabolic animals in the lower plot would be even more extensive if larger bradymetabolic myliobatiform rays and tachymetabolic tuna were included. Note that dinosaurs are either close to or above a corrected encephalization quotient value set at the level of the lowest EQ techymetabolic animals.

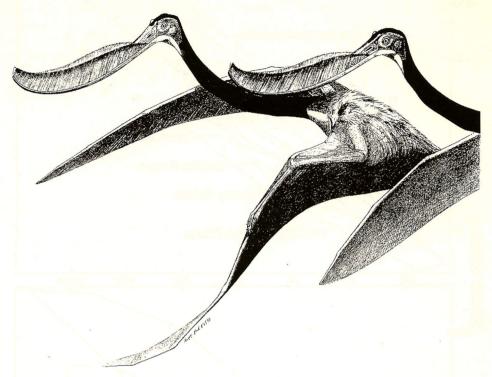


Figure 7 The small size of the main body of the cranium of *Pterodaustro guinazui* (figures based on a complete skull and skeleton) shows that, despite their high level energetics, insulation, and flight, pterosaurs had reptilian sized brains.

single modern example has failed to do so. The argument that non-tachymetabolic, fast growing therapsids confirm the viability of this combination depend upon the questionable assumption that they were not tachymetabolic—there being good evidence that they were tachymetabolic at the edentate level. The concept of fast growing reptilian dinosaurs and therapsids is entirely speculative, and will always remain so in the absence of any living analogues.

#### MESOZOIC CLIMES WERE WARM AND BENIGN

Myth: The Mesozoic was an age of nonseasonal warmth, where even the poles supported extensive forests. In terms of modelling dinosaur physiology, this takes the form of exposing the subjects to relatively benign thermal conditions that appear to favor warmth loving reptiles (Spotila *et al.*, 1973; Paladino *et al.*, 1990).

Reality: It is true that the Mesozoic climate was more moderate than today's. However, Barron and Washington (1982) and Sloan and Barron (1990) have stressed that it was not in fact equable, and that continental interior and polar locales with resident dinosaur faunas experienced cold winters. This leads to the problem of downplaying the severe conditions that dinosaurs in such places as the interior of

Mongolia and the Kogosukruk delta (see Spicer and Parrish, 1990) regularly experienced. In particular, none of the models examining dinosaurs as inertial homeotherms has calculated the heat drain inspired by strong wind chills and evaporative cooling during winter storms. The reduction of fat insulation in the latter half of winter would render reptilian model dinosaurs especially vulnerable to such conditions. The scarcity or absence of small and large crocodilians in well watered interior and polar dinosaur bearing locales confirms that winter conditions were too harsh to support bradymetabolic archosaurs (Paul, 1988b).

#### DINOSAURS WERE MIGRATORS EXTRAORDINAIRE

Myth: This is a recent development that reverses the traditional view that dinosaurs were reptiles unlikely to move very far in a given year. The new model proposes that dinosaurs migrated up to 6400–9200 km roundtrip each year, especially to avoid the sunless, florally dormant polar winters (Hotton, 1980; Paul, 1988b; Currie, 1989). This is especially important to help reptilian model dinosaurs to avoid the winter cold.

Reality: The new model of migrating dinosaurs is valid only up to 2500 km. Modern polar winters are far harsher than the worst seen in the Mesozoic, and the migratory abilities of large, long legged polar ungulates and carnivores are broadly comparable to those of dinosaurs. Polar mammals do not migrate farther than 2500 km roundtrip per year; beyond this point the energy consumption levels probably are too high to make it worthwhile even for such high energy animals (Paul, 1988b). Migrating herds are limited by the locomotory performance of their young, and subyearling hadrosaurs and ceratopsids making their first migrations had shorter limbs than gracile juvenile caribou, so dinosaurs were not better migrators than ungulates. It is unlikely, therefore, that polar dinosaurs, living under relatively benign winter thermal and floral conditions, migrated any farther than their modern mammalian counterparts if they had similar energy expenditure levels. If these dinosaurs had reptilian energetics, their movements would have been even more severely limited. The continent spanning distances that some have proposed are therefore not realistic.

Certain tropical ungulates migrate from 500 to perhaps 1250 km roundtrip per year in search of the best feeding conditions (Paul, 1988b), some tropical and subtropical dinosaurs may have done the same.

#### SAUROPODS DROPPED LARGE CALVES

Myth: The large pelvic canals and minimum size of sauropods indicates that they gave birth to large calves, which would be advantageous for such highly mobile giants (Desmond, 1976; Bakker, 1986).

Reality: This reasonable idea has been contradicted by new finds of tiny sauropod hatchlings and eggshells in nest (Mohabey, 1987). It may not be possible for the members of a clade to abandon calcified eggshells once they have evolved, and the disparity between the size and intrauterine development of 2 kg hatchlings and large newborn calves would be extreme, so it is probable that all sauropods were oviparous. As outlined below, this probably had strong advantages for sauropods.

#### HERBIVOROUS DINOSAURS JUST ATE PLANTS

Myth: It is generally thought that prosauropods, sauropods, and ornithischians limited their diets to assorted plant matter.

Reality: Some ornithischians, such as adult broad beaked ankylosaurs, iguanodonts and hadrosaurs, probably were full time herbivores. However, the sharp beaks, premaxillary teeth, and speed of small adult ornithopods were well suited for hunting nonflying insects and small animals, and scavenging carcasses. The small heads and slender necks of prosauropods and sauropods suggest that they may have picked up small animals on occasion, and even scavenged carcasses. The parrot beaks and shearing teeth, powered by massive jaw muscles, of protoceratopsids and ceratopsids suggest that they were omnivores, rather like suids and entelodonts. They may have competed with theropods to feed on carcasses. In all the adult examples, animal tissue probably only made up about a tenth or less of the total diet, so the effect on energy-flow dynamics in dinosaur communities was probably modest at best.

#### BIG THEROPODS DID NOT HUNT FOR A LIVING

Myth: The big theropods, tyrannosaurs especially, were too big and slow to hunt prey, so they only scavenged (as per Halstead and Halstead, 1981; Barsbold, 1983). Reality: I have discredited this myth in detail elsewhere (Paul, 1988a). Suffice it to say that it is hardly likely that a 6 tonne animal with a 1.3 m long head, filled with massive jaw closing muscles that powered rows of teeth up to 150 mm long, and able to run like a great bird, would go hungry waiting for herbivores to drop dead for it. The problem of hunting safety for giant predators was solved by the use of hit-and-run tactics in which they quickly delivered crippling wounds, and then left the prey until it was too weak to be a threat. Confirming that big theropods were an active threat to big herbivorous dinosaurs is the array of armor, weaponry, and speed that the latter often employed to protect themselves (see below).

#### DEFENSIVE NEEDS WERE NOT A DRIVING FORCE BEHIND THE EVOLUTION OF DINOSAURIAN WEAPONRY AND ARMOR, AND INTRASPECIFIC COMBAT WAS RELATIVELY SAFE

Myth: In modern ungulates, horns evolved primarily for intraspecific purposes (Janis, 1982). Defense is at most a secondary consideration, and thermoregulation is another important function. Intraspecific weapons are designed to minimize damage on both sides. The horns of ceratopsids likewise developed for safe intraspecific combat, and they and armored dinosaur tail clubs and spikes developed as heat radiators (Farlow and Dodson, 1975; Horner and Gorman, 1988; Rigby, 1989).

Reality: As usual, the real situation is much more complex. Field observation and paleobiological research have demonstrated that anti-predator defense is a primary function of the weaponry of many modern and recent ungulates (Kruuk, 1972; Schaller, 1972; Sinclair, 1977; Kingdon, 1982; Guthrie, 1990). There are grades of defensive versus intraspecific function of weaponry, with rhinos, Cape buffalo, eland, bison, sable and so forth aggressively defending themselves with their horns

under normal circumstances. Guthrie (1990) shows that certain features of some ungulate horns are often designed to severely wound opponents of their own species.

As shown above, heat radiation is not as important as often thought, and it is probably not the driving force behind dinosaur horns, clubs and spikes, although they could be used for such purposes. The horns of most ceratopsids are very long, sharp, dangerous weapons, well designed to wound attacking predators. The single, non-interlocking nasal horns of many species were also good for seriously injuring opponents during intraspecific combat. The tail spines of *Stegosaurus* were arrayed in a pin cushion fashion that enhanced their wounding ability (Paul 1987a). Ankylosaur tail clubs had sharp dorso-lateral rims that would have enhanced the effect of their impact. Ankylosaur armor is most similar to the protective cuirasses of glyptodonts and turtles.

#### PACHYCEPHALOSAURS BUTTED HEADS, NOT PREDATORS

Myth: Pachycephalosaurs butted their heads together at high speeds.

Reality: Such classic domeheads as *Stegoceras* and *Pachycephalosaurus* lacked any co-locking devices to help stabilize their head upon impact. Instead, the round domes would have bounced off each other erratically like billard balls, placing dangerous lateral torques on the neck. This suggests they instead rammed the sides of their opponents, including predators.

## ARCHAEOPTERYX HUNTED DRAGONFLIES AND BUTTERFLIES

Myth: Protobirds were terrestrial hunters of flying insects that learned to fly by leaping after insects (as proposed by Caple *et al.*, 1983). A number of recent illustrations have taken this to the extreme of showing *Archaeopteryx* chasing dragonflies, others show it chasing butterflies or moths.

Reality: It is unfortunate that the question of the origin of bird flight has entrenched itself into two camps—one favoring arboreal gliding, the other terrestrial leaping—because interbranch leaping would result in the improvement of aerodynamic control surfaces seen in the terrestrial leaping scenario. The latter scenario suffers from a lack of any living analogues, and it may be unfeasible for energetic reasons (Paul, 1988a). As for hunting dragonflies, they are perhaps the supreme insect aerialists in terms of speed and agility. Even high performance birds have great trouble pursuing them. *Archaeopteryx* and other protobirds would have been hopelessly outmatched, and restorations of them hunting dragonflies are most unrealistic. Jurassic protobirds could not pursue moths and butterflies, because these insects did not appear until the Cretaceous (Crepet and Friis, 1987).

#### FLYING IS SO VERY HARD TO DO

Myth: Most vertebrates get around in one or more of three ways, swimming, walking, and flying. These locomotory modes evolved in this order, and it is generally believed that swimming is the easiest, and flight the most difficult, of them. Reality: Swimming is easy, slow, sprawling gaits are relatively unchallenging, and

the per unit energy demands of flying are very high. However, it is easier to fly than to walk with an erect gait, or to run with any gait. Do not believe this? A child can build a good working model of an airplane and get it to fly, including even a helicopter model with complex aerodynamic controls. The AeroVironment QN project built a fairly realistic flapping flight model of a giant pterosaur whose basic flight stability was provided by a low power, on board, computer. Only a modest investment of resources would result in much higher fidelity bird or pterosaur models. In contrast, it has not yet proven possible to construct a robot that walks with a speed and agility anywhere near that of a human, even on a level floor (Moravec, 1988).

Both flying and erect walking are highly dynamic processes. One reason that flight is fairly easy is because flying machines and beings are usually built to be inherently stable, it takes effort to tip them over. In contrast, walking and running are controlled falls, with disaster looming at every step. In addition, air is a relatively simple and open medium to progress through. Walking beasts are continually threatened with a complex surface topography that can trip them up. The ease of flight is confirmed by the rapidity with which insects learned to fly after they took up terrestrial habits, and by the small brains found in insects and pterosaurs. These brains are modified for flight purposes, especially for processing the optical data so critical for aerialists, but their overall computing power is no greater than it is in sprawling gait insects and reptiles (see above).

Flight evolved after walking simply because it is necessary to do the latter before

one can do the former.

# THE PNEUMATIC BONES AND AIRSACS OF BIRDS AND PTEROSAURS GREATLY REDUCE THE MASS OF THEIR SKELETONS, AND THEIR SPECIFIC GRAVITIES

Myth: In order to reduce their mass and improve flight performance, birds have thin walled, air sac filled bones. These adaptations were taken to extremes in pterosaurs.

Reality: Prange et al. (1979) have shown that, as a percentage of total body mass, the skeletons of nonflying and flying birds and mammals make up similar percentages of total mass at any given body size. Likewise, the airsacs of flying and nonflying birds alike lower their specific gravities only about 10% compared to other tetrapods (Paul, 1988a). The body volume/mass ratios of even albatross and frigate birds indicate at most a 25% reduction in density due to internal airspaces. There is no a-priori reason to believe that pterosaurs had significantly lower skeletal weights or specific gravities (see below).

#### BIG PTEROSAURS WERE ULTRALIGHT AIRBEINGS

Myth: Large pterosaurs such as the pteranodontids and azhdarchids were much lighter in mass relative to their wingspans and areas than are birds of similar size. Their thin walled bones were also lighter and weaker than those of birds. These factors indicate that large pterosaurs were slow, fragile fliers (Bramwell and Whitfield, 1974; Desmond, 1976; Brower, 1983; Pennycuick, 1986).

Reality: Most volume estimates of the body of *Pteranodon* (including mine) agree that, relative to wingspan-area, it had a body about as large as more gracile birds. The body and legs of azhdarchids are even larger relative to their wings. This means that the very low mass estimates assume unrealistically low specific gravities of

0.2–0.3. In span, length, bone dimensions, and overall volume, azhdarchids were much larger than 7.5 m span, 80–120 kg *Argentavis*. Assuming viable specific gravities, then a 5.9 m span *Pteranodon* massed 20–25 kg, and 11 m span *Quetzalcoatlus* massed some 250 kg (Paul, 1990b). This places large pterosaurs in the same mass/wingspan-area range as birds, and 12 m class sailplanes and ultralight aircraft (see Figures 8 and 9).

The thin walled bones of pterosaurs were braced by an extensive set of internal struts, giving them great strength at low weight (Wellnhofer, 1988).

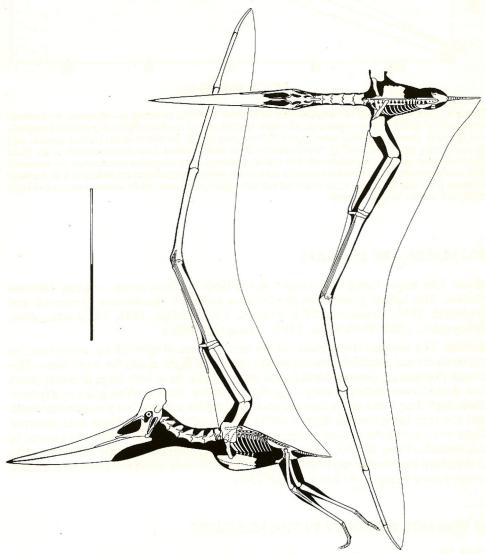


Figure 8 A two view skeletal restoration of lightly built *Pteranodon ingens*, based primarily on the skull and skeleton of USNM 12167 scaled up to fit the complete, 5.9 m span wing of SMM 2085. The volume/mass ratio of this restoration is similar to earlier estimates. Mass derived from a model and other means, with a specific gravity of from 0.57 to 0.7 (with the value of the beak assumed to be  $\sim$ 0.25) is 20–25 kg. Scale bar equals 1 m.

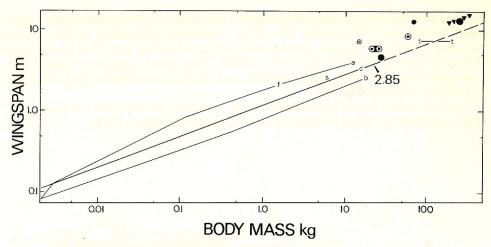


Figure 9 The relationship of wingspan and body mass in birds, including a—albatross, b—bustard, c—condor, s—swan and t—Argentavis, ultralight aircraft and 12 m class sailplanes (inverted triangles), and the giant pterosaurs Pteranodon ingens (5.9 m span) and P. sternbergi (8 m) (dotted circles), and Quetzalcoatlus sp. (4.7 m) and Q. northropi (11–12 m) (solid circles). Low mass estimates of the giant pterosaurs that assumed unrealistically low specific gravities or an atrophied musculature are indicated with small symbols, mass estimates derived from more reasonable parameters are indicated with the large symbols. Note that the higher mass estimates still leave giant pterosaurs lightly loaded compared to large birds, and similar to light aircraft.

#### BIG FLIERS ARE SOARERS

Myth: The largst living and extinct flying birds are low power, energy efficient soarers. The largest pterosaurs should have followed this pattern (Bramwell and Whitfield, 1974; Desmond, 1976; Brower, 1983; Padian, 1983; McGowan, 1984; Pennycuick, 1986; Wellnhofer, 1988; Alexander, 1989).

Reality: The heaviest living fliers, swans and bustards of up to 18 kg, never soar, so big birds do not establish soaring as the preferred flight mode for large fliers. The largest pterosaurs, pteranodontids and azhdarchids, have very large pectoral crests that should have anchored very large flight muscles. Azhdarchids additionally have thick, high drag inner wings that are poorly suited for soaring, but give great strength and leverage for powerful flight muscles. These adaptations indicate that powered flight was an important form of large pterosaur flight, probably the primary one in azhdarchids (Paul, 1990b). This is energetically feasible because the estimated ratio of sustained metabolic output to standard metabolic rate is similar in azhdarchids and swans power flying at 60 km/h (about 25/1).

#### IT WAS NOT AS WINDY IN THE MESOZOIC

Myth: Because the polar-equatorial temperature gradient was not as strong in the Mesozoic, winds were not as strong. This favored the evolution of slow, lightweight pterosaurs (Bramwell and Whitfield, 1974; Desmond, 1976; Brower, 1983).

Reality: Climatic modelling by Barron and Washington (1982) suggests that Cret-

aceous winds were not significantly weaker than they are today. If so, then pterosaurs would have needed to be about as strongly built and fast as birds.

# PTEROSAURS WERE INCOMPETENT, SPRAWLING QUADRUPEDS: NO, THEY WERE AGILE, ERECT LEGGED BIPEDS

Myths: A largely European school sees pterosaurs as bat-like quadrupeds, with limited mobility on the ground (Bramwell and Whitfield, 1974; Pennycuick, 1986; Wellnhofer, 1988). A largely American school sees them as agile, dinosaur/bird-like bipeds (as per Padian, 1983).

Reality: Pterosaurs were not bats, nor were they dino-birds. They were like bats in some way, like birds in others, and had many unique features that indicate they were highly flexible and adept on the ground. It is clear that at least some pterosaurs—the filter feeders and the giant azhdarchids that had to regularly wade in shallow waters and take off from the ground with horizontally held bodies—must have been good runners, and their hip joints are broadly similar to those of other taxa (Paul, 1987a, b). However, pterodactyloids lack a strong set of bipedal adaptations (Pennycuick, 1986; Paul, 1987a, b), and the pterosaur forelimb is stronger, and has more robust digits, than the legs. Articulation studies in work show that their fore and hindlimbs were able to assume a narrow trackway, with the humerus held horizontal, and the femur as erect as in many birds (see above). This shows that pterosaurs were good quadrupedal walkers and runners (Paul, 1987a, b). Rhamphorhynchoids probably walked and ran bipedally with a horizontal body, pterodactyloids may have walked bipedally with a vertical body posture (Bennett, 1990), and all could dash bipedally to take off.

# LAGOSUCHIANS ARE NOT IN THE DINOSAURIA, TOOTHED BIRDS ARE NOT MEMBERS OF AVES, AND PROSAUROPODS AND SAUROPODS ARE SAUROPODOMORPHS

Myth: Gauthier (1986) excludes toothed Mesozoic birds from Aves in an attempt to stabilize the group. Most workers leave the lagosuchians out of the Dinosauria, and prosauropods and sauropods are often united in the Sauropodomorpha.

Reality: These three cases are used to illustrate a complex set of problems in archosaur classification. The exclusion of birds from Aves will never be accepted by ornithologists, so it is taxonomic whistling in the wind. Nor should this application of extreme cladistic taxonomic principles receive approval. It is an overreaction to the problems inherent in classifying life forms, and a misguided attempt to deny that the biology of animal groups should play a role in the effort to classify them. The limiting of Aves to only those species that are within the clade encompassed by living examples is entirely a matter of arbitrary convenience of cataloging that has no biological or scientific basis. In terms of adaptations, the toothed birds are birds, and all birds should, and certainly will, remain in Aves. Likewise, the lagosuchians, with their light heads atop S-curved necks, and their long, erect, digitigrade, mesotarsaled legs, were in all important regards dinosaurs. Giving a new name to the clade that includes lagosuchians and other dinosaurs, such as Ornithodira, tells us nothing about the biology of these animals (but does contribute to the numbing cladistic proliferation of names). It all comes down to commonsense—if it walks like a duck,

flies like a duck, and quacks like a duck, it's a duck! Placing lagosuchians in the Dinosauria tells us exactly what these little dinosaurs were.

The common unification of prosauropods and sauropods in a single group is a more subtle denial of the group's biology, as well as a potentially unrealistic reflection of their relationships. The exact interrelationships of basal herbivorous dinosaurs remains uncertain because of the lack of an adequate data base, and it is likely to remain so because of the limited number of characters that can be used to sort out relationships in the basal members of closely related groups, and the presence of extensive parallels and reversals in such taxa. It is therefore quite possible that prosauropods are directly ancestral to segnosaurs and/or ornithischians, and are a sister group to sauropods, or are ancestral to all three, or to none, and so on. In many cases the alliance of prosauropods and sauropods in the Sauropodomorpha would be incorrect. As it is, the Sauropodomorpha is more a reflection of the shared small headed, long necked nature of its members, than it is of their detailed relationships. It would promote stability to recognize the distinctive biology of the two groups. The sauropods are derived giants with short, rigid trunks and specialized, elephantine limbs, and are quite different from the flexible backed, primitive limbed prosauropods, which had partially developed cheek muscles. These differences should be formally recognized.

# REVERSALS CAN BE LARGELY NEGLECTED IN STUDIES OF DINOSAUR PHYLOGENETICS

Myth: Advanced cladistic works on dinosaur phylogenetics need pay little attention to the possibility that reversals complicate understandings of their relationships.

Reality: Reversals of morphology are probably very common in evolution, especially since this often does not require the development of new genetic instructions, but rather the release of a suppressed set of old instructions. An important example of this phenomenon may have occurred in the bird-like Cretaceous theropods. Features otherwise found in secondarily flightless birds suggest the theropods were secondarily flightless also, and that they experienced a set of reversals that returned them to a preflight status (Paul, 1988a). The forward direction of the pubes of some of these theropods may also represent a reversal from an archaeoptrygian-dromaeosaur condition, caused by the deepening of the tail, and a reduction of the size of the forelimbs. Another example of a notable reversal is the development of auxiliary hyposphene-hypantrum vertebral braces in theropods, followed by their subsequent loss in birds. This suggests that ornithischians may have lost the same structure if they descended from prosauropods and segnosaurs, which have these extra braces (contra Gauthier, 1986). If phylogenetic studies are to have any meaning, they must take into account the possibility of major reversals. Of course, this is not an agreeable task, since it greatly complicates such efforts.

# COMPUTERS ARE POWERFUL TOOLS FOR STUDYING DINOSAUR PHYLOGENETICS

Myth: Some of the latest phylogenetic studies on dinosaurs have been based on computer generated cladograms (Gauthier, 1986). This is promoted as the most powerful method for exploring possible phylogenetic patterns.

Reality: Within the next few decades human scientists may well become obsolete in the face of competition from self-aware robotic computers (Barrow and Tipler, 1986; Moravec, 1988). As they evolve towards this level, computers will become increasingly valuable tools for dinosaur research, and they are already useful for certain kinds of data processing. However, current generation computers are still very simple devices—even the Connection Machine supercomputer boasts only 65,000 simple parallel processors—that lack one of the most powerful tools for scientific investigation. This is commonsense judgement that allows, via the complex interaction of mass parallel processors and reflective circuitry, the discerning of broad patterns from a large body of data. They are also severely constrained by the limited amount of data and alternative scenarios they can handle (the travelling salesman problem), and by the limitations of their human programmers. Until these problems are rectified, human brain generated phylogenetic studies will remain important.

# DINOSAURS WERE INHERENTLY VULNERABLE TO CLIMATIC DISRUPTIONS

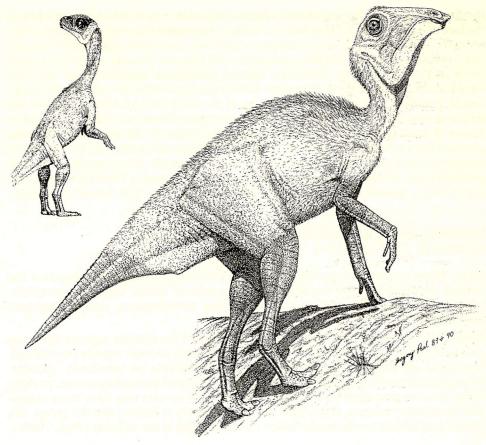
Myth: Many scenarios of dinosaur extinction continue to assume that dinosaurs had limited thermoregulatory capabilities that rendered them, whether embryonic, juvenile, or adult, to increasing or decreasing temperatures, and to increased seasonality.

Reality: Recent years have seen a wide expansion of the climatic regimes dinosaurs are known to have lived in, which ranged from deserts to polar winters (see above). Nor were all dinosaur habitats as seasonally equable as previously thought. Dinosaurs themselves appear to have been sophisticated thermoregulators, perhaps at the avian-mammalian level. Although individual species may have been vulnerable to climatic changes, at this time there is no reason to believe that the group, as a whole, was subject to wholesale failure due to changes in the weather (Paul, 1988c).

# BIG DINOSAURS WERE K-STRATEGISTS THAT WERE VULNERABLE TO EXTINCTION

Myth: It has generally been assumed that big dinosaurs were vulnerable to the kinds of disruptions that can lead to the loss of big, slow breeding, low population (K-strategist) mammals. Most scenarios of dinosaur extinction tacitly assume that large dinosaurs were relatively easy to kill off.

Reality: Unlike large mammals, which drop a large calf every one to six years, large dinosaurs had extremely high rates of reproduction, laying from two dozen to perhaps many dozens of small eggs each year (Figure 10). Along with their fast growth, this gave dinosaurs a very high recovery potential, well above the 6–12% per year population expansion that can be achieved by large mammals (Owen-Smith, 1988). At the same time, these dinosaurs enjoyed much the same survival and recovery abilities of large mammals, including high resistance to starvation, and the ability to disperse long distances both to avoid starvation, and to recover after heavy losses. This means that dinosaurs combined many of the best r-strategy recovery features usually associated with small, fast breeding animals, and the best K-strategy survival and recovery features inherent in large animals. This remarkable ability to live through and quickly recover from crises should have made them highly resistant to extinction, further complicating efforts to explain their loss.



**Figure 10** The small size of baby dinosaurs such as 70 g *Mussaurus patagonicus* and 800 g *Hypacrosaurus* sp. facilitated the large clutches that gave large dinosaurs reproductive rates and recovery potentials much greater than those of equivalent sized adult mammals. Figures are to same scale.

## THE SCALE OF THE K/T EVENT WAS UNIQUE FOR THE MESOZOIC

Myths: One scenario, the extinction of dinosaurs and pterosaurs, was due to the impact of a bolide of exceptional size, that left a crater of from 100–300 km in diameter. In another scenario, the extinction of these archosaurs was the result of super-vulcanism that led to the formation of the Deccan traps.

Reality: An increasing amount of evidence indicates that giant impacts and supervulcanism are much more frequent events than has been realized. Three Mesozoic craters of 70–100 km diameter have already been identified from the Late Triassic to Late Jurassic. Full exploration of the earth's surface is certain to reveal many more such Mesozoic structures, and it is highly probable that some of these, or craters that have been lost to subduction, will be substantially larger. Trap formation also occurred multiple times in the Mesozoic, and some of these traps appear to be more extensive than the Deccan traps. This suggests that any K/T impacts and volcanics were not unique in scale. This is important because the world dinosaur fauna survived the many earlier events in good order, with no indication of any substantial size and diversity squeezes having occurred (Paul, 1988c).

## THE LAST DINOSAURS RESTED UNDER THE SHADE OF TALL HARDWOODS

Myth: Because angiosperms were the most abundant large plants in the Late Cretaceous (Cenomanian-Maastrichtian), artists (including myself) have often included tall hardwood trees in their late Mesozoic landscapes.

Reality: While large conifer logs are common in Mesozoic sediments, the diameter of angiosperm wood did not exceed 10 cm until the Cenozoic (Crane, 1987). This means that Late Cretaceous dinosaurs lived in dwarf angiosperm woodlands and shrublands where the trees were only a few meters tall, a rather monotonous short stature flora broken only by isolated individuals and stands of towering conifers and other nonflowering trees.

#### THERE IS MORE THAN ONE WAY TO RESTORE A DINOSAUR

Myth: At the end of a heated discussion, often I have heard the retort, "well, there is more than one way to restore a dinosaur!"

Reality: A dubious statement at best, it is becoming less and less true as we learn more and more about the actual appearance of dinosaurs. After all, each taxa had a particular form and appearance in life, and in many cases we know what this form was (Paul, 1987a). Hadrosaurs have downcurved rather than straight anterior dorsal columns, soft dorsal frills are often preserved, and their skin is well documented. The knees of giant theropods, ornithopods, and ceratopsids articulated correctly only when they were flexed like those of birds, they did not have the straight knees of elephants (Paul, 1987a). Of course, there are many other things we do not know, and many areas remain open to dispute. Even so, I have noticed that the above statement is usually voiced when the speaker has run out of specific arguments for their case. So it contains little useful information, and it encourages the anything goes attitude that long plagued the field of paleorestoration.

#### CONCLUSION

At the best, some of the myths outlined above are hurtful to the science of dinosaurology because there is a good chance that they are wrong in part or in whole, and yet are widely accepted as fact without proper substantiation. Many others of the above myths are patently false, being contradicted by modern biology and other sciences. False concepts must be abandoned before we can better understand the true nature of dinosaurs and the world they lived in. For example, as long as it is believed that sauropods were dimwitted, weak herbivores unable to eat the few ounces per bite needed to sustain a high metabolic rate, and were in constant danger of overheating, then it is hardly possible to see them as anything other than bradymetabolic reptiles. If on the other hand they are seen as social, fast growing, tree wrecking herbivores of exceptional power, well able to take in and process fodder equalling 1 or 2% of their body mass per day that descended from tiny,

energetic protodinosaurs, and used bulk insulation and heat storage along with hyper-elevated body temperatures to thermoregulate during severe droughts, then it is difficult to avoid the conclusion that they were highly energetic beasts in the manner of elephants.

In other examples, hypothesis of the origins of bird flight will be distorted as long as the difficulty of achieving flight is exaggerated. The flight of big pterosaurs will also be misunderstood if it is believed that big fliers must be soarers, and that giant pterosaurs were light in mass. The idea that big animals share a similar inertia driven thermoregulation is not at all useful when it is obvious that big reptiles and mammals exhibit a strong, graded correlation between their levels of metabolism, anatomy, and activity. The extinction of dinosaurs can only be understood when it is realized how resilient these fast breeders were, and that they survived a number of giant impacts. Emerging myths, such as that ectotherms can grow fast, or that dinosaurs migrated continental distances, threaten to lead the field further astray.

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