

On the Origin of Dinosaurs and Mammals

By
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Abstract

The coincidence in time of incipient rifting of Pangea and the origin of dinosaurs during the Carnian age (230-225 Ma) of the Late Triassic suggests a fundamental link between the two. That link may have been the onset of Earth expansion, triggered by the Pangean thermal anomaly and resulting in a 20% reduction in surface gravity. In reduced gravity, animals will have less skeletal mass and thinner bones than equally massive animals adapted to normal gravity; a significant increase in maximum body size will also ensue. These predictions, inferred from allometric scaling principles and supported by biomedical space research and gravity tolerance experiments, are borne out in the fossil record: the Late Triassic witnessed the transition from Paleozoic faunas dominated by relatively small and robust synapsid reptiles (therapsids) to Mesozoic faunas dominated by large and gracile diapsid reptiles (archosaurs), including many families of gigantic dinosaurs.

Dynamical principles of locomotion indicate that a gravity reduction will lower the speed at which animals change gait. In adapting to reduced gravity, the advanced thecodonts may have shifted from a bipedal symmetrical running gait to a bipedal asymmetrical hopping gait, much as the Apollo astronauts did on the Moon. This behavioral shift by the thecodonts engendered fundamental structural changes, including the fully erect gait and obligatory bipedal pose that characterized primitive and many advanced dinosaurs. Like kangaroos, the ectothermic archosaurs may have relied on elastic storage and rebound to hop at high speeds over long distances at a low metabolic cost, which gave them a competitive edge over the proto-endothermic therapsids. The latter became restricted to small-scale niches left vacant by the dinosaurs. In the primitive shrew-like mammals, a high surface-area-to-volume ratio increased metabolic requirements and thus hastened the development of the high-grade mammalian physiology.

Triassic archosaurs were the first vertebrates capable of sustained powered flight. In reduced gravity, the capacity for sustained powered flight may have evolved directly from the archosaurs' bipedal hopping gait.

Reduced gravity during the Jurassic implies a subsequent increase in gravity to its modern value. A post-Jurassic gravity increase (associated with terrestrial contraction?) may have fostered the transition from faunas dominated by large, high-browsing sauropods in the Jurassic to faunas dominated by smaller, low-browsing ornithischian dinosaurs in the Cretaceous. Finally, a gravity increase in the latest Cretaceous may have played a role in the wholesale extinction of the remaining dinosaurs at the K-T boundary.

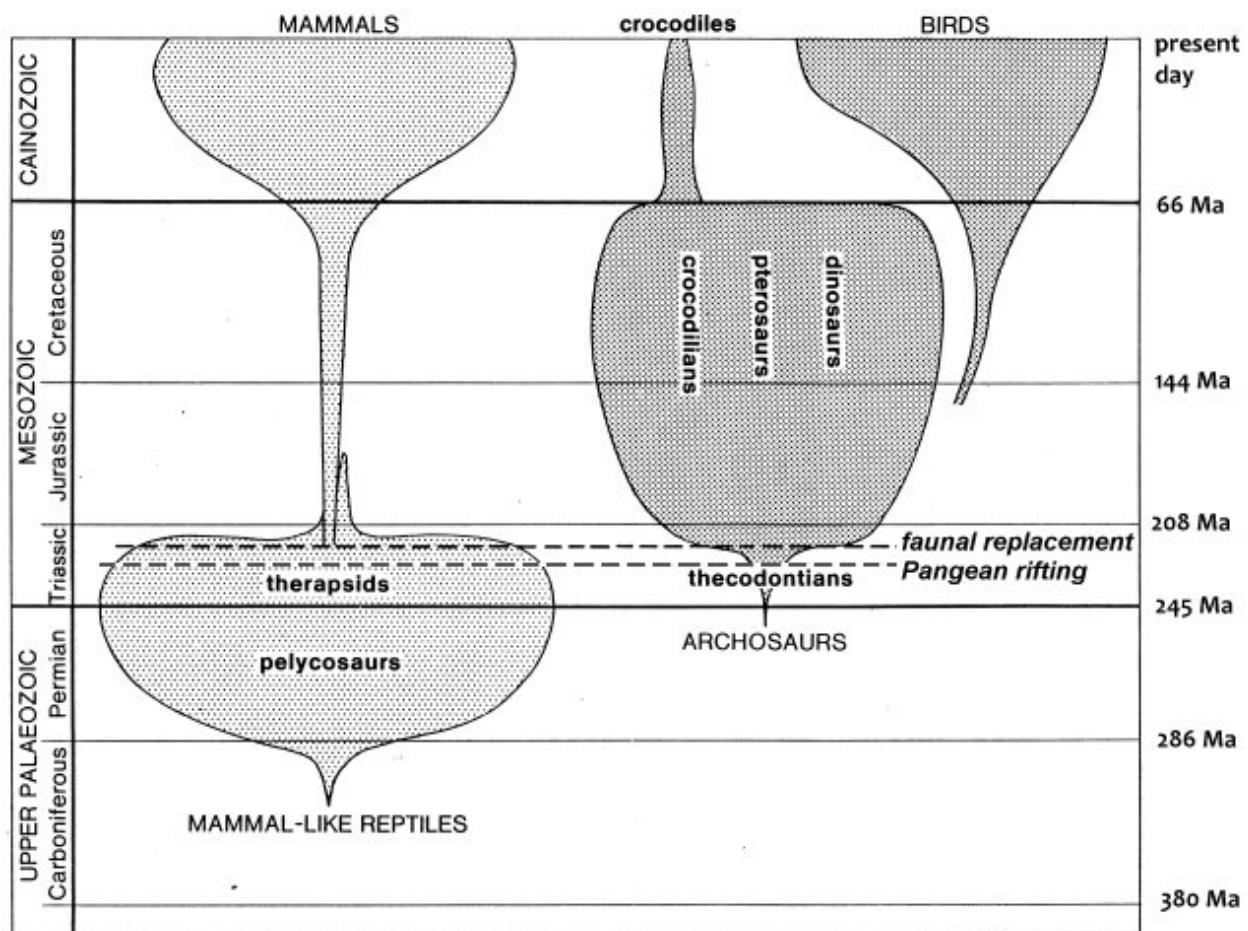


Figure 1. The relative fortunes of ‘higher’ vertebrates since the Late Paleozoic. (Modified after Charig 1979; “Faunal Replacement” datum from Charig 1979; “Pangean rifting” datum from Cousminer and Manspeizer 1976, Nadon and Middleton 1984, and Veevers 1989.)

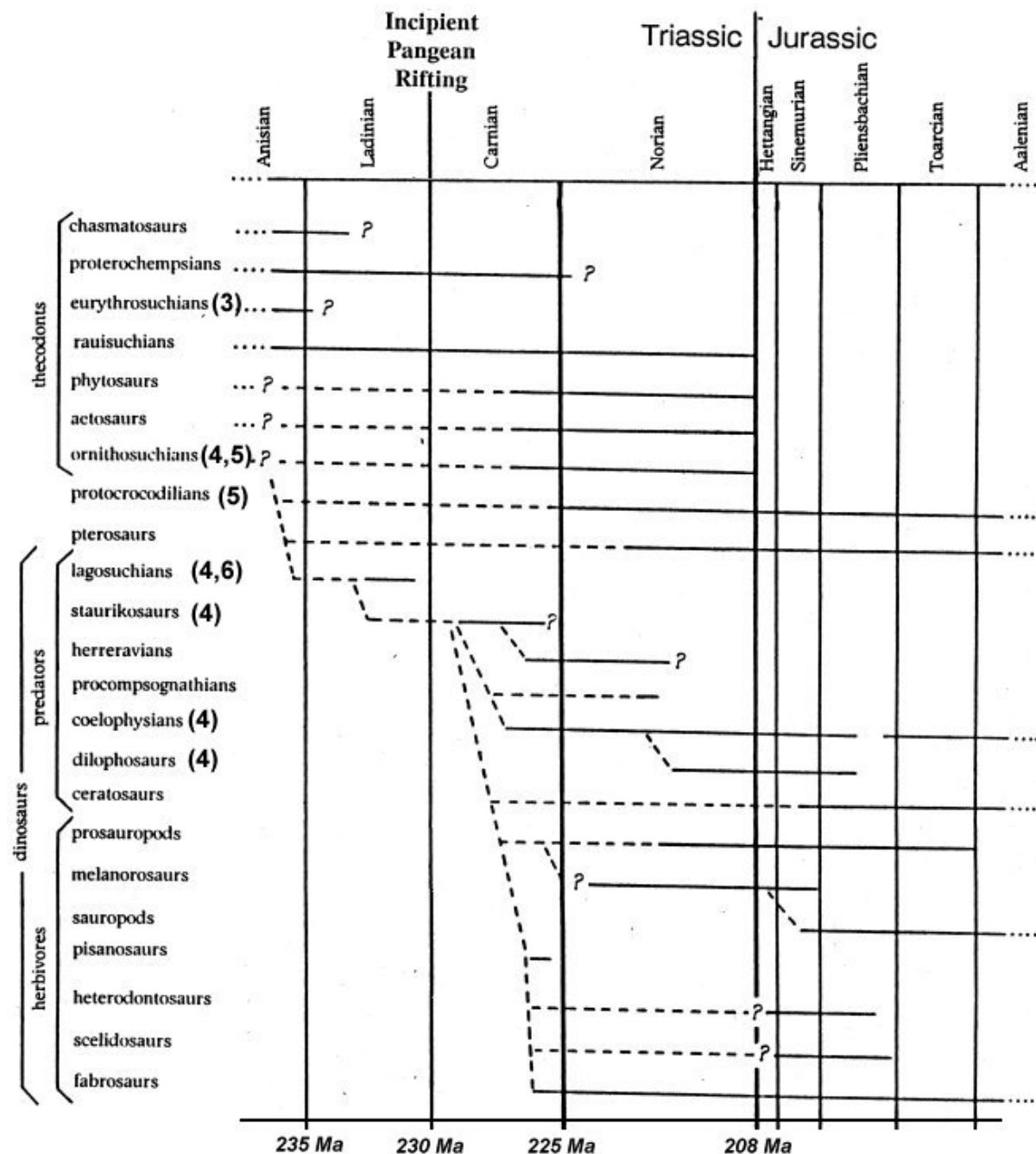


Figure 2. The phylogeny of archosaurs. The numbers in parentheses refer to figures presented elsewhere in this paper in which those animals are depicted. (Redrawn after Paul 1988; “Pangean rifting” datum from Cousminer and Manspeizer 1976, Nadon and Middleton 1984, and Veevers 1989.)

Introduction

Increasingly precise geological data indicate that the Pangean singularity – final supercontinent coalescence and initial rifting – occurred during the Carnian age (230-225 Ma) of the Late Triassic.¹ Coincidentally, dinosaurs originated during the Carnian age² at almost precisely the same time and were dominant by the end of the Triassic (208 Ma). (See Figures 1 and 2.) Despite an increasing wealth of fossil evidence, many important dinosaur adaptations – including giantism, bipedality, and powered flight – have never been adequately explained. The dinosaurs’ remarkable success at the expense of the once-dominant mammal-like reptiles also remains an open question. In an attempt to solve these problems, it is hypothesized here that the thermal anomaly associated with the Pangean singularity³ actually signals the onset of a brief episode of global swelling during the Early Mesozoic which caused, as a direct consequence, a slight reduction in surface gravity. Such a change in the geophysical environment would have had a profound affect on vertebrate evolution; it will be argued that many of the dinosaurs’ unique adaptations, and their evolutionary success at the expense of the mammal-like reptiles, were made possible by a decrease in surface gravity during the Triassic and Jurassic.

Skeletal Scaling in Reduced Gravity

It is true that we can seldom test a paleontological hypothesis with a live experiment. What we can do is perform ‘thought experiments.’ We can erect hypotheses, deduce their consequences, and then we can see whether these consequences are borne out by the fossil data.

– Steven M. Stanley⁴

Although gravity is a universal force measured in absolute terms, its tangible influence on living things can and does vary. Aquatic animals, such as fishes and whales, are essentially ‘immune’ to gravity’s influence because their buoyancy in water offsets their weight. All land-living animals, however, are subject to gravitational stress. Yet even on land, gravity’s influence is variable. The relative influence of gravity (and most other physical forces) varies with size and scale; forces dominant at one scale of nature become inconsequential at another. Extremely small animals less than 1 mm in length, for example, inhabit a Gibbsian world dominated by cohesive forces; larger animals live in a Newtonian world dominated by gravity.⁵ The insect kingdom straddles gravity’s frontier.

¹ Cousminer and Manspeizer, 1976; Nadon and Middleton, 1984.

² Benton, 1988.

³ Veevers, 1989.

⁴ Stanley, 1981.

⁵ Went, 1968.

In terrestrial vertebrates, the skeleton provides structural support against the crushing stress of weight. With increasing body size, body weight increases at a faster rate than the weight-supporting capacity of the skeleton. Body weight is proportional to volume, and volume is proportional to the cube of linear dimensions. The strength of bone, on the other hand, is proportional to its cross-sectional area, and area is proportional to the square of linear dimensions. Thus, if linear dimensions l are doubled, body weight will increase by a factor of eight – $2l^3$ – while bone strength increases only by a factor of four – $2l^2$. Accordingly, with increasing body size, animals will devote a larger fraction of their body mass to the skeleton.

A change in relative bone dimensions and bone mass with increasing body size is a prime example of scaling, which has been described as “the structural and functional consequences of changes in size and scale among otherwise similar organisms.”⁶ Galileo may have been the first to realize that an increase in body size makes it “necessary to change the ratio between [bone] thickness and length either by increasing the thickness or by diminishing the length.”⁷ On the assumption that static strength is the primary determinant of relative bone dimensions, Galileo concluded that bones are scaled for constant-stress similarity, according to which bone length l is related to diameter d as $l \propto d^{1/2}$.

Although the general idea behind Galileo’s reasoning is valid, his scaling formula turned out to be rather inaccurate in detail. Bones typically are somewhat thinner than constant-stress scaling would predict. In order to improve upon Galileo’s insight, some recent workers have suggested that scaling is based on “elastic rather than strength criteria.”⁸ According to the principle of elastic similarity, bones “should be scaled in such a way as to deform under gravity in a geometrically similar fashion.”⁹ In other words, the ratio of bone-deformation-to-bone-length will remain constant with increasing size. The principle of elastic similarity yields a proportionality of $l \propto d^{2/3}$. Thus, bones scaled for elastic similarity would be thicker than geometrically similar bones – $l \propto d^1$ – and thinner than bones scaled for constant-stress similarity – $l \propto d^{1/2}$.

Characteristic	General Formula	Similarity Formulas		
		Geometric	Elastic	Constant-stress
Proportions	$l \propto d^x$	$X = 1$	$X = 2/3$	$X = 1/2$
Bone Lengths	$l \propto M^{x/(x+2)}$	$l \propto M^{1/3}$	$l \propto M^{1/4}$	$l \propto M^{1/5}$
Bone Diameters	$d \propto M^{1/(x+2)}$	$d \propto M^{1/3}$	$d \propto M^{3/8}$	$d \propto M^{2/5}$
Skeletal Mass	$s \propto l d^2$ $M_{Skel} \propto s$	$(M^{1/3})(M^{1/3})^2$ $M_{Skel} \propto M^{3/3}$	$(M^{1/4})(M^{3/8})^2$ $M_{Skel} \propto M^{8/8}$	$(M^{1/5})(M^{2/5})^2$ $M_{Skel} \propto M^{5/5}$

Table 1 – Comparison of Similarity Formulas¹⁰

⁶ Schmidt-Nielsen, 1984.

⁷ Galileo, 1638, 1954 edition.

⁸ McMahon, 1973; Rashevsky, 1960.

⁹ Alexander, 1982a.

¹⁰ After Calder, 1984.

Each of these scaling formulas can, within limited domains, account for the known facts, but none of them is universally valid. Leg dimensions in adult ungulates, for example, seem to be scaled for elastic similarity but those of mammals in general are not. (Mammalian leg lengths correspond more closely to the value predicted by geometric similarity.) In many cases, different bones within the same animal are scaled differently. In ground-running birds, such as quails and ostriches, the vertical leg bones (tibiotarsus and tibiometatarsus) are much longer than any of the scaling formulas would predict but come closest to the values predicted by geometric similarity. The horizontal bones (femur and toes), on the other hand, fall in between the values predicted by geometric and elastic similarity. Yet in both sets of bones the diameters correspond exactly with the values predicted by constant-stress similarity.¹¹ At best, this bewildering situation suggests that individual bones are scaled according to the types of stress they are most likely to encounter; at worst, it proves that bone scaling defies rigorous analysis.

Another shortcoming of all of these scaling formulas is their unanimous prediction of isometric skeletal scaling. (See Table 1.) In fact, as mentioned above, animals devote a relatively larger fraction of their mass to the skeleton as body size increases.

It seems obvious that a reduction in gravity, and the consequent reduction in body weight, should have some affect on relative bone dimensions. But it is not at all clear from these scaling formulas what affect, if any, a gravity (and weight) reduction would have on relative bone dimensions. If bone dimensions are a function of mass (as shown in Table 1), then a change in gravity would have no effect. If, on the other hand, they are a function of weight (mass times gravity), then a gravity reduction would result in thinner and shorter bones, and therefore an overall reduction in body size. Both conclusions seem wrong. Galileo based his scaling principle on the capacity of bones to support their own weight: a reduction in gravity therefore would permit thinner bones. But that inference is not implicit in the above formulations. And with respect to elastic similarity, bones are proportioned so that they will deform in a geometrically similar fashion irrespective of body weight. Clearly, a reduction in gravity would have no effect on bone elasticity.

The problem of bone scaling has perplexed and so far eluded some of the most outstanding minds. Perhaps the best we can hope for is a scaling formula based on empirical similarity.¹² But even a strictly empirical approach cannot account for the differences in relative bone dimensions found among different species and indeed within individual animals.

Fortunately, the scaling of the skeleton as a whole offers more promise. It is well known that the percentage of body mass devoted to the skeleton increases with size.¹³ In mammals, the statistically derived allometric scaling formula¹⁴ is

¹¹ Calder 1984.

¹² Alexander, 1982a.

¹³ Prange, et al., 1979.

¹⁴ As modified by Schmidt-Nielsen, 1984.

$$M_{Skel} = 0.0343M_{Body}^{1.083} \quad (1)$$

For birds, the formula is

$$M_{Skel} = 0.0406M_{Body}^{1.068} \quad (2)$$

Stated simply, Equations (1) and (2) indicate that the skeleton of a one-gram mammal should account for 3.43% of its total body mass, and it should account for 4.06% of body mass in a one-gram bird. An exponent greater than one indicates non-isometric scaling: the fraction of body mass devoted to the skeleton will increase with increasing body size.

A comparison of Equations (1) and (2) belies the common assumption that birds, as an adaptation for flight, have lighter skeletons than mammals. In fact, these empirical regressions indicate that birds actually devote a slightly larger fraction of their body mass to the skeleton than do mammals, especially at the low end of the scale. With increasing body size, however, the skeletal mass of mammals approaches and, above 100 kg in body mass, surpasses that of birds. Nevertheless, the two formulas yield very similar values between 10 kg (at which size a mammal would devote 7.2% of its mass to the skeleton and a bird 7.6%) and 1000 kg (10.6% for mammals and 10.3% for birds). Above one metric ton, the two formulas diverge but this is considerably larger than any living bird and is at the upper end of the mammalian size range.

Although Equation (1) represents a ‘best fit’ regression of available terrestrial mammal data, and includes animals ranging in size from a 3.5-gram shrew to a 6.6 metric ton elephant, it is rather inaccurate when applied to large-scale mammals. It predicts, for example, that a 6.6 ton elephant will devote 13% of its body mass to the skeleton when in fact the value is closer to 27%.¹⁵ (The two equations predict, respectively, that a mammal with 27% bone mass would weight 65 kilotons, and a similarly proportioned bird 1.3 megatons!) This gap between theory and fact does not invalidate the basic method: it merely reflects skewing toward the low end of the scale and demonstrates the pitfalls of extrapolating beyond the sample range.

On the assumption that the need for structural support is most acute in large-scale animals, Equation (1) can be adjusted to achieve a closer agreement between the predicted and actual skeletal mass for large-scale mammals. Based on a trial-and-error method, the following allometric formula was found to predict that a 10 kg dog would have 14% skeletal mass, a 67 kg human 17% skeletal mass, and a 6.6 ton elephant 27% skeletal mass, all of which are approximately correct.¹⁶

$$M_{Skel} = 0.0584M_{Body}^{1.098} \quad (3)$$

The revised exponent (1.098) in Equation (3) is still within the range of statistical error of the Equation (1) exponent (1.083 ± 0.021) but the revised coefficient (0.584) is

¹⁵ Prange et al., 1979.

¹⁶ Ibid.

considerably larger than the Equation (1) coefficient (0.0343). This means that instead of devoting 3.43% of body mass to the skeleton, a 1-gram animal would devote 5.84%. Accordingly, Equation (3) is least accurate with respect to very small animals (a 6.3-gram shrew has 4.8% skeletal mass. Equation (1) predicts 4.0% skeletal mass and Equation (3) 7.0%) but it is much more accurate than Equation (1) for animals above 10 kg.

The important point here is that skeletal mass increases out of proportion to body mass, which suggests that the need for skeletal support increases with body size. The fact that gravitational stresses also increase with size implies that weight (mass times gravity) is the crucial factor in the hyperallometric scaling of skeletal mass. This notion is borne out in whales. The body mass of a whale is buoyantly supported in water, which relieves much of the stress on its skeleton. Accordingly, the skeletal scaling exponent in whales is much lower than in terrestrial mammals and, indeed, approaches isometry:¹⁷

$$M_{\text{Skel}} \propto M_{\text{Body}}^{1.024} \quad (4)$$

The fact that the skeleton of whales seems to “scale strictly in proportion to body size... [s]uggests that when there is no need to support the body in a gravitational field, the skeleton is not required to scale out of proportion to body size.”¹⁸

If gravitational stress is responsible for the hyperallometric skeletal scaling of land-living animals, then the complete absence of gravitational stress (zero g) should permit isometric scaling. In zero g, skeletal mass should increase in direct proportion to body mass: “In the absence of gravity... geometric similarity must be obeyed.”¹⁹ This, in turn, implies that in reduced gravity, the allometric exponent would fall between the 1 g value of 1.098 (Equation (3)) and the hypothetical zero g value of 1.000. Thus, for example, at .75 g, the exponent would be 1.0735, while at .25 g it would be 1.0245. Because we are dealing with exponents, these seemingly negligible differences yield very substantial results.

Three Predicted Consequences of a Gravity Reduction

If the skeletal scaling exponent is a function of gravity, then a reduction in gravity will have three important consequences (all else being equal):

- Animals adapted to low gravity should have less bone mass than animals of equal mass adapted to normal gravity.
- In reduced gravity, bones of a given length would tend to be thinner and bones of given thickness, longer.
- If there is a limit on the amount of body mass that can be devoted to the skeleton, then a gravity reduction should permit a considerable increase in size and mass of the very largest land animals.

¹⁷ Schmidt-Nielsen, 1984.

¹⁸ Ibid.

¹⁹ Economos, 1983.

The first prediction – that animals adapted to low gravity should have less bone mass than an animal of equal mass in normal gravity – follows from the assumed dependency of skeletal scaling on gravity. The second prediction – that bones would become thinner and longer – follows the first prediction and from the fact that bone dimensions are related to skeletal mass as $l d^2 \propto M_{\text{skel}}$. Since the proportionality of bone diameter to bone length is $d \propto l^x$ (where $x > 1$), a reduction in skeletal mass will result in a reduction in the scaling exponent x . In other words, all else being equal, bones of given length would tend to be thinner, and bones of given thickness, longer. Both of these expectations are supported by biomedical space research: bone thinning and an overall reduction in bone mass is one of the best-known side effects of weightlessness.

Bones are quite sensitive to changes in gravitational stress.²⁰ Upon entering zero g (or, more accurately, micro g), bone growth slows down immediately and eventually ceases altogether. In laboratory rats sent into space, the rate of bone formation dropped to half the control rate in earth-bound rats even though total body mass remained constant. “Without exception, each rat formed more bone after than during flight.” Since “the greatest changes occur in weight bearing bones, changes in mechanical loading are undoubtedly important.”²¹ Similarly, in astronauts and cosmonauts, “the first reaction to a decrease in stress is decalcification.” There is a significant increase in urinary and fecal calcium and other bone-related minerals; the rate of calcium loss is about 0.5% of the total calcium content per month.²² “These results are indicative of an alteration in bone structure, as confirmed by an increase in urinary hydroxyproline, a degradation product of bone collagen.”²³

Bone thinning and the loss of bone mass in zero g are not at all surprising. Since the skeleton must be strong enough (at least) to support body weight, the complete absence of body weight in zero g means that the need for weight support is also completely absent; as a result, the bones and skeleton degenerate. A similar thing happens to bed-ridden invalids: their bones and muscles atrophy from lack of use. Because of the complete elimination of mechanical stress, prolonged exposure to zero g creates symptoms not unlike osteoporosis, a degenerative bone malady. “Theoretically, it seems possible that bone could be reduced and decalcified so far that a return to terrestrial conditions and normal body weight would increase the stresses... so much that they would go beyond the upper tolerance level.”²⁴

The third predicted consequence of a reduction in gravity is closely related to the first two. If there is a limit on the amount of body mass that can be devoted to the skeleton, and skeletal scaling is a function of gravity, then a gravity reduction should permit a considerable increase in maximum body size. In reduced gravity, animals will be able to achieve body sizes not possible under normal 1 g conditions because they can devote a smaller fraction of their body mass to the skeleton. Assuming that animals cannot exceed

²⁰ See Smith, 1975, for an excellent review of “gravitational biology.”

²¹ Morey and Baylink, 1978.

²² Shapland and Rycroft, 1984.

²³ Lenfant and Chiang, 1982.

²⁴ Kummer, 1972.

27% bone mass (the value for elephants), a 20% reduction in gravity would permit roughly an order of magnitude increase in body size. Applying the gravity reduction conversion method described above to Equation (3), the skeletal scaling formula at 0.8 g would be:

$$M_{\text{Skel}} = 0.0584 M_{\text{Body}}^{1.079} \quad (5)$$

Using this formula, the mass of an animal with an elephant-like skeleton (27% of body mass) would be 250 metric tons; a human-like animal (17% skeletal mass) would be 750 kg and a dog-like animal (14% skeletal mass) would be 65 kg. These surprising results indicate that even a small reduction in gravity will have a huge effect on skeletal mass, especially in large-scale animals.

Vertebrate Evolution in Reduced Gravity

What affect, then, would a gravity reduction have on vertebrate evolution? Basic skeletal design, of course, is genetically determined; and since modern evolutionary theory denies the inheritability of acquired traits, the loss of bone mass experienced by an individual exposed to low gravity would not be transmitted to its offspring.²⁵ However, if it is beneficial for animals to have the lowest possible bone mass,²⁶ then evolution in reduced gravity should favor those varieties with a genetic tendency toward lightweight skeletons: animals with low bone mass (perhaps expressed as a low genetically-coded skeletal growth allometry) would have a competitive edge over animals equipped with more massive skeletons. Moreover, because such animals would devote relatively less body mass to the skeleton, they should be able to grow much larger than animals with more robust skeletons and there should be an increase in the size of the very largest land animals. Because of its magnified effect on large animals, a 20% reduction in gravity would, in effect, foster the evolution of giants – animals with the skeleton of an elephant but the mass of a whale.

If there was a reduction in gravity during the Middle-to-Late Triassic, then the animals that evolved afterwards should have been more gracile and lightly constructed than those that had gone before, and they should have been able to grow much larger. Both predictions are borne out by the fossil evidence.

²⁵ Cf. Smith, 1975.

²⁶ Calder, 1984.

The Synapsid-Diapsid Succession

We cannot deny this drastic and fundamental change in the nature of the vertebrate land fauna, or that many new adaptations, many new life-styles appeared in the latter half of the Triassic period. But why did it happen at all, why did produce such great diversity, and why was it (in a geological sense) so sudden and simultaneous?

– Alan Charig²⁷

The Triassic was a period of rapid and fundamental change. Prior to the Triassic, in the Late Permian, advanced mammal-like reptiles, known as therapsids, overwhelmingly dominated the terrestrial vertebrate fauna. In some fossil locales, therapsids account for 90% of the genera; “other reptiles seem for the most part to have been crowded out.”²⁸ And despite mass extinctions at the end of the Permian, the mammal-like reptiles were still very common in the Early Triassic. Yet by the end of the Triassic, the therapsids were all but extinct and the world belonged to dinosaurs. (See Figure 1.)

Therapsids and dinosaurs belonged to two distinct subclasses of reptiles: the therapsids were synapsid reptiles and the dinosaurs were diapsids. Synapsid and diapsid reptiles were only very distantly related, having diverged from the basal reptile stock during the Pennsylvanian period 100 million years before the Triassic. The first synapsid reptiles appeared in the Early Pennsylvanian (Fig. 1) and soon became the preeminent terrestrial vertebrates. Among the earliest synapsids were the pelycosaurs, the so-called ‘primitive mammal-like reptiles.’ Dominant in the Late Pennsylvanian and Early Permian, the pelycosaurs were succeeded in the Late Permian by their descendants, the therapsids, which flourished into the Triassic.

The immediate ancestors of mammals, therapsids were already approaching a mammalian level of physiology and thermal control;²⁹ they were certainly the most advanced animals of their day. But in the Middle Triassic, the therapsids began to encounter fierce competition from an assemblage of diapsid reptiles known as thecodonts, stem members of the superorder Archosauria and the direct ancestors of dinosaurs, crocodiles and pterosaurs. By the end of the Triassic, the therapsids were on the brink of extinction; their descendants, the mammals, barely survived into the Jurassic and beyond.

The diapsid lineage originated in the Late Pennsylvanian about 20 million years after the appearance of the earliest synapsids. Diapsids were rather obscure during the 80 million years of synapsid supremacy. They began to make their presence felt only in the Late Permian with the appearance of the proterosuchian thecodonts but did not begin to seriously challenge the therapsids until the Middle Triassic. Unlike their contemporaries, the mammal-like reptiles, the early diapsids do not reveal any indication of significant

²⁷ Charig, 1979.

²⁸ Colbert, 1965.

²⁹ Kemp, 1982; Bennett and Ruben, 1986; Guillette and Hotton, 1986; cf. Bakker, 1971.

physiological advancement.³⁰ Thecodonts almost certainly were less advanced physiologically than the therapsids and were on a par perhaps with their descendants, the crocodiles. Nevertheless, thecodonts proved eminently successful against the therapsids. But their sojourn was brief. Victims of their own success, thecodonts did not survive the Triassic.

Taxonomists classify reptiles according to the number and location of diagnostic openings, or fenestrations, in the skull.³¹ Indeed, the names ‘synapsid’ and ‘diapsid’ refer to this.³² The synapsid – ‘fused arch’ – skull is characterized by a single diagnostic fenestration behind the eye (postorbital) whereas the diapsid – ‘twin-arched’ – skull has two postorbital fenestrations. Thus, whereas the skull of the mammal-like synapsid reptiles was typically solid and thick-boned with only a single small opening behind the eye, the diapsid skull was much more open and lightweight, and perforated by two or more fenestrations. In archosaurs, the skull was further lightened by a large anteorbital fenestra; and in advanced thecodonts and primitive dinosaurs there was still another opening in the jaw – the lateral mandibular fenestra. What is the significance of these structures?

Skull design obviously cannot be attributed to any single causal factor. Skull fenestrations, in addition to reducing weight, also serve to anchor jaw muscles. Conversely, bone thickening in the roof of the skull, which occurred in both synapsids (e.g. dinocephalians) and diapsids (pachycephalosaur dinosaurs), can be attributed to head-butting behavior associated with sexual or territorial combat. But despite these complications, basic skull structure does give some indication of the osteological differences embodied in these two lines of reptiles. In general, the solid-skulled synapsid reptiles had massive and thick-boned skeletons whereas the skeletons of the open-skulled diapsids, and the dinosaurs in particular, were slender and lightly constructed.

Therapsids were typically compact with their mass concentrated in the trunk. Despite their relatively small size (compared, that is, to dinosaurs), therapsids possessed heavily constructed skeletons with short, stout limbs, broad flat feet, a short tail, massive skull, and virtually no neck. Variations from this type depended on size and scale: the large herbivores (e.g. *Moschops*) were the most heavily built while the smaller carnivores (e.g. *Lycaenops*) were leaner and more refined in structure. (Fig. 3.)

³⁰ Cf. Bakker, 1986.

³¹ MacLean, 1986.

³² Osborn, 1903.

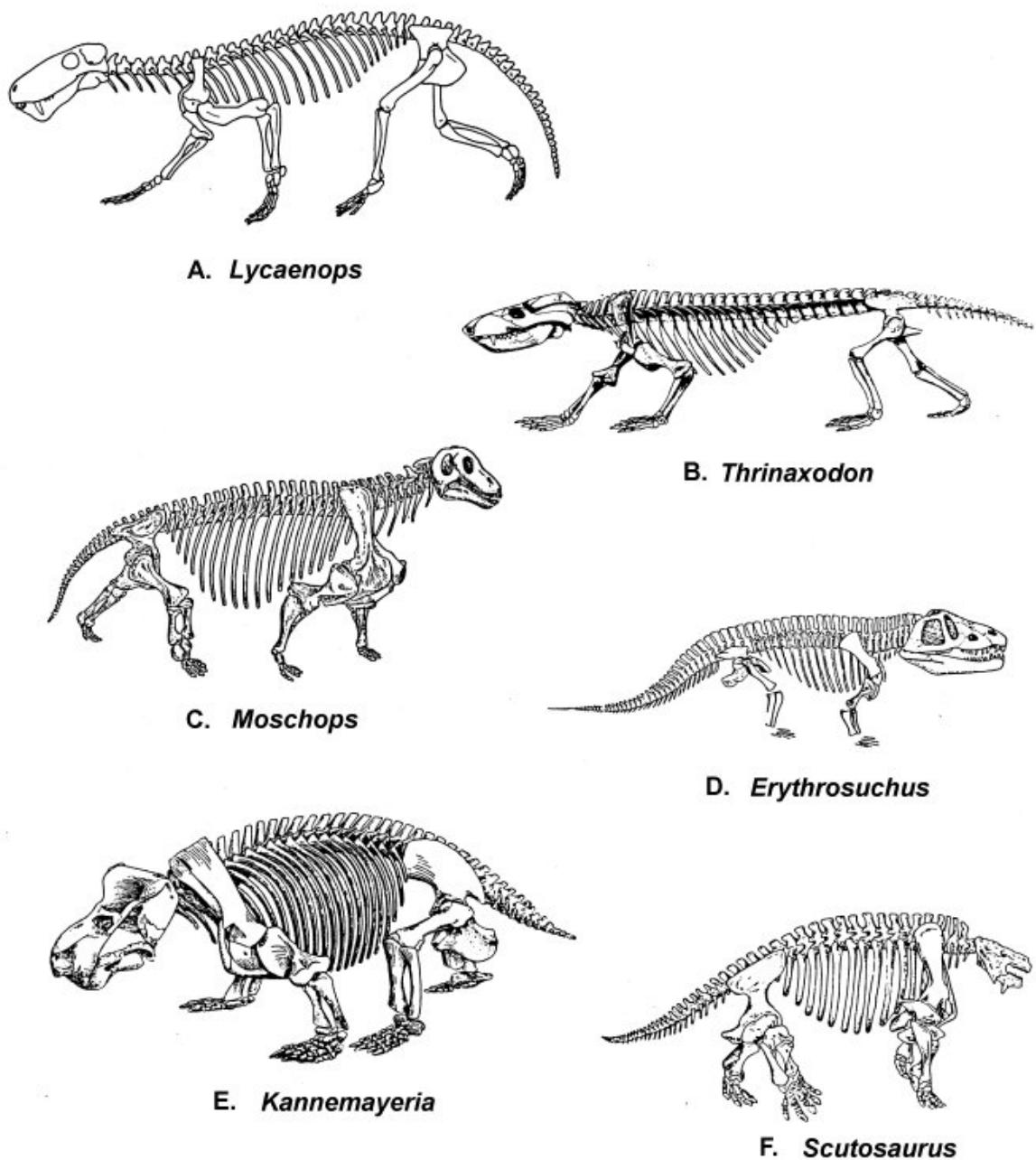


Figure 3. Some reptiles from the Permo-Triassic. Note the robust morphology and stout bones. A. *Lycaenops*, dinocephalian therapsid, Late Permian, length 1 m, from Colbert (1948). B. *Thrinaxodon*, cynodontian therapsid, Early Triassic, length 50 cm, from Brink (1956). C. *Moschops*, dinocephalian therapsid, Late Permian, length 5 m, from Gregory (1957). D. *Erythrosuchus*, proterosuchian thecodont, Early Triassic, length 5 m, from Heune (1936). E. *Kannemayeria*, dicynodontian therapsid, Early Triassic, length 3 m, from Pearson (1924). F. *Scutosaurus*, pareiasaur, Late Permian, length 2 m, from Gregory (1951). Figures are not drawn to scale.

The skeletal design embodied in the therapsids seems to have been established at the dawn of reptile evolution or even earlier, when the first vertebrates appeared on land. Indeed, most Paleozoic reptiles were even more robust than modern mammals and reptiles of comparable size. “[T]he limbs of early reptiles [from the Pennsylvanian] are almost invariably much shorter relative to shaft diameter than in living reptiles.” For example, “medium-sized cotylosaurs… had much shorter limbs than similar-sized iguanids or agamids [lizards]; the large cotylosaurs had much shorter, stockier limbs than the largest living lizards, the big monitors.”³³

Nearly all of the early therapsids were heavily constructed. The dinocephalians, from the Early Permian, were “massive animals that must have frequently weighed a thousand pounds or more in life.” From the dinocephalians there arose two new lines of mammal-like reptiles, “with one branch, the titanosuchians, becoming large, ponderous carnivores, and the other, the tapinocephalians, becoming large and equally ponderous herbivores.”³⁴

“Thick-skulled predators,” the titanosuchians were exemplified by *Jonkeria*, “a large lumbering carnivore” whose “body was robust and the limbs… very stout.” These hunters “could not have been very fast or agile, so it is to be presumed that they preyed upon the largest and clumsiest of the vegetarians.” Among their prey were the pareiasaurs, “heavy, ungainly animals with capacious bodies, strong limbs and broad feet, and thick solid skulls.” Tapinocephalians, the plant-eating cousins of the titanosuchians, “were equally as large, and one might say equally as clumsy as the pareiasaurs. They rival the pareiasaurs in the heaviness and thickness of the skull, a skull in which the temporal opening behind the eye is much reduced and the bones are exceedingly thick.”³⁵

Many families of mammal-like reptiles went extinct at the end of the Permian. But those that survived retained the thick-boned morphology of their forebears. Dicynodonts (Fig. 3E.), the most abundant herbivores of the Permo-Triassic, “were slab-sided animals with short, heavily muscled limbs and short tail. Their plantigrade feet no longer sprawled so far to the sides as those of their pelycosaurian forebears, but they had lost the lizardlike gracility of pelycosaurs without gaining the mammalian slenderness of living dogs and cats. The body form of dicynodonts is roughly comparable to that of such robust mammals as beavers [and] badgers, but the limb bones of dicynodonts are more robust than those of even the most stout-bodied mammals.”³⁶ The meat-eating cynodonts – the ancestors of mammals – also survived the Permian extinctions. More gracile than the dicynodonts, the largest cynodonts possessed short erect limbs; in size and morphology, they resembled robust wolves. (Fig. 3B.)

The Triassic Transition and the Rise of the Diapsid Reptiles

³³ Bakker, 1971a.

³⁴ Colbert, 1965.

³⁵ Ibid.

³⁶ Hotton, 1986.

Selection pressures during the Permo-Triassic favoring stout thick-boned animals must have been very strong indeed. The morphologic pattern described above was not limited to the therapsids, or even to synapsid reptiles, but seems to have been characteristic of tetrapods in general. “A remarkable parallel to the therapsids were the pareiasaurs, common in the Mid and Late Permian.”³⁷ The pareiasaurs (Fig. 3F.), previously mentioned, were anapsid reptiles (characterized by no diagnostic skull fenestra), unrelated to the therapsids. Significantly, even the proterosuchian thecodonts, from the Late Permian and Early Triassic, had thick bones and were massively constructed (Fig. 3D). Despite their diapsid pedigree, the proterosuchians were “clumsy reptiles with stout bodies and generally short tails and frequently with large skulls.”³⁸ These “awkwardly built” animals represent a sterile side branch of the thecodonts and “are not in themselves truly ancestral archosaurs.”³⁹

In contrast to the robust and thick-boned reptiles that flourished throughout the Late Paleozoic, many of the archosaurs and other diapsid reptiles that emerged during the Early Mesozoic were very slender and lightly constructed. Ornithosuchian thecodonts, the vanguard of the archosaur revolution, burst upon the scene during the Lower Triassic. *Euparkeria* (Fig. 4A), one of the earliest ornithosuchians, “is in many regards an almost ideal ancestor for later archosaurian types.”⁴⁰

Many workers have commented on the lightweight construction of the archosaur skeleton and skull, a characteristic already evident in *Euparkeria*. “There is obviously a strong evolutionary trend among these early thecodonts to reduce as much as possible the amount of bone in the skull and jaw thereby cutting the weight of the structure.” The reduction in bone mass was also evident in the post-cranial skeleton: “The lightness, one might say the fragility of the thecodonts is at once striking and apparent. The bones were delicately formed and many of them such as the long bones of the legs were hollow as are the bones in birds.”⁴¹

The lightweight construction of the archosaur skeleton is most clearly evident in the early dinosaurs: there were all extremely gracile with long slender limbs and necks (Fig. 4). ‘Coelurosaur,’ the name given to the most primitive group of dinosaurs, literally means ‘hollow reptile’, a reference to the animals’ hollow bones. “These were relatively small forms, very lightly built, with thin-walled bones. The skull was small, the orbits large, the neck relatively long and slender. Coelurosaurs of slender build were already common in the Late Triassic.”⁴²

Coelophysis, a coelurosaur from the Late Triassic, whose name literally means ‘hollow form,’ is typical of these early dinosaurs (Fig. 4D). “The skeleton is approximately 2.5 meters long and extremely lightly built. The limbs are long and slender, and the bones

³⁷ Bakker, 1971a.

³⁸ Colbert, 1969.

³⁹ Romer, 1968.

⁴⁰ Romer, 1966.

⁴¹ Colbert, 1967.

⁴² Romer, 1966.

are hollow.”⁴³ “The neck is very long and flexible enough for the head to reach the pelvic region. The tail is enormously long and, although the individual vertebrae are themselves long, the end is again flexible.”⁴⁴ The skull “epitomizes the light, flexible construction of paper-thin bony sheets and slender struts.”⁴⁵ This basic body plan persisted despite a significant increase in size: *Dilophosaurus*, a coelurosaur from the Early Jurassic, was 6 m long (Fig. 4E.).

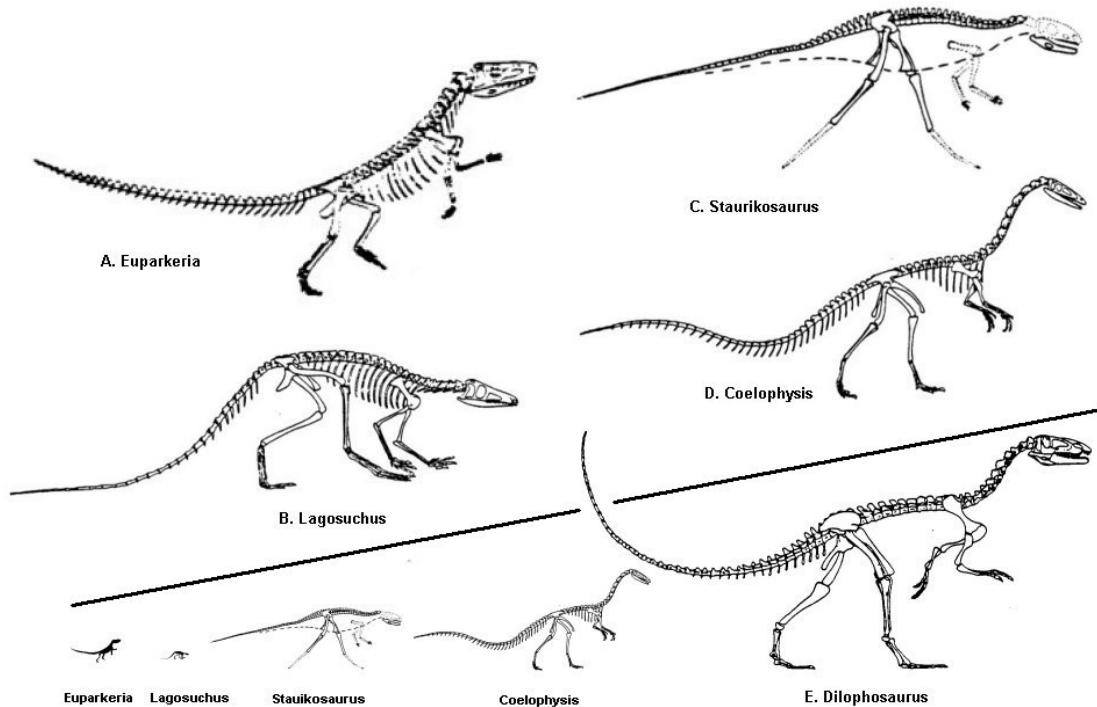


Figure 4. From thecodonts to dinosaurs. Note the gracile morphology and slender bones. A. *Euparkeria*, ornithosuchian thecodont, Early Triassic, length 50 cm, from Ewer (1965). B. *Lagosuchus*, ornithosuchian thecodont, Middle Triassic, length 30 cm, from Bonaparte (1978). C. *Staurikosaurus*, very primitive saurischian dinosaur, Middle-Late Triassic, length 2.1 m, from Galton (1977). D. *Coelophysis*, theropod dinosaur, Late Triassic, length 2.5 m, from Colbert (1972). E. *Dilophosaurus*, theropod dinosaur, Early Jurassic, length 6 m., from Welles (1984). The figures below the diagonal line are drawn to scale.

Another group of Triassic dinosaurs, the prosauropods, were similarly constructed, though they were somewhat larger and more robust than the coelurosaurs. In *Anchisaurus*, “[t]he neck was probably long, slender and flexible, as was the back, giving these animals a rather long-bodied look.”⁴⁶ Neck elongation was especially acute in *Massospondylus*. (Extremely long necks also characterized the Jurassic sauropods: *Mamenchisaurus*, a 22-meter sauropod from the Late Jurassic, had a neck 10 meters long.) Unlike the coelurosaurs, most prosauropods were only partially bipedal.

⁴³ Carroll, 1988.

⁴⁴ Halstead and Halstead, 1981.

⁴⁵ Bakker, 1986.

⁴⁶ Norman, 1985.

Melanorosaurus, a ten-meter-long prosauropod from the Middle and Late Triassic, was a quadruped.

During the Late Triassic, gracility and elongated extremities (legs, neck and tail) were the norm rather than the exception. For example, the earliest (sphenosuchian) crocodiles (Fig. 5), which descended from thecodonts and appeared in the Middle Triassic, were very lightly constructed. In contrast to modern amphibious crocodiles, which are quite robust, the Triassic crocodiles “had very long slim limbs and were almost certainly agile, terrestrial forms.”⁴⁷ *Terristrisuchus*, for instance, has been characterized as “extremely gracile.”⁴⁸ Several primitive crocodiles, such as *Hesperosuchus* and *Gracilisuchus* (Fig. 5E), were facultatively bipedal and were originally thought to be thecodonts. To be sure, most of these early crocodiles were quite small, less than a meter in length, but they and their cousins, the dinosaurs, were almost always more lightly constructed than therapsids of similar size.

(Exceptions to this trend toward lightly built skeletons and elongated limbs and necks included the phytosaurs and aetosaurs, both of which were armored quadrupedal thecodonts, and the rhynchosauroids, relatives of modern lizards. Most of these groups were extinct by the end of the Triassic.)

Even the most distant relatives of the dinosaurs were built along similar lines. In the ancestors of the giant marine reptiles, “the one noticeable specialization is a considerable elongation of the neck vertebrae.”⁴⁹ Colbert found this ‘specialization’ especially puzzling: “Every now and then the paleontologist encounters a fossil that baffles him thoroughly, a specimen that defies all attempts to explain how it could have lived. The characters of the skeleton are so grotesque that one is hard pressed to guess what they mean in terms of adaptation to the environment. Such a fossil is *Tanystropheus* from the Middle Triassic of Europe.”⁵⁰ What Colbert found so baffling was the animal’s incredibly long neck. *Tanystropheus* was only two or three meters long but its long serpentine neck accounted for half that length (Fig. 5D). Although its limbs, tail and skull were well proportioned, each of the ten neck vertebrae were grossly elongated. Indeed, *Tanystropheus* was so bizarre that early workers believed that the neck and body came from different animals – the neck belonging to a pterosaur and the body to a dinosaur. Recently, a worker has suggested “that the adult life must have been spent in the water, for it is difficult to envisage how such a long neck could be supported on land.”⁵¹ Where have we heard that before?

⁴⁷ Carroll, 1988.

⁴⁸ Ibid.

⁴⁹ Romer, 1966.

⁵⁰ Colbert, 1965.

⁵¹ Paraphrased in Carroll, 1988.

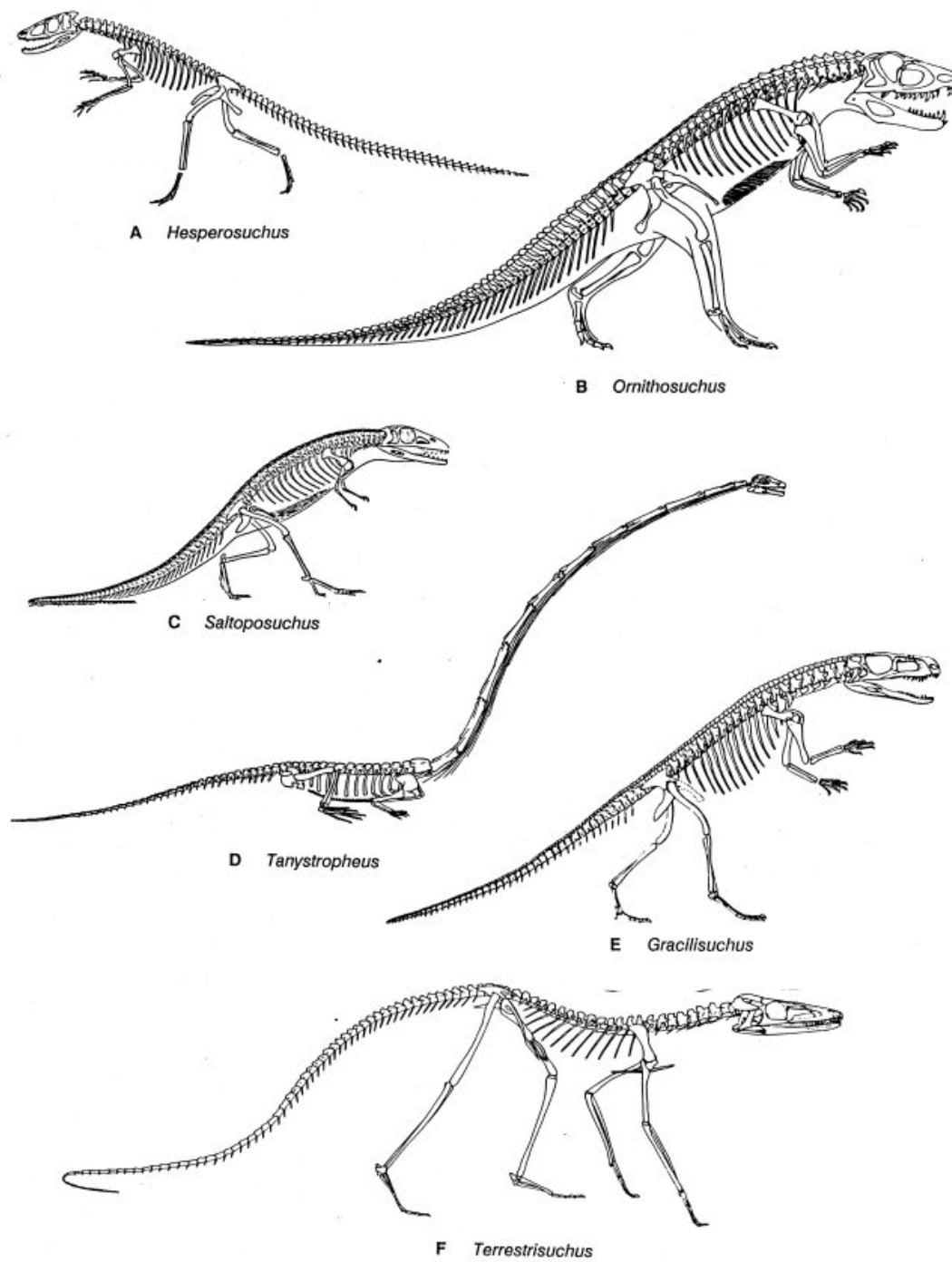


Figure 5. Some non-dinosaur diapsid reptiles from the Triassic. Note the dinosaur-like morphology. A. *Hesperosuchus*, sphenosuchian crocodile, Late Triassic, length 1.3 m, from Colbert (1952). B. *Ornithosuchus*, ornithosuchian thecodont, Late Triassic, length 4 m, from Walker (1964). C. *Saltoposuchus*, sphenosuchian crocodile, Late Triassic, length 1 m, from Huene (1936). D. *Tanystropheus*, protorosaur, Middle Triassic, length 3 m, from Wild (1973). E. *Gracilisuchus*, sphenosuchian crocodile, Late Triassic, length 30 cm, from Romer (1972). F. *Terrestrisuchus*, sphenosuchian crocodile, length 50 cm, from Crush (1984). Figures are not drawn to scale.

Summary

“Vertebrate paleontology is comparative osteology in the time dimension.”⁵² Skeletal scaling principles and biomedical space research suggest that natural selection in reduced gravity will favor bone thinning, a relative decrease in skeletal mass, and an increase in the uppermost limit to body size. These predictions are borne out in the fossil record: the Late Triassic witnessed the proliferation of gracile, long-limbed and lightly-constructed diapsid reptiles (thecodonts and dinosaurs) at the expense of the synapsid (mammal-like) reptiles, animals that were much more compact, cumbersome and massively-constructed. Giant dinosaurs, such as *Melanosaurus*, were already present in the Late Triassic, followed soon thereafter by the largest of all land-living animals, the sauropods.

Dinosaur Giantism

The sauropods began their long evolutionary history as giants; one might say that geologically speaking they became instantaneous giants, because the first of these great dinosaurs is found in rocks of very early Jurassic age.

– Edwin H. Colbert⁵³

Barapasaurus, from the Early Jurassic, was one of the first true sauropods. At twenty-five meters in length,⁵⁴ *Barapasaurus* was the largest animal that had yet evolved. Prior to the Mesozoic, the largest land animals were herbivorous pelycosaurs from the Permian, sprawling quadrupeds that rarely exceeded four or five meters in length. The very existence of *Barapasaurus* demonstrates that powerful selection pressures favoring giantism were at work during the Mesozoic, pressures that simply were not operative during the Paleozoic. But more important, the appearance of *Barapasaurus* so early in the age of dinosaurs belies the notion that the evolution of dinosaur giantism was a protracted and incremental process, à la Cope’s Law.⁵⁵ Although dinosaur giantism did not reach its zenith until the Late Jurassic, gigantic dinosaurs appeared quite early.

Every schoolchild knows that dinosaurs were the largest land animals that ever lived. Yet professional paleontologists are forever pointing out that ‘not all dinosaurs were giants.’ And indeed, *Compsognathus*, from the Late Jurassic, was quite small, about the size of a chicken. But for the most part, dinosaurs were big – very big. Estimates of median dinosaur mass range from 500 kg to 5 metric tons; and a safe estimate, perhaps a bit conservative, would be one ton. The biggest finds on record may well have exceeded 100 tons, about the size of a Blue Whale. And given the astronomical odds against the fossil preservation of any given animal, it is nearly certain that larger dinosaurs existed but were not preserved or have not yet been found.

⁵² Davis, 1963.

⁵³ Colbert, 1983.

⁵⁴ Galton, 1986.

⁵⁵ Bakker, 1980.

During the Jurassic Period, giant dinosaurs were the rule not the exception. Eighty percent of the biomass from the Late Jurassic Morrison formation of the western United States consisted of stegosaurs and sauropods; the latter average 20 tons.⁵⁶ Nevertheless, everything about these giants belies their enormous size: “Surprisingly, the joint surfaces of the [sauropods] limbs are poorly defined, and there must have been a good deal of cartilage in the carpus and tarsus as well. The capacity for the cartilage to yield under pressure and conform to a shape that would most effectively distribute the force produced by the weight of the body was apparently more important than the greater per unit strength of bone.”⁵⁷

The bipedal theropods were of course much smaller than the giant sauropods. But many of these ‘small’ dinosaurs were still quite large. Until recently, Tyrannosaurus, from the Late Cretaceous, was thought to be the biggest biped, but other theropods of equal or even larger size from the Late Jurassic have been unearthed.⁵⁸ The mass of these ‘small’ dinosaurs was ‘only’ four or five tons.

The typically large size of the dinosaurs, and the comparatively small size of modern mammals, has been quantified by Nicholas Hotton.⁵⁹ Based on 63 dinosaur genera, Hotton’s data yield an average generic mass in excess of 850 kg (about the size of a grizzly bear) and a median generic mass of nearly 2 tons (comparable to a giraffe). This contrasts sharply with extant mammals (788 genera) whose average generic mass is 863 grams (a large rodent) and a median mass of 631 grams (a smaller rodent). The smallest dinosaur was bigger than two-thirds of all living mammals; the majority of dinosaurs were bigger than all but 2% of living mammals.

Robert Bakker believes that Hotton has overstated the size difference.⁶⁰ Bakker maintains that the modern fauna – dominated by very small mammals and devoid of very large ones – is atypical in the history of mammals. Yet even when all of the mammals smaller than the smallest dinosaur (4 kg) are excluded from Hotton’s data set, the size gap between the mammals and dinosaurs is only marginally reduced: the average generic mass of mammals is raised to 36 kg (a large dog) and median mass is raised to 25 kg (a smaller dog). Both values are still orders of magnitude less than dinosaurs.

In order to balance the scales as it were, Bakker compared Late Jurassic dinosaurs with mammals from the Miocene and Pliocene, which Bakker characterized as “the Age of Mammal Giants.”⁶¹ But Bakker’s histograms (which, incidentally, do not include any mammals under 1 kg) still reveal a significant in difference in size.⁶² A comparison of

⁵⁶ Bakker, 1980.

⁵⁷ Carroll, 1988.

⁵⁸ Geotimes, Feb. 1990.

⁵⁹ Hotton, 1980.

⁶⁰ Bakker, 1980.

⁶¹ Bakker, 1980.

⁶² Both Hotton (1980) and Bakker (1980) depicted their data on log-vs-linear histograms, with body mass given as the log values. Hotton split his sizes into 0.1 log ranges; Bakker lumped his data into 1-log ranges. My numbers are extrapolated from these histograms. With respect to Bakker’s histograms, I

Miocene mammals with Late Jurassic dinosaurs (from the Tendagaru formation) yields a median mass of 316 kg for both mammals and dinosaurs, but an average specimen mass of 125 kg for the mammals versus 418 kg for the dinosaurs. The size difference is much more pronounced when comparing Pliocene mammals with Morrison dinosaurs. The average and median mass of Pliocene mammal species was about 300 kg and 316 kg, respectively, versus an 1895 kg average mass and 3162 kg median mass for Jurassic dinosaurs from the Morrison formation. When compared to the modern fauna, the Miocene-Pliocene may have been an age of giants, but it pales in comparison to the Late Jurassic.

Bakker's desire to narrow the size gap between mammals and dinosaurs stems, in part, from his personal belief that dinosaurs were ecologically and physiologically similar to mammals. Hotton, by contrast, rejects dinosaur endothermy as unnecessary and untenable. He argues that size alone could have enabled dinosaurs to maintain a constant body temperature (mass homeothermy). But quite apart from the problem of dinosaur physiology (discussed later), no one on either side of the debate has been able to explain why dinosaurs grew so large, or why animals of dinosaurian dimensions were limited to the Mesozoic.

Accustomed with the typically large size of dinosaurs, most scientists take dinosaur giantism for granted. As a result, they tend to ignore or belittle the very real mechanical problems associated with size. But to early workers, the large size of the 'terrible lizards' was a problem of the first order. William Buckland, who lived in the mid-nineteenth century, believed the earliest known dinosaurs, *Megalosaurus*, *Iguanodon*, and *Hylaeosaurus*, which he and his wife discovered, were "the most gigantic of all quadrupeds that have ever trod upon this planet."⁶³ Acutely aware of the problems of size and unjaded by familiarity with the dinosaurs, the Victorians reconstructed these dinosaurs as heavily muscled sprawling quadrupeds. Yet, as we now know, the dinosaurs in question were only medium-sized, and they were bipeds to boot.

When the first sauropod was discovered in the 1840s, Richard Owen believed it to be much too large to live on land and therefore decided that it must have been a marine lizard. His name for it – *Cetiosaurus*, or 'whale-lizard' – reflected this belief. However, the discovery of weight-bearing limbs proved that *Cetiosaurus* was in fact a land dweller, a notion that Owen found difficult to accept. Accordingly, he decided that *Cetiosaurus* must have spent its life in lagoons and swamps, where its enormous mass could be supported buoyantly in water.⁶⁴ Thus was born the amphibian theory of sauropods.

Many leading paleontologists have subscribed to the amphibian theory. "The legs of sauropods were large," wrote A.S. Romer in 1966, "but even so, it seems doubtful whether they could have borne so many tons of weight. For his reason [and others], it appears probable that the sauropods were amphibious types that spent most of their lives in lowland swamps and lagoons where they were buoyed up by the water, and the

assigned a median value for each size class – thus, animals in the size range $10^2 - 10^3$ grams were assigned a mass of $10^{2.5}$ grams.

⁶³ Quoted in Desmond, 1976.

⁶⁴ Desmond, 1976.

problems of support and locomotion were greatly simplified.”⁶⁵ Bjorn Kurten concurred: “It must be assumed that the sauropods normally dwelt in water, where their weight would cause no trouble, since it was buoyed up by the water.”⁶⁶

This amphibian theory of sauropods was held almost universally until Bakker convincingly demonstrated that sauropods did not live in water but were actually land-dwellers, more like high-browsing giraffes than wallowing hippos.⁶⁷ The long erect limbs and deep rib cage of sauropods are similar to those of elephants and other large terrestrial mammals, and quite unlike the short, stubby limbs and barrel-shaped torso of hippos, which spend most of their lives in water. Moreover, sauropod fossils are typically found in well-drained floodplain or fluvial deposits, and not in lakes or swamps.

Bakker believes that dinosaurs were the Mesozoic analogues of modern terrestrial mammals, with sauropods being the dinosaur equivalent of giraffes. He makes a convincing case. But in solving the problem of sauropod ecology and behavior, Bakker has unwittingly reopened the problem of dinosaur giantism. In removing these giants to dry land, Bakker has thrown out the sauropods with the swamp water, for the *raison d'être* of amphibian sauropods – the reason they were relegated to the swamps in the first place – was their gigantic size. Bakker, of course, maintains that sauropods were not anomalously large and hence denies that there is any problem at all. Calculations of sauropod bone strength by Alexander lend support to this view,⁶⁸ but Alexander's conclusions are only as good as his estimates of dinosaur mass, which I suspect are probably low. For example, Colbert estimated that *Brachiosaurus* had a mass in excess of eighty tons⁶⁹ whereas Alexander's estimate is less than fifty.⁷⁰

Perhaps the most relevant analysis of terrestrial giantism is by Economos.⁷¹ Citing centrifugal hypergravity experiments, Economos noted that “small mammals could adapt and survive for extended periods of time in stronger fields than large mammals. If terrestrial gravity is expresses as 1G, a mouse tolerates 7G, a rat 5G, a dog and chicken 3G; the approximate value for man is about 1.7G. Conceivably, as the magnitude of the tolerable field or ‘gravitational tolerance’ decreases with increasing body mass, an upper limit for body size would be reached, that ‘largest’ mammal having a gravitational tolerance equal to terrestrial gravity.” From these data, Economos derived the following power-law function that relates body mass m (in kg) to gravitational tolerance G_{\max} .

$$G_{\max} = 4 m^{-0.14} \quad (6)$$

Based on Equation (6), Economos calculated that the maximum possible body size for land mammals – where G_{\max} equals one – “is found to be about 20,000 kg, which agrees with the estimated body mass of *Baluchitherium*.”

⁶⁵ Romer, 1966.

⁶⁶ Kurten, 1968.

⁶⁷ Bakker, 1971b.

⁶⁸ Alexander, 1985; Alexander, 1989.

⁶⁹ Colbert, 1962.

⁷⁰ Alexander, 1989.

⁷¹ Economos, 1981.

At 20 tons, *Baluchitherium*, a rhinoceros from the late Oligocene and early Miocene, was the largest of all land mammals, living or extinct. Compared to a modern rhino or elephant, *Baluchitherium* was truly gigantic. But according to Bakker, 20 tons was only the average size of Morrison sauropods. Larger sauropods, of 50 or even 100 tons, are known to have lived. How did they support themselves? Economos, together with an earlier generation of paleontologists, opted for the amphibian solution: “Apparently, the buoyancy of water has made possible the evolution of sea mammals much larger than the largest land species. (This was also true of dinosaurs.)”⁷² Bakker, however, has shown that sauropods were land-dwellers; hence, they could not rely on buoyancy to support their bulk. Thus, we have a paradox: either 20 tons is the maximum size for a land animal, in which case Bakker is wrong about the terrestrial habits of sauropods, or else Economos is wrong and land animals larger than 20 tons can exist.

There is, of course, a simple solution to this paradox, a solution that validates Bakker’s empirical findings without violating Economos’s theoretical analysis. Reduced gravity during the Jurassic would have permitted land animals to achieve body sizes not possible under present-day conditions. In a previous section, it was argued based on the skeletal scaling Equation (3) that a 20% reduction in gravity would permit an order of magnitude increase in body mass of the very largest land animals without any increase in the fraction of body mass devoted to the skeleton. The mass of the largest sauropods was probably about 100 tons. It is therefore worth noting that for $G_{\max} = 0.8G$, Economos’s Equation (6) yields a maximum body size of about 100 metric tons.

Locomotion in Reduced Gravity

Practically all the work done in walking and running is against gravity.

– Rodolfo Margaria⁷³

When American astronauts went to the Moon in the late 1960s and early 1970s, they discovered that walking and running, the normal bipedal gaits of humans on Earth, were ineffective on the Moon where gravity is 1/6 that of Earth. But the astronauts discovered that by modifying their locomotive behavior, and shifting to a skipping or hopping gait, they could move about quickly with relatively little effort or exertion. The Apollo astronauts adapted to lunar gravity by changing gait. Dimensional analysis, based on the principle of dynamic similarity, helps explain why they did this and provides a simple and elegant approach to the problem of gait selection.

Dynamic similarity is an application of the pendulum principle – the interaction between gravity and inertia. “Motions are said to be dynamically similar if they could be made identical by uniform changes of the scales of length and time.”⁷⁴ Thus, two pendulums of

⁷² Economos, 1981.

⁷³ Margaria, 1976.

⁷⁴ Alexander, 1982a.

different lengths but identical angular amplitude are dynamically similar. Likewise, two running animals with different leg lengths but the same ratio of stride-length-to-leg-length are also dynamically similar. Mathematically, pendulums (and running animals) are dynamically similar if they have equal Froude numbers – $\mathbf{u}^2/g\mathbf{l}$ – where \mathbf{u} is a characteristic speed, \mathbf{g} the acceleration of gravity, and \mathbf{l} a characteristic length. When Froude numbers are applied to animal locomotion, \mathbf{u} refers to forward velocity and \mathbf{l} to leg length.

It has been found that animals ranging in size from small rodents to horses use similar gaits and equal values of (stride length/leg length) at any given Froude number. More to the point, gait transitions tend to occur at particular Froude numbers. “Men break into a run and kangaroos and crows change from walking to hopping at Froude number around 0.6, about the same as the Froude numbers at which quadrupedal mammals change from walking to a faster symmetrical gait.”⁷⁵ In order to achieve maximum speed, quadrupeds will shift from a symmetrical gait, such as a trot, to an asymmetrical gait, such as a gallop. Thus gait transition occurs at Froude numbers between 2 and 3.

Dimensional analysis of gait transition helps explain the problems encountered by the Apollo astronauts when they attempted to walk and run in lunar gravity, and why they found skipping and hopping to be so effective. Gravity is one of the Froude number variables. If gait transition occurs within a narrow range of Froude numbers, then a reduction in gravity will necessarily lower the speed at which a human astronaut (or any other animal) shifts to a higher gait.

The Mechanics, Dynamics and Energetics of Animal Locomotion

These considerations are brought into sharper focus by understanding the mechanics, dynamics and energetics of animal locomotion. Bipeds are capable for four distinct gaits: walking, running, ‘skipping’, and hopping. Adult humans normally employ the first two gaits, but children, because of their high energy and low mass, frequently shift to a ‘skipping’ gait at intermediate speeds. Hopping is unnatural for humans but is quite common in small mammals and birds and, of course, kangaroos. Quadrupeds on the other hand, have a much larger repertoire of gaits: walk, amble, trot, pace, canter, transverse gallop, rotary gallop, bound and pronk.⁷⁶ For our purposes, these nine gaits can be reduced to four – walk, trot, gallop, and bound. Hind limb movement in these quadrupedal gaits is mechanically similar to the four bipedal gaits.

⁷⁵ Alexander and Jayes, 1983.

⁷⁶ Hildebrand, 1985.

Bipeds	Quadrupeds	Temporal Spacing of Footfalls	Leg-pair Swing	Characteristic Phase	Relative Stride	
					Rate	Length
Walk	Walk	Symmetrical	Alternating	Supported	Low	Short
	Amble				High	
Run	Trot			Suspended	Medium	
	Pace				High	
'Skip'	Canter	Asymmetrical	Synchronized	Aerial	Low	Long
	Gallop					
Hop	Bound					
	Pronk					

Table 2 – A Comparison of Bipedal and Quadruped Gaits

As shown in Table 2, these four gaits differ with respect to footfall sequence, characteristic phase, stride rate, and stride length. Walking and running (trotting) employ alternating leg swings; they are said to be symmetrical gaits because the spacing of footfalls is evenly distributed through time. The two gaits differ in that walking is a supported gait – at least one foot is on the ground at all times – while running (trotting) is a suspended gait – all feet are off the ground momentarily while the body is suspended in midair between footfalls. Skipping (galloping) also employs a suspended phase; but unlike running (trotting), skipping is an asymmetrical gait: footfalls are unevenly distributed through time and leg-pair motion is synchronized. Finally, hopping (bounding) is an asymmetrical gait characterized by an aerial phase, which is simply a prolonged suspended phase when the animal is propelled high off the ground.

For any gait, animals tend to move at their most ‘comfortable’ or economical speed. They change gait for energetic reasons.⁷⁷ Changing gait minimizes the metabolic cost of locomotion at higher speeds, much as shifting to higher gears in an automobile lowers engine speed and conserves fuel.

Walking, the slowest form of locomotion, is also the most economical. It relies on gravity as its primary energy source.⁷⁸ The gravitational potential energy acquired at the beginning of each step, when the body is raised through the leverage action of the legs and feet, is converted into kinetic energy (forward motion) during the second (downward) phase as the body falls forward under gravity. This is known as ‘ballistic walking’.⁷⁹ Walking is a supported gait: balance and stability are maintained by keeping at least one foot on the ground at all times.

Because ballistic walking is powered by gravity, muscular exertion is kept to a minimum with obvious energy-saving benefits. The optimum speed of ballistic walking – the most comfortable and efficient speed – is probably dictated by the natural frequency of the

⁷⁷ Alexander, 1982b; Bennett, 1985.

⁷⁸ Margaria, 1976; Alexander, 1982b; McMahon, 1984.

⁷⁹ McMahon, 1984.

pendulum-like limbs. Swinging the legs faster or slower than their natural frequency requires the application of muscle power. Otherwise, muscles need only provide enough energy to help support the body, overcome inertia when beginning to walk, raise the body at the beginning of each step, and lift the feet between steps. Because it uses gravity and inertia instead of muscles and metabolism, walking is very efficient at low speeds.

The speed of locomotion is the product of stride length times stride rate. In walking, stride length is limited by leg length and the arc swept out by the legs swinging from the hips. Consequently, stride length cannot be increased without introducing a suspended phase, i.e. by shifting to a running gait. The only way to walk faster than normal is by increasing stride rate. But swinging the legs faster than their natural frequency requires muscular exertion. Therefore, as walking speed increase, there comes a point at which ballistic walking is no longer practical. The muscles are doing most of the work so the economies provided by ballistic walking no longer apply. Moreover, the application of muscle power enables the animal to propel itself forward and float momentarily between steps – the suspended phase – which effectively increases stride length. At this point, a biped will abandon walking and begin to run, and a quadruped will begin to trot.

With respect to energetics, walking and running are radically different gaits. Whereas a walking biped *falls* forward under gravity, a running biped *propels* itself forward by applying muscular (i.e. metabolic) energy to its leg-levers. Running speed can be raised by increasing stride rate, stride length, or both. Stride rate is increased by swinging the legs faster than their normal frequency (by applying additional muscle power to the legs) and by bending the legs (shortening their length) during the recovery stroke when the feet are off the ground.⁸⁰ Stride length is increased by introducing a suspended phase: a running or trotting animal will ‘leap’ from one step to the next and ‘float’ forward momentarily between steps when both feet are off the ground. The suspended phase is the characteristic dynamic state of running. But the application of muscle power to the legs in order to increase stride rate and stride length requires metabolic input and naturally incurs an oxygen debt. Hence, a walker will always outdistance a runner; the latter will eventually ‘run out of gas.’

Gravitational potential energy is effectively wasted when an animal runs or gallops.⁸¹ Nevertheless, a vertical component is required to elevate the animal high enough off the ground to enable it to move its legs forward during the suspended phase. In suspended gaits, the vertical component is equal to body weight; the animal’s center-of-mass remains at a relatively constant elevation above the ground. If, however, the vertical component *exceeds* body weight, the animal will be propelled vertically as well as forward: the center-of-mass follows a parabolic ballistic path between footfalls. When this occurs, the animal has shifted to an aerial gait, i.e. hopping in bipeds, and bounding or pronking in quadrupeds.

In many respects, hopping is a blend of walking and running; it combines the best of both worlds. Like walking, it converts the gravitational potential energy acquired at the height

⁸⁰ Gray, 1968.

⁸¹ Margaria, 1976.

of each jump into the kinetic energy of forward motion. (In specialized hoppers, such as kangaroos, much of this gravitational energy is converted into elastic energy stored in tendons upon impact, and then converted into kinetic energy during the next power phase.⁸² More on this in the next chapter.) Like running, hopping employs a suspended phase (or, more accurately, an aerial phase), with both feet off the ground, in order to increase stride length. However, this protracted aerial phase reduces the duty factor (i.e. the fraction of each step cycle when the feet are on the ground) and therefore requires a reduction in stride rate that, as in walking, approaches the natural frequency of the limbs; the limbs swing leisurely back and forth between footfalls. The reduction in stride rate is more than offset by the enormous increase in stride length.

But hopping is also quite different than walking and running. Walking and running are symmetrical gaits: footfalls alternate – first one foot, then the other – to ensure stability and balance. Hopping, however, is an asymmetrical gait and footfalls are concurrent which permits the two legs to apply their power simultaneously. This has two benefits. First, it minimizes lateral displacements in the center-of-gravity and helps maintain inertial stability during the aerial phase when the feet are off the ground. It also allows the animal to land squarely on both feet in preparation for the next step. Second, having both legs kick simultaneously creates a much more forceful power stroke. Thus, whereas a running biped must apply a downward force that is approximately equal to body weight, a hopping biped can apply a force with no real limit, and well in excess of body weight.

For obvious reasons, aerial gaits are generally limited to small, lightweight animals such as birds, kangaroo rats, squirrels and dik-diks. (The one notable exception, the kangaroo, is discussed in the next two chapters.) Because aerial gaits require a vertical component that exceeds body weight, only the very smallest and lightest animals have the requisite power (relative to body weight) to propel their bodies off the ground.

This rather lengthy analysis of tetrapod locomotion helps explain why the Apollo astronauts abandoned walking and running in favor of skipping and hopping. In reduced gravity, the decrease in gravitational potential energy requires a corresponding decrease in kinetic energy and hence a reduction in forward velocity. Reduced gravity also makes the limb-pendulums swing more slowly: “at reduced gravity, such as on the surface of the Moon, the period of the system increases and the step frequency correspondingly decreases.”⁸³ Accordingly, walking speed on the Moon is much lower than it is on Earth and does not exceed 2 km/hr.

The reason that running on the Moon proved so difficult is less obvious but is still basically the same. The forceful application of leg power in the running gait not only propelled the astronauts forward but also launched them high off the surface, which effectively disrupted the rhythm of their normal symmetrical gait. In other words, because of their high stride rate, the astronauts’ legs and feet were positioned for the next step before their bodies had floated back to the surface. In reduced gravity, therefore, the

⁸² Dawson, 1977.

⁸³ Margaria, 1976; see also McMahon, 1984.

aerial hopping gait was doubly beneficial: it enabled the astronauts to take advantage of their high power-to-weight ratio *and* permitted a lower stride rate as well.

The Affect of a Gravity Reduction on the Evolution of Animal Locomotion

What affect, then, would a gravity reduction have on the evolution of tetrapod locomotion? Dimensional analysis indicates that a gravity reduction will lower the speed of gait transition and thus enable animals to shift to higher gaits at lower speeds. At the same time, a reduction in gravity will tend to favor lower stride rates. This suggests that when shifting from a walk to a higher gait, animals may bypass the suspended gaits (running, trotting and galloping), which employ high stride rates, and go directly to aerial gaits (hopping, bounding or pronking) for which a high stride rate is not necessary. The reduction in body weight would make aerial gaits all the more attractive. The experience of the Apollo astronauts supports these expectations.

The astronauts, of course, were already bipedal when they went to the Moon. Their morphology was such that shifting to a bipedal hopping gait required merely a minor change in *behavior*. But early archosaurs were quadrupeds; the shift to an obligatory bipedal gait involved fundamental changes in body structure. In the next chapter, we will discuss archosaur locomotion and limb mechanics and the possible role played by a gravity reduction in the evolution of archosaur locomotion and morphology.

Bipedality and the Fully Erect Gait

The reason predatory dinosaurs became bipedal is not at all clear. [...] The only thing that can be said in the end is that bipedalism was a serendipitously crucial adaptation....

– Gregory S. Paul⁸⁴

The earliest known biped was the Early Triassic thecodont *Euparkeria*. (Fig. 4A). Though normally quadrupedal, this small reptile was capable of shifting to a bipedal gait when moving quickly. In the Middle and Late Triassic, bipedality became increasingly common among the thecodonts and evolved independently in several lineages including the one that led to the dinosaurs. The oldest known dinosaur, *Staurikosaurus* from the Late Triassic, was a biped. (Fig. 4C).

All dinosaurs, with the possible exception of the sauropods,⁸⁵ descended from bipedal ancestors. All of the carnivorous theropods, from *Staurikosaurus* in the Late Triassic to *Tyrannosaurus* in the Late Cretaceous, were obligatory bipeds. Among the herbivorous dinosaurs, all of the early ornithischians, such as *Fabrosaurus*, from the Early Jurassic, were obligatory bipeds; most of the later ones, such as *Iguanodon* from the Jurassic and *Hadrosaurus* from the Cretaceous, were at least habitual bipeds. Stegosaurs and sauropods were quadrupedal, but many of them, including such giants as *Diplodocus*,

⁸⁴ Paul, 1988.

⁸⁵ Stahl, 1974

were capable of rearing up on their hind limbs and tail to browse in the treetops. Indeed, of all the dinosaurs, only the armored ankylosaurs and horned ceratopsians, from the Cretaceous Period, seem to have been obligatory quadrupeds, incapable of ever assuming a bipedal pose.

The question of how and why bipedality evolved has received surprising little ink or attention. Perhaps paleontologists regard the problem as uninteresting or unimportant. But the ubiquity of dinosaur bipeds, contrasted with the rarity of bipeds among other large animals, suggests otherwise. Why did bipedality evolve? What selective advantages did it confer that made it preferable to a four-legged pose? And why was it so common among the dinosaurs?

Evolution of the Fully Erect Gait

It is generally agreed that the fully erect gait is the absolute diagnostic feature that sets dinosaurs apart from all other reptiles, including thecodonts. Although it is important to distinguish between the anatomical changes associated with the fully erect gait, on the one hand, and the shift to a bipedal gait, on the other,⁸⁶ their concurrent development in the early archosaurs suggests that the two were intimately related.

By most accounts,⁸⁷ there were three phases in the evolution of archosaur locomotion and gait: (1) the primitive *sprawling gait*; (2) the intermediate *semierect gait*; and (3) the advanced *fully erect gait*. The most primitive thecodonts, the proterosuchians, were sprawling quadrupeds. The more advanced ornithosuchian thecodonts and crocodiles had a variable semierect gait; some of them were incipient bipeds. And the earliest dinosaurs, which descended from the ornithosuchians, were obligatory bipeds with a fully erect gait.

The primitive sprawling gait “probably was already standardized at the end of the Devonian or beginning of the Carboniferous, long before the first reptile appeared.”⁸⁸ In the sprawling gait, the upper limbs extended horizontally from the pelvis and shoulder and are joined at the knees and elbows to vertical lower limbs, in an inverted L- shape. Leg motion describes a wide sweeping arc of the upper limbs with complex long axis rotations of the lower limbs. The proterosuchian thecodonts, from the Late Permian, were, like most of their contemporaries, low-slung sprawling quadrupeds showing “little if any trend towards bipedalism that was so marked in archosaur evolution.”⁸⁹ (See Fig. 3.)

Beginning with *Euparkeria* in the Early Triassic, all thecodonts above the proterosuchian grade were equipped with a variable semierect gait. When it moved slowly or stood still, *Euparkeria* held its hind limbs in a horizontal sprawling position; but when it ran, the legs were brought beneath the body into a more upright configuration. The semierect gait effectively raised the body higher off the ground, narrowed the trackway, increased

⁸⁶ Charig, 1972

⁸⁷ Bakker, 1971a; Desmond, 1976; Charig, 1979.

⁸⁸ Bakker, 1971a.

⁸⁹ Colbert, 1969.

stride length, and permitted faster locomotion. Deflecting the hind limbs down and inward greatly simplified leg motion by bringing it closer to the ideal of a freely swinging pendulum, a condition that was ultimately achieved in the dinosaurs. It also enabled *Euparkeria* to shift from a quadrupedal to a bipedal gait when moving quickly.⁹⁰

During the Middle Triassic, when the mammal-like reptiles were being challenged by a “bewildering variety of thecodonts,”⁹¹ bipedality and an increasingly upright gait continued to develop in tandem in several thecodont lineages. In the advanced ornithosuchian thecodonts, such as *Lagosuchus*, an animal very close to the common ancestry of the dinosaurs, the limbs were almost fully erect as indicated by a sharply inwardly turned femoral head approaching the dinosaurian condition. (Figs. 4B and 6.) The rauisuchians, largest of all Middle and Late Triassic thecodonts, “evidently attained a vertical posture independently of the lineage that led to the dinosaurs.”⁹² Many of the ornithosuchians, rauisuchians, and even some sphenosuchian crocodiles showed a strong tendency toward bipedal locomotion as indicated by their disproportionately long hind limbs.

The final stage of archosaur limb development – the fully erect bipedal gait – was achieved by the dinosaurs and is clearly evident in *Staurikosaurus* (Fig. 4C) and *Herrerasaurus*, two of the earliest known dinosaurs.⁹³ In the fully erect gait, (also known as the fully improved gait), leg motion is restricted to the parasagittal plane (essentially vertical and limited to fore-and-aft movement) with no long axis rotation.⁹⁴ In dinosaurs, the fully erect gait was maintained by a sharply inturned and cylindrical femoral head that fit snugly into a perforated acetabulum (hip socket). In addition, the tibia tended to be dorsoventrally flattened and bowed.⁹⁵

Associated with the development of the fully erect bipedal gait were important modifications in the lower limb elements – the metatarsals and feet. In the sprawling reptiles, the pose was plantigrade: the metatarsals served as proximal foot elements – the ‘heel’ – that helped distribute body weight over the substrate. But in shifting to an upright gait, the thecodonts and dinosaurs adopted a digitigrade pose: the metatarsals were raised off the ground and converted into distal leg elements and the foot was essentially reduced to the digits alone. In thecodonts, the foot was pentadactyl; in dinosaurs, tridactyl.

Dinosaur Hip Structure and Limb Mechanics

Paleontologists generally agree that the advances in archosaur gait and locomotion played some role in the dinosaurs’ rapid and remarkable evolutionary success. Just what that role was, or what advantage it conferred, remains an open question. How it relates to the problem of dinosaur bipedality is also unclear. Bakker has interpreted the fully erect gait

⁹⁰ Ewer, 1965.

⁹¹ Bakker, 1980.

⁹² Carroll, 1988.

⁹³ Benton, 1988.

⁹⁴ Bakker, 1971a; Charig, 1972.

⁹⁵ Padian, 1986.

as indicating that dinosaurs employed mammal-like or ostrich-like gaits, i.e. the quadrupeds galloped and the bipeds ran. This capacity for high speed locomotion would have given the dinosaurs a significant edge over the slower mammal-like reptiles, animals still burdened, according to Bakker,⁹⁶ by the primitive sprawling gait. Because high-speed running and galloping gaits presumably require a high aerobic exercise metabolism, Bakker⁹⁷ has argued that dinosaurs must have been advanced endotherms, comparable to mammals and birds.

The link between the fully erect gait, on the one hand, and physiology, on the other, is central to Bakker's theory of dinosaur endothermy. John Ostrom, though more circumspect than his erstwhile student, is in general agreement. In modern tetrapods, the correlation between endothermy and an upright posture "is virtually absolute and surely is not merely coincidental."⁹⁸ But despite this correlation, Ostrom is careful to note that "no cause-and-effect relationship between posture and physiology has been established."⁹⁹

Correlation is not causation. Posture and physiology *may* be related, but not necessarily. By the same token, the relationship between posture and gait is also problematic. The dinosaurs' erect limb architecture certainly indicates a capacity for high-speed locomotion. At the very least, this undermines traditional ideas about dinosaur sluggishness. But does it necessarily imply high *running* speeds? This is the crux of the debate over dinosaur physiology. High speed running requires a high-grade physiology. But if dinosaurs, and in particular bipedal dinosaurs, did not run, then the need for high metabolic rates disappears. Although most advocates of dinosaur endothermy insist that dinosaurs ran, close examination of dinosaur hip structure suggests otherwise.

A running biped employs a suspended, symmetrical gait (see Table 2). Each step taken by a running biped produces a lateral shift in the center-of-mass resulting in a slight rotation of the body about the long axis.¹⁰⁰ In order to compensate for these displacements, a running animal must be able to shift its feet laterally – to the left and right – in order to maintain stability, especially when moving over irregular terrain.¹⁰¹

In modern cursorial mammals, the femoral head articulates with the pelvis in a flexible ball-and-socket configuration; this allows considerable freedom of leg movement and permits lateral adjustments of footfalls. "Mammals have capitalized on the capability of the ball-joint for quick adjustments of footfall, to evolve the fast cursorial locomotion of horses and camels, not to mention the acrobatics of dik-diks and mountain goats."¹⁰² Bipedal dinosaurs, however, did not possess a ball-and-socket hip structure. In dinosaurs, the femoral head was cylindrical and fit hinge-like into a deep hip socket that constrained leg motion to a narrow parasagittal plane of travel. According to Nicholas Hotton, such

⁹⁶ Bakker, 1971a; cf. Kemp, 1982 and Sues, 1986.

⁹⁷ Bakker, 1968, 1971a, 1972, 1980, 1986.

⁹⁸ Ostrom, 1980.

⁹⁹ Ibid.

¹⁰⁰ Hotton, 1980; McMahon, 1984.

¹⁰¹ Hotton, 1980.

¹⁰² Ibid, 1980.

an inflexible hip configuration would have made it impossible for dinosaurs to make lateral adjustments of footfalls: “Without comparable flexibility of the hip articulation, dinosaurs could not have attained comparable cursoriality. Small dinosaurs may have been disproportionately more agile than large ones, if instability of the hip imposed less rigid constraints on animals of lighter weight, but *the structure of the dinosaur hip joint would have precluded the speed and flexibility of mammals.*”¹⁰³ (Emphasis added.)

Hotton’s analysis calls into question Bakker’s assumption that bipedal dinosaurs were high speed *runners* and thus undermines one of his principal arguments in favor of dinosaur endothermy. But Hotton’s alternative¹⁰⁴ – that dinosaur hip structure limited them to a leisurely walking gait – is also difficult to accept given the dinosaurs’ highly specialized lower limb elements. Why would a walking animal need the flexibility provided by the mesotarsal joint? Why would a walking animal require clawed tridactyl feet? Claws provide traction, but traction is superfluous for a walking animal, which is powered by gravitational potential energy rather than leg power. And why would walking animals need dorsoventrally bowed limbs, structures clearly ‘designed’ to withstand the stresses associated with high speed locomotion? As Bakker has argued, all of these features are suggestive of high speed running, but as Hotton has shown, the dinosaur hip structure rendered high speed bipedal running impossible.

Dinosaur limb architecture is a paradox: dinosaurs had the legs and feet of a runner but the hips of a walker. Their long flexible limbs should have enabled them to run with great speed, yet their hinge-like hip joint prevented them from doing so. Clearly, dinosaurs were ‘designed’ for some other form of locomotion – a gait faster than a walk but more stable than a run. And in bipeds, the *only* plausible alternative to walking and running – the *only* gait that satisfies these requirements – is hopping.

At first glance, hopping would seem even less stable than running. But, in fact, the opposite is true: hopping is potentially *more* stable. A running biped employs a symmetrical gait: it pushes off the ground with one foot (powered phase), floats forward inertially while both feet are off the ground (suspended phase), and lands on the opposite foot in preparation for the next step (recovery phase). The consequent lateral displacements require compensatory adaptations (e.g. ball-and-socket hip, flexible pelvis, etc.) to enable the animal to maintain dynamic stability. By contrast, a hopping biped employs an asymmetrical gait: it uses *both* limbs simultaneously to push off the ground (powered phase) and to land (recovery phase). The force vector generated by the dual leg kick of a hopping biped is directed downward and to the rear, which launches the animal upward and forward with little if any lateral deviation. Accordingly, a bipedal hopping gait does not suffer from the dynamic instability inherent in the alternating running gait.

¹⁰³ Ibid, 1980.

¹⁰⁴ Ibid, 1980.

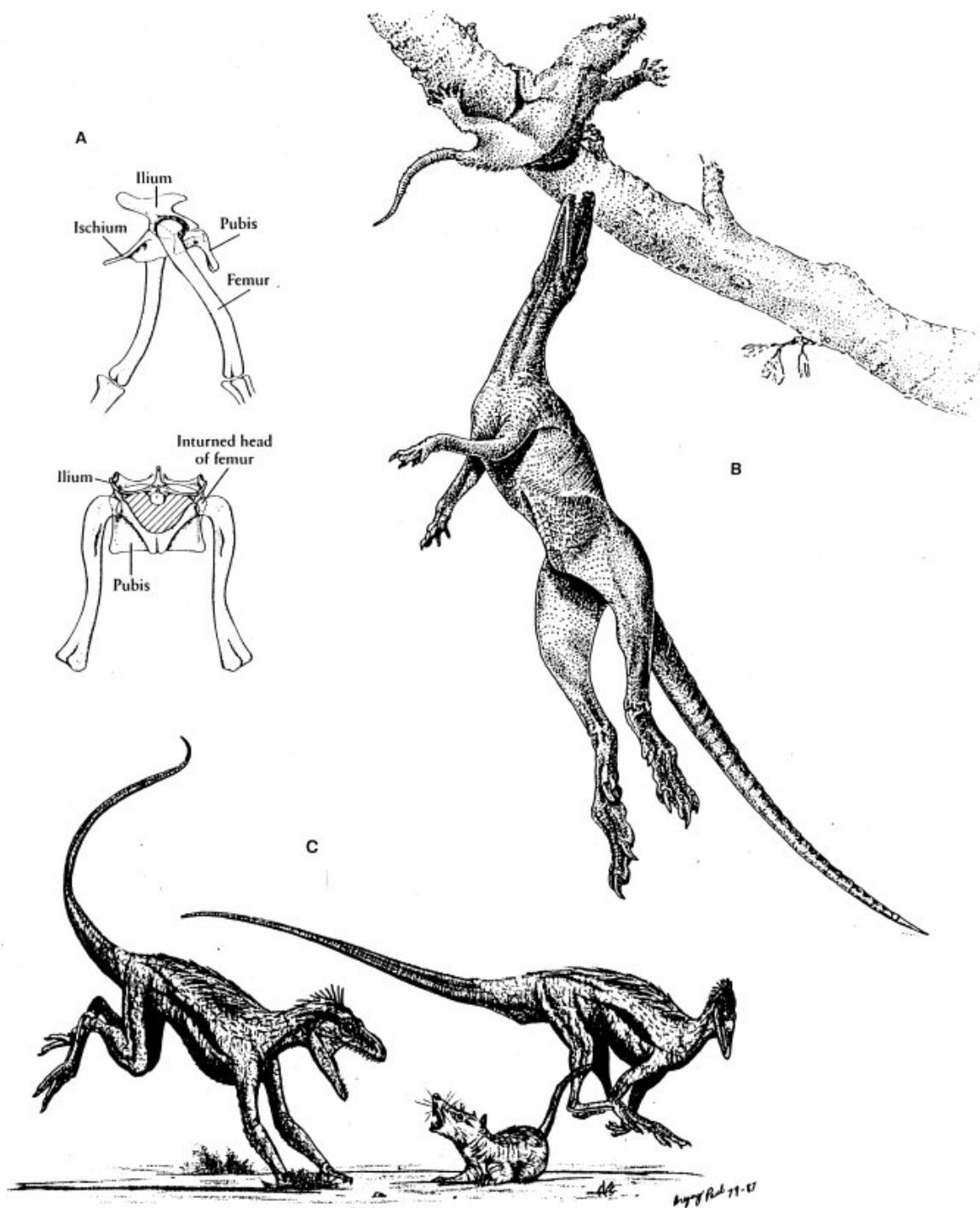


Figure 6. Lagosuchids in action. Note the asymmetrical gait. A. The pelvis and rear limbs of the lagosuchid thecodont *Lagerpeton*. B. Robert Bakker's (1986) depiction of *Lagosuchus* assaulting an early mammal. C. Gregory Paul's (1988) depiction of a similar encounter.

The instability of a symmetrical running gait requires a capacity for lateral adjustment of footfalls, a capacity that dinosaurs lacked. But in an asymmetrical hopping gait, the capacity for lateral adjustments is not only unnecessary, it is downright undesirable. Any deviation in leg motion from a purely fore-and-aft (parasagittal) plane will create a destabilizing torque and impair a hopping animal's ability to land squarely on both feet upon completion of the aerial phase. Hence, for a well-adapted hopping biped, leg motion should ideally be constrained to the parasagittal plane; and this is precisely the way dinosaur hips and limbs were designed.

The Bioenergetics of Bipedal Hopping

Selection for bipedal hopping can account for the dinosaurs' peculiar hip structure. More importantly, hopping offers unique bioenergetic benefits that no quadrupedal gait can match. Thus, it may help explain why the early archosaurs preferred bipedal hopping over quadrupedal trotting or galloping and why bipedality became fixed in the dinosaur lineages.

Gait selection in tetrapods is based in large measure on economic factors, i.e. achieving maximum speed with the least expenditure of energy. Quadrupeds shift from a ballistic walking gait to an aerobic trotting gait at intermediate speeds and, at high speeds, break into a gallop. Galloping is only marginally more efficient than trotting at high speeds, but it nevertheless is very expensive because it, too, relies on metabolic input.¹⁰⁵ However, the situation is quite different with respect to bipeds.

In bipeds, maximum speed is achieved by hopping. Hopping, like galloping, is an asymmetrical gait. But whereas galloping incurs a high metabolic cost, the metabolic cost of bipedal hopping is much lower and, indeed, actually *declines* with increasing speed. This fact is amply demonstrated by studies of kangaroo locomotion.

Kangaroo hopping is powered, to a very large extent, by elastic energy stored in large leg tendons that are anchored in the tail. The gravitational potential energy acquired at the height of each jump is converted upon impact into elastic energy, which is then converted into kinetic energy to propel the animal upward and forward in its next hop.¹⁰⁶ Because of its reliance on elastic storage and rebound, a high-speed hopping gait offers energy economies not available to animals that run or gallop. Treadmill studies have revealed that "once the [kangaroo] began to hop the [metabolic] cost leveled off and even decreased."¹⁰⁷ "Beginning at a speed of about 17 k.p.h. (11 m.p.h.), hopping appears to be more economical of energy than quadrupedal locomotion is."¹⁰⁸ Consequently, "the storage and release of spring energy makes sustained jumping more energy efficient than the quadrupedal gallop...."¹⁰⁹

¹⁰⁵ Bennett, 1985.

¹⁰⁶ McMahon, 1985.

¹⁰⁷ Dawson, 1977.

¹⁰⁸ Ibid.

¹⁰⁹ Emerson, 1985.

The evolutionary advantages of such an efficient gait are obvious. Kangaroos are marsupial mammals whose basal metabolic rate is only about 70% that of advanced placental mammals. “Since marsupials have a low metabolic rate, it is possible that they have a low maximum energy output and consequently a reduced potential for speed of locomotion. The bipedal hopping of kangaroos... could be a mechanism that helps overcome this limitation. Also important for a metabolically limited animal, particularly for a kangaroo ranging over the semiarid interior of Australia, would be economy in long-distance travel.”¹¹⁰

Bakker argues that the dinosaurs’ long erect limbs indicate a capacity for high-speed locomotion. Based on dinosaur trackways (discussed below), he believes that their preferred gait was asymmetrical running. Since a high-speed running gait requires a high aerobic exercise metabolism, dinosaurs could not have retained the cold-blooded metabolism of ‘Good Reptiles.’ Rather, they would have needed a high-grade warm-blooded physiology comparable to mammals and birds. But this line of reasoning assumes that dinosaurs ran; and, as we have seen, dinosaur hip structure probably rendered running impossible. However, if dinosaurs hopped, then high speeds would have been entirely possible without any increase in physiological grade.

Ironically, Bakker may still turn out to be correct about dinosaur physiology but in a way he never imagined. Locomotion is a form of work and work generates heat. One of the interesting side effects of the kangaroos’ elastic hopping gait is overheating. (They avoid heat stress by licking their richly vascularized forearms, which dissipates excess heat through evaporation.¹¹¹ Is it possible that the reason that marsupials are the only large hopping mammals is that the heat generated by elastic hopping would kill placental mammals?) This raises the intriguing possibility that endothermy evolved as a *consequence* of dinosaur locomotive behavior, and not the other way around, as Bakker would have it. Elastic hopping provides a non-metabolic internal heat source. If dinosaurs ultimately became ‘warm-blooded,’ as their bone histology implies,¹¹² then perhaps the energy needed to sustain high metabolic rates was generated mechanically by elastic hopping behavior.

Hopping and Obligatory Bipedality

Bipedal hopping behavior can solve many problems concerning dinosaur morphology, limb mechanics and physiology. It may also help explain the origin of obligatory bipedality. This claim may at first glance seem paradoxical or even tautological. Hopping *is* a bipedal gait. How can a bipedal gait itself be a cause of bipedality? The answer, I suggest, is that the two adaptations – the one behavioral, the other structural – evolved in tandem; that hopping and bipedality reinforced one another so as to engender and ‘perfect’ the obligatory bipedal gait.

¹¹⁰ Dawson, 1977.

¹¹¹ Ibid.

¹¹² De Ricqles, 1980.

As mentioned above, a capacity for bipedal locomotion was already evident in the ornithosuchian thecodont *Euparkeria*. Unlike the fully bipedal dinosaurs, *Euparkeria* was merely a facultative bipedal, i.e. capable of shifting to a bipedal gait when moving quickly but otherwise remaining quadrupedal. How and why *Euparkeria* was able to shift to a bipedal gait when running is not difficult to conceive. When a quadruped accelerates, the turning couple generated by the hind limbs against the body tends to rotate the body about the hips and momentarily lift the fore limbs off the ground.¹¹³ This transient effect is quite natural and commonly occurs in many otherwise quadrupedal animals, such as the quarter horse rearing up as it bolts from the starting gait or the crocodile lunging after prey on its two hind limbs. It is the biological analogue of the biker performing a ‘wheelie’ as his motorcycle accelerates.

In mammals, this tendency to rear up on the hind limbs is dampened because the center-of-mass is located near the shoulders. If, however, the center-of-mass is located nearer the hips, as it was in *Euparkeria*, then this tendency to rear up on the hind limbs is amplified.¹¹⁴ All thecodonts above the proterosuchian grade possessed long, muscular tails, and disproportionately long hind limbs. These characters are thought to have originally been adaptations associated with the presumed aquatic lifestyle of ancestral thecodonts, but they turned out to be ideally suited for incipient bipedality.

The transient biomechanical forces generated during acceleration promoted bipedality in the early thecodonts. This capacity for two-legged locomotion was undoubtedly a necessary prerequisite for the eventual adoption of an obligatory bipedal gait in archosaurs. But was it a sufficient cause? Probably not. Modern crocodiles are structurally similar to the thecodonts and they occasionally break into a bipedal gait when accelerating, but crocodiles are not bipeds; their normal gait is quadrupedal. Why, then, did the thecodonts and dinosaurs become permanently bipedal? Morphology and mechanics alone are not sufficient to bring about the shift to obligatory bipedality; crocodiles prove that. Hence, something else must have been involved, something that not only *enabled* archosaurs to assume a permanent bipedal gait but *required* them to do so. That ‘something,’ I suggest, was hopping.

Having been ‘preadapted’ for bipedal running, thecodonts need only have made a minor change in their locomotive behavior in order to shift from a symmetrical running gait to an asymmetrical hopping gait. Since hopping employs elastic energy and incurs a low metabolic cost, the early archosaurs may have shifted to a bipedal hopping gait because it was the most economical high-speed gait available. Hopping enabled the thecodonts to move quickly with a minimal expenditure of energy. To the extent that such a gait was beneficial (and if it conserved energy, it almost certainly *was* beneficial), bipedal hopping behavior would have been reinforced and perfected by Natural Selection.

Evolutionary success is largely a matter of differential reproductive success. Anything that enhances reproductive success is, by definition, beneficial and improves the odds in the Darwinian ‘struggle for life.’ Although the shift to an asymmetrical hopping gait was

¹¹³ Gray, 1968.

¹¹⁴ Ibid.

only a minor behavioral change, it had enormous evolutionary implications. It was perhaps *the* single most important event in the early history of the archosaurs. Henceforth, the evolutionary path toward an obligatory bipedal hopping gait became inexorable. Over time, the ‘invisible hand’ of Natural Selection shaped the course of thecodont evolution by weeding out the less proficient hoppers and allowing those more adept at hopping to survive and reproduce. Selection for hopping-proficiency inevitably engendered modifications in thecodont morphology, which, in positive feedback, further improved thecodont hopping behavior. It became perfected in dinosaurs.

Selection for hopping would have induced structural changes that optimize structural stability. A well-adapted hopping biped will ‘bounce’ up and down, not unlike a pogo stick rider, with no lateral deviations. Moving forward requires simply that the hopping animal (or pogo stick rider) lean forward, redirecting the force vector toward the rear, per Newton’s Second Law. Whereas a running animal can adjust its footfalls to accommodate lateral shifts in the center-of-mass, a hopping animal (like a pogo stick rider) cannot. It must be *perfectly* balanced at all times, and *especially* during takeoffs and landings. Thus, parasagittal limb motion ensured that the force transmitted through the legs and feet was directed vertically downward and horizontally to the rear, with no lateral deviations. Moreover, the demands of dynamic stability, and the need for exquisite balance with little if any margin for error, would exert selection pressures favoring animals whose center-of-mass was located directly above the hips. In this manner, selection for bipedal hopping led eventually to a permanent bipedal pose, with the animal perfectly balanced about the hips.

Successful bipedal hopping requires exquisite balance during all phases of locomotion, from takeoff to landing. Once this problem of dynamic stability was solved, a well-adapted biped would have no difficulty in maintaining a stable bipedal pose *even when it was not moving at all*. Put another way, by fulfilling the needs of *dynamic* stability, Natural Selection would, as a matter of course, also solve the problem of *static* stability. The ornithosuchian thecodonts began as habitual bipedal runners, but obligatory bipedality became fixed in their descendants only *after* they had already shifted to a hopping gait. Thus, with respect to the evolution of dinosaur posture and limb mechanics, form followed function.

Bipedal hopping offers a simple and straightforward solution to the mystery of obligatory bipedality. The quadrupedal thecodonts became incipient bipeds because biomechanics and anatomy allowed (or compelled) them to do so. Their descendants began hopping because such a gait proved more economical than running or galloping. Once this behavioral shift occurred – once thecodonts began to hop – the path to obligatory bipedality became fixed by Natural Selection. The permanent bipedal pose was a natural consequence of the perfection of bipedal hopping behavior. Indeed, the two adaptations evolved in tandem.

Hopping explains why dinosaur limb motion was restricted to the parasagittal plane and why dinosaurs were equipped with a rigid cylindrical hip structure. The dinosaurs’ long flexible limbs provided maximum power; their hinge-like hip socket ensured perfect fore-

and-aft limb motion directing the limb thrust vertically downward and to the rear with no lateral deviations. Hopping behavior also accounts for the retention by dinosaurs of a long muscular tail, similar to that of kangaroos, but completely absent in modern ground birds, such as ostriches, to which dinosaurs are so frequently compared. The kangaroo tail serves as both a counterbalance and an anchor for thick tendons needed for elastic hopping. Ostriches, by contrast, are runners and not hoppers, so they have no tail. Which of the two animals do dinosaurs more closely resemble? And if dinosaurs were runners, why did they retain a long heavy tail?

The analogy between bipedal dinosaurs and hopping kangaroos is not new. Joseph Leidy first suggested it in the mid-nineteenth century.¹¹⁵ But over the years, the idea of hopping dinosaurs has fallen into disfavor; practically no one believes it today. The reasons for this are two-fold, neither of which I consider compelling. First, the sheer size of most dinosaurs would seem to preclude bipedal hopping. Of course, this problem becomes less acute if gravity were reduced during the Mesozoic which is the thesis defended here. The second reason is a negative one – the complete absence of hopping dinosaur trackways. “There are literally thousands of predatory dinosaur trackways that show two or more steps,” writes Gregory Paul, “and they always, *always*, show that theropods strode like humans and birds. They never hopped like some birds and kangaroos.”¹¹⁶ (Emphasis in the original.) Although Paul acknowledges that “Bipedal hopping is somewhat more energy-efficient [than running] at least at moderate speeds, but, as their trackways show, dinosaurs never hopped.”

Paul’s unequivocal rejection of dinosaur hopping based on the absence of hopping footprints is somewhat surprising given his mistrust of negative evidence expressed elsewhere in his book on predatory dinosaurs.¹¹⁷ For example, when faced with the complete absence of *running* trackways left by large theropods, Paul writes: “It cannot be proven that large theropods were slow by their trackways because, as I’ve explained, this would be another case of unfair use of negative evidence. Someday the prints of a 5-tonne theropod running at high speed may be found and settle the issue once and for all. Until and unless that happens, we must turn to the design and stressing of the theropod skeleton for evidence of their speed.” And, we might add, for evidence of their gait as well. Paul wants it both ways: the absence of *hopping* footprints proves beyond all doubt that dinosaurs did not hop; yet denying high speed running behavior based on the absence of *running* footprints is an “unfair use of negative evidence.” Paul and I may disagree when it comes to dinosaur paleontology, but we are in complete agreement when it comes to epistemology: absence of evidence is not evidence of absence.

Bipedal hopping, and the analogy with modern kangaroos, solves many problems about the early dinosaurs, especially the development of the fully erect bipedal gait and the adoption of a permanent bipedal pose. The kangaroo analogy also allows us to dispense with the purported need for stepped-up metabolic rates (though it may have actually provided the energy source for a heightened metabolism). By hopping in a kangaroo-like

¹¹⁵ Leidy, 1858.

¹¹⁶ Paul, 1988.

¹¹⁷ Ibid.

manner, and utilizing elastic storage and rebound, dinosaurs could have moved quickly and effortlessly for sustained periods, and covered great distances at a low metabolic cost. Thus, there is no need for them to have advanced beyond the ectothermic physiology of their ancestors, the thecodonts, or their cousins, the crocodiles. With this in mind, we may conceive of the early dinosaurs as being little more than ‘hopping crocodiles’ – a compelling and frightening creature, and one that must have terrorized our ancestors, the protomammals.

Dinosaur Physiology and the Origin of Mammals

If gravity were halved, we should get a lighter, slenderer, more active type needing less energy, less heat, less heart, less lungs, less blood.

– D’Arcy Wentworth Thompson¹¹⁸

Any comprehensive theory of dinosaur evolution must also tackle the problem of mammal origins and evolution. Dinosaurs and mammals both originated during the Late Triassic. For 140 million years, the dinosaurs were the preeminent land vertebrates while our ancestors endured a long ‘mammalian dark age’ that ended only when the dinosaurs went extinct at the end of the Cretaceous. Most dinosaurs were large and many were gigantic. Mesozoic mammals, by contrast, were quite small; most of them were shrew- or rat-size and the largest was only about the size of a house cat. That the dinosaurs helped suppress the mammals is beyond all doubt; how they achieved that feat is still a mystery.

Advocates of dinosaur endothermy maintain that a ‘warm blooded’ physiology and an upright gait gave the dinosaurs a competitive edge over the mammals. The fact that mammals were also endothermic, or at least the physiological equals of the dinosaurs, casts doubt on this interpretation. Moreover, the pattern of Mesozoic evolution was emerging even before the first true dinosaur or mammal had evolved. By the Middle Triassic, the thecodonts were already gaining the upper hand over the therapsids from which mammals descended. Most paleontologists agree that therapsids were quite advanced physiologically and were possibly endothermic. Were thecodonts also endothermic? Bakker claims that they were warm blooded¹¹⁹, yet crocodiles, which descended from thecodonts, are not.

Implicit in most theories of dinosaur endothermy is the assumption that ‘warm blooded’ animals always have a competitive advantage over ‘cold blooded’ animals, that endothermy is somehow intrinsically superior to ectothermy. This assumption is quite reasonable given the dominance of endotherms – mammals and birds – in the modern fauna. But the assumed superiority of endotherms is not necessarily true, for while endotherms are quite diverse and eminently successful in modern habitats, they pay a price for that success, a price that under different circumstances may have been too dear.

¹¹⁸ Thompson, 1917, 1961ed.

¹¹⁹ Bakker, 1986.

Bakker maintains that among the various advantages of endothermy is a fast growth rate and fast breeding rate.¹²⁰ He points out that while large mammals reach sexual maturity in a few months, large reptiles, such as alligators and tortoises, require several years. From an evolutionary point of view, writes Bakker, “their slow growth is a mistake. Alligators would be much better competitors if they could match the rate of growth of mammals and birds. The primary Darwinian goal for each and every species is to breed – breed early, breed often. In the swamp, there is only a limited supply of food to eat or burrows to hide in or logs to bask on. And the species that fills the swamp with offspring monopolizes the natural economy. Moreover, fast rates of reproduction are powerful evolutionary weapons; they provide the enormous advantage of coping with predators or surviving climactic catastrophes.”¹²¹

I am frankly puzzled by Bakker’s reasoning. He claims that alligators “would be much better competitors if they could match the rate of growth of mammals or birds.” Better competitors? If I am not mistaken, alligators have proven to be very competitive and have, indeed, dominated their niches for over 200 million years! They have survived countless climatic catastrophes and other mass extinction events, including the ‘Great Dying’ at the end of the Cretaceous that wiped out the dinosaurs. Nothing succeeds like success, and the alligators and their kin have been remarkably successful, arguably the most successful land animals that ever lived. They must be doing something right.

Bakker’s assertion that breeding early and often is somehow intrinsically superior to the alternative – breeding late and infrequently – is also doubtful. To be sure, flooding an ecosystem with offspring is a very successful strategy, especially for invertebrates and ‘lower’ vertebrates. But it is not widely employed by ‘higher’ vertebrates because, among other reasons, it precludes a high degree of parental care because parental nurturing has a high energy cost and increases vulnerability to predation. A common argument in favor of dinosaur endothermy is that dinosaurs had complex social organizations similar to that of modern mammals. But alligators also have complex social systems – a high degree of parental care and protection, community hunting tactics, etc.¹²² – so warm-bloodedness is not a prerequisite.

In advancing his own views on dinosaur physiology, Bakker argues that “reptiles cannot exploit their full potential for growth because their cold-blooded physiology makes them less effective in gathering food in the wild than a warm-blooded creature.” He describes how biologists study animal diets by examining stomach contents. “What is found in Alligators is surprising – on average, big crocodilians are empty, or nearly so. Compared to the average lion or hyena, a Nile crocodile spends most of its life fasting.”¹²³ Again, the *implication* here is clear – an empty stomach implies inferiority. But once again, the actual *message* is the opposite. The fact that a crocodile can survive and flourish on very little food – to the extent that it “spends most of its time fasting” – is no liability but a

¹²⁰ Ibid.

¹²¹ Ibid.

¹²² Pooley and Gans, 1976.

¹²³ Bakker, 1986

genuine advantage. In sharp contrast to the insatiable demands of a warm-blooded physiology, which requires endotherms to be highly active in the search for food and therefore makes them more vulnerable to both predators and starvation, the cold-blooded physiology of a crocodile is very frugal and allows the animal to lead a very passive life, a life lying in ambush for some unsuspecting (and hyperactive) mammal or bird.

The altogether Whiggish notion of inherent endotherm superiority is seriously flawed, especially when applied to the archosaurs. It has been argued here that the early dinosaurs were little more than ‘hopping crocodiles’ – animals powered by a relatively ‘primitive’ cold-blooded physiology but, because of their reliance on elastic hopping, capable of great mobility and sustained speed. As such, they would have been irresistible predators, especially when compared with their competition, the therapsid reptiles. Ousted from the niches for large-scale animals, therapsids declined in size, number, and variety during the Middle and Late Triassic. Their descendants, the mammals, were reduced to trivial little insectivores that barely survived into the Jurassic and beyond. Though dinosaurs began as predators, they quickly radiated into the niches left vacant by the therapsids. By the end of the Triassic, dinosaurs such as *Plateosaurus* had become the dominant herbivores.

Therapsids already had a relatively advanced physiology by the Triassic Period.¹²⁴ The demands of such a physiology forced them to be more active than the ectothermic archosaurs and thus made therapsids more vulnerable to predation. But, whereas the archosaurs could move quickly and effortlessly in an elastic hopping gait, therapsids were limited by their limb architecture to a slower ballistic walking or aerobic trotting gait. Significantly, therapsids probably could not gallop. Anatomical evidence of galloping behavior appears only in the earliest mammals from the Late Triassic.¹²⁵ By this time, however, the mammals had already been driven into niches for extremely small animals that dinosaurs never exploited.

The progressive reduction in the size of the incipiently endothermic mammal-like reptiles would have increased their energy requirements. This was an inevitable consequence of scale – the increase in the surface-area-to-volume ratio. Heat loss is a function of surface area, and small animals have a larger surface area relative to body mass than do big animals. Small mammals, therefore, must produce more internal heat to offset the heat loss through their skin. Consequently, the trend toward increased metabolic rate would have accelerated as therapsid body size decreased.¹²⁶

Given the energetics of bipedal hopping, the evolutionary success of the early dinosaurs over the advanced mammal-like reptiles may have resulted from the fact that dinosaurs remained ‘cold blooded’ at a time when environmental conditions favored low energy animals. Adapted to reduced gravity, the ancestral dinosaurs were, as D’Arcy Thompson wrote, “lighter, slenderer, more active types needing less energy, less heat, less heart, less

¹²⁴ Kemp, 1982.

¹²⁵ Crompton and Jenkins, 1979.

¹²⁶ Baur and Friedl, 1980.

lungs, less blood.”¹²⁷ Unable to compete with dinosaurs for medium- to large-scale niches, the mammal-like reptiles and their descendants became progressively smaller over time which intensified their metabolic requirements.

The Origin of Vertebrate Flight

Vertebrate flight appeared for the first time in the Late Triassic and evolved independently in at least two separate lines of diapsid reptiles.¹²⁸ The pterosaurs descended from thecodonts and appeared in the Late Triassic. Birds probably descended from small bipedal theropods; the most famous flying theropod is *Archaeopteryx*, which lived during the Late Jurassic.

The debate over the origin of flight has raged for over a century with no end in sight.¹²⁹ Two theories are preferred: (1) the ‘arboreal’ – or top-down – theory according to which flying archosaurs began as gliders; and (2) the ‘cursorial’ – or bottom-up – theory according to which the feathered forelimbs of small running theropods were converted from insect-snares into flapping wings. The two theories essentially represent competing sides in the form vs. function debate. The arboreal theory has function on its side: powered flight evolved in tree dwelling animals that were already habitual gliders. The cursorial theory has form on its side: the earliest flying animals, such as *Archaeopteryx*, are remarkably similar in their anatomy to contemporary theropods and almost certainly descended from them. Both theories have much in their favor, but neither is flawless nor entirely convincing. For example, it is difficult to conceive how or why the transition from running to flying happened, or what possible benefit it conferred.

Without delving too deeply into this debate, the theory defended here suggests a third alternative – a variation of the bottom-up theory – that may help explain how and why powered flight evolved. It has been argued that the advanced thecodonts and primitive dinosaurs were hopping bipeds. As we have noted, a bipedal hopping gait is characterized by a prolonged aerial phase. An increased ability of small hopping archosaurs to remain aloft between footfalls may have led eventually to sustained, powered flight. But how did this happen? What benefit did it confer?

Many small dinosaurs are thought to have been insectivores. It is possible that some of them fed by leaping into swarms of flying insects and using their fore limbs as insect snares. If so, the capacity to gather more insects by remaining aloft for longer periods-of-time would have proven beneficial; it would have engendered structural changes in the fore limbs, both to make them better insect snares *and* (perhaps serendipitously) to provide more lift. Anything that improved the ability to hunt flying insects – including the development of long feathered forelimbs – would have been advantageous and seized upon by Natural Selection, leading inexorably to the capacity for sustained powered flight.

¹²⁷ Thompson, 1917, 1961ed..

¹²⁸ Carroll, 1988.

¹²⁹ Feduccia, 1980.

Seen in this light, powered flight is nothing more than a hopping gait with an infinite aerial phase and zero duty factor; it evolved as a natural byproduct of archosaur locomotion and hunting behavior. The morphology of primitive flying archosaurs, such as *Scleromochlus*,¹³⁰ a possible pterosaur-ancestor from the Late Triassic, is not inconsistent with this ‘saltational’ theory of flight.

Irrespective of how or why flight originated, it certainly would have been facilitated in reduced gravity. And reduced gravity would also help explain the extreme gracility of *Archaeopteryx* (e.g. the small size of its sternum) when compared to modern birds of similar size.

The Great Dying

If maximum animal size can serve as a valid paleogravity indicator, then gravity reached its minimum – 0.8 g – during the Late Jurassic when the largest dinosaurs existed. Since gravity today is higher, gravity must have increased between the Late Jurassic and the present, in conjunction perhaps with a contraction of the Earth.

During the Cretaceous Period, dinosaurs were generally smaller than their Jurassic forebears. (Bakker contrasts the ‘high browsers’ of the Jurassic with the ‘low browsers’ of the Cretaceous.¹³¹) Ornithischian dinosaurs, such as the ornithopods and ankylosaurs, succeeded the sauropods as the dominant herbivores. Ornithischians were much smaller than sauropods and were relatively more robust than theropods of similar size.¹³² Similarly, the most common Cretaceous sauropods, the titanosaurs, were smaller, stockier and had shorter necks than the great Jurassic giants. Indeed, the very last dinosaurs to evolve, the ceratopsians from the Late Cretaceous, were robust quadrupeds. Altogether different than the gracile bipeds of the Late Triassic, the ceratopsians were almost mammal-like in their appearance and structure.

What then of the Great Dying? With the exception of the amphibious crocodiles, no land animal larger than 20 kg survived the extinction event at the Cretaceous-Tertiary boundary. Many marine families also perished. Plants, on the other hand, seem to have escaped relatively unscathed. If, as has been argued, a gravity reduction at the beginning of the Mesozoic played a role in the origin of dinosaurs, then perhaps their extinction at the end of the Mesozoic was related to a gravity increase.

Estimates of Global Expansion

Plate tectonic theory assumes an equivalence between global spreading and subduction rates. For every square kilometer of new crust created by seafloor spreading, an equal

¹³⁰ Carroll, 1988.

¹³¹ Bakker, 1978.

¹³² Romer, 1966.

amount of old crust must be consumed by subduction. However, if the rate of subduction is less than the spreading rate, then a net increase in surface area would result and the Earth would expand.¹³³

Though currently out-of-favor among geoscientists, the Earth expansion hypothesis has a long and venerable history. It was first proposed in the 1920s and 30s, by O.C. Hilgenberg and others. More recently, S.W. Carey¹³⁴, L.C. King¹³⁵, and H.G. Owen¹³⁶ have been the most vigorous advocates of expansion. Their work deserves much wider recognition than it has received. Although I have been greatly influenced by their ideas, consideration of the possible effects of gravity variations on dinosaur evolution, discussed herein, leads to somewhat different conclusions regarding the extent and rate of post-Pangean Earth expansion as well as the possibility of Late Mesozoic contraction. I am fully aware that these conclusions conflict with most Earth expansion models, not to mention the reigning plate tectonic paradigm.

The paleontological evidence discussed herein suggests that gravity during the Late Permian and Early Triassic was 1 g or slightly higher, as indicated by the robust morphology of the mammal-like reptiles. Assuming constant mass, this indicates an Earth of current dimensions, or somewhat smaller, during the Permo-Triassic. Using the thecodonts and dinosaurs as crude ‘paleogravity indicators,’ expansion and the reduction in gravity began in the Middle-to-Late Triassic with gravity reaching a minimum of 0.8 g sometime during the Jurassic. (The dating of the onset of expansion corresponds with the views of both Carey and King, though both believe that expansion continued into the Cenozoic.)

According to classical physics, $g \propto r^2$; at constant mass, a reduction in gravity to 0.8 g requires a radius 11.8% larger than at present. The current radius of the Earth is 6371 km; its surface area ($4\pi r^2$) is 5.1×10^8 km². At 0.8g, the radius would be 7123 km with a total surface area of 6.41×10^8 km²; therefore, the net increase was 751 km in radius and 1.31×10^8 km² in surface area.

Staurikosaurus, the oldest dinosaur, appeared in the Carnian age of the Late Triassic (225-230 Ma); *Barapasaurus*, the first truly gigantic dinosaur, appeared in the Early Jurassic, some 40-45 m.y. later. If total expansion occurred during this interval, then surface area increased at an average rate of $2.9\text{-}3.3$ km² yr⁻¹. Extending the expansion interval to the end of the Jurassic (144 Ma), when the largest dinosaurs existed, yields an average rate increase of $1.5\text{-}1.6$ km² yr⁻¹ over a period of 80-85 m.y. Thus, creation of seafloor at the rate of 3 km² yr⁻¹ through seafloor spreading, together with the subduction of 1.5 km² yr⁻¹ between 230-144 Ma, would produce the required additional surface area and increased radius. Although these rates of spreading and subduction are extreme

¹³³ Steiner, 1977.

¹³⁴ Carey, 1976; Carey, 1988.

¹³⁵ King, 1983.

¹³⁶ Owen, 1983.

when compared to modern rates,¹³⁷ i.e. a high rate of spreading and a low subduction rate, they certainly are not unreasonable.

Conclusion

A 20% reduction in gravity during the Triassic and Jurassic, caused by Earth expansion, may have played a crucial role in the origin and evolution of dinosaurs. In reduced gravity, evolutionary selection pressures would favor (1) a relative decrease in skeletal mass, (2) a relative decrease in bone thickness, and (3) an increase in the uppermost size limit of land animals (Fig. 7). These predictions, deduced from skeletal scaling principles, and supported by gravitational tolerance experiments and biomedical space research, are borne out by the fossil evidence. During the Mid-to-Late Triassic, the small, robust, and exclusively quadrupedal synapsid reptiles (therapsid-dominated faunas) were supplanted by larger gracile and bipedal diapsid reptiles (dinosaur-dominated faunas). Gigantic sauropod dinosaurs were already present in the Early Jurassic and were the dominant herbivores in the Late Jurassic.

The principle of dynamic similarity indicates that a gravity reduction will enable land animals to shift to higher gaits at lower speeds. The ancestral archosaurs (ornithosuchian thecodonts and early theropod dinosaurs) may have shifted from a facultatively bipedal symmetrical running gait to an obligatory bipedal asymmetrical hopping gait, much as the Apollo astronauts did in reduced lunar gravity. Such a shift in locomotive behavior may have engendered significant changes in archosaur limb architecture: hind limb elongation; the development of the mesotarsal joint; clawed, tridactyl feet; and a hinge-like hip articulation that restricted limb motion to the parasagittal plane in the fore-and-aft direction. Perfection of the bipedal hopping gait enabled early dinosaurs to assume a permanent two-legged pose.

Bipedal hopping in modern kangaroos is powered by elastic storage and rebound. By analogy, a bipedal hopping gait would have enabled the early dinosaurs to achieve high speeds and cover great distances at a low metabolic cost. This economical high-speed gait gave the ectothermic archosaurs a significant advantage over the slower, though physiologically more advanced, mammal-like reptiles. Seen in this light, the early dinosaurs may be conceived as little more than ‘hopping crocodiles.’ Excluded from niches for medium- and large-scale animals, the therapsids became progressively smaller; the reduction in body size and consequent increase in surface-area-to-volume ratio increased their metabolic requirements and thus accelerated the development of the high-grade mammalian physiology.

Aerial locomotion would have been facilitated in reduced gravity. Triassic archosaurs were the first vertebrates capable of powered flight. Pterosaurs descended from thecodonts, and birds descended from small theropod dinosaurs. Bipedal hopping suggests an alternative explanation for the origin of powered flight that contrasts with the

¹³⁷ Chase, et al., 1975; Steiner, 1977.

traditional cursorial and arboreal theories. The capacity to remain aloft for longer periods-of-time during the aerial phase of each hop, augmented by modifications of the fore limbs, may have made the small bipedal archosaurs more proficient consumers of flying insects and thus caused selection pressures to favor sustained powered flight.

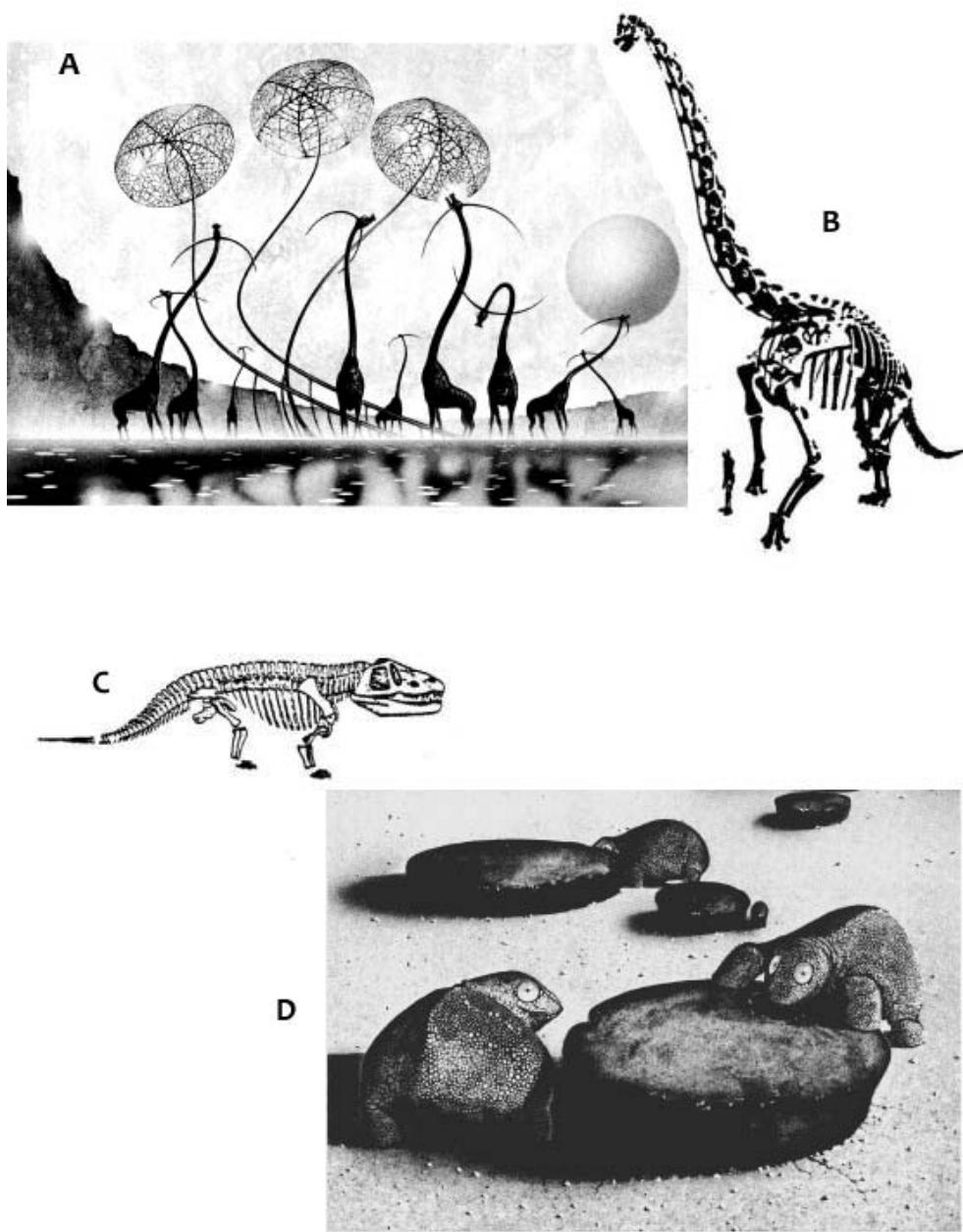


Figure 7. A. An artist's vision of life on a low-gravity planet: "weaker gravity would release both trees and animals from gravitational constraint and make them shoot upward to become taller and more slender." The balloon-like structures are 'trees.' (Bylinsky 1981; drawing by W. McLoughlin.) B. The Late Jurassic sauropod *Brachiosaurus* with human skeleton for scale, from Glut (1976). C. The Early Triassic proterosuchian thecodont *Erythrosuchus*, from Huene (1936). D. A fanciful view of life on a high-gravity planet where "the opposite effect would be seen: animals getting squatter, their legs and necks getting thicker." (Bylinsky 1981; drawing by W. McLoughlin.)

Finally, reduced gravity in the Triassic and Jurassic implies a subsequent increase in gravity to its modern value. The transition from the Jurassic faunas dominated by large, high-browsing sauropods to the Cretaceous faunas dominated by smaller, low-browsing ornithischian dinosaurs, is consistent with a gravity increase during the Cretaceous period. It is also possible that a catastrophic increase in gravity at the K-T boundary played a role in the mass extinction of the remaining dinosaurs.

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