Terramegathermy in the Time of the Titans: Restoring the Metabolics of Colossal Dinosaurs

GREGORY S. PAUL AND GUY D. LEAHY
3109 N. Calvert St. Side Apt., Baltimore MD 21218 and
2405 Bailey Hill Rd., Eugene OR 97405

INTRODUCTION

Among dinosaurs, megadinosaurs (those over one tonne) have been considered among the best candidates for having had low metabolic rates (LoMRs). Spotila et al (1991) argued that big dinosaurs were gigantotherms that shared thermal characteristics with the large leatherback sea turtle, and Dodson (1991) suggested that giant dinosaurs lived in the slow lane compared to giant mammals. Coulson (1979), Bennett (1991) and Ruben (1991) restored big dinosaurs as "good reptiles" powered by bursts of reptilian hyperanaerobiosis rather than the sustained tachyaerobiosis that powers birds and mammals. Farlow (1990) suggested that large dinosaurs were "damned good reptiles" with fluctuating metabolic rates (MRs), and in 1993 he argued that dinosaurs used a combination of rapid reproduction and intermediate metabolic rates (InMRs) to grow bigger than land mammals. All the above workers, and McNab (1983) and Dunham et al. (1989), have modeled big dinosaurs as LoMR or InMR inertial homeotherms that maintained constant body temperatures on a daily basis.

Why land giants must be tachyaerobic. - We will outline arguments that megadinosaurs had high metabolic rates (HiMRs) similar to those of megamammals, except for a few InMR forms in both groups. Our hypothesis starts with a simple observation. On land all classic reptiles with LoMRs have weighed about one tonne or less (Figs. 1 & 2). Many HiMR land mammals have exceeded one tonne, and the largest approached 20 tonnes (Figs. 1 & 2). This differs from the marine realm, where 6-15 tonne basking and whale sharks have LoMRs, environmentally dependent body temperatures, and are more sluggish than the much more energetic and hotter running whales of the same size. Therefore, when we are asked (again and again) why some dinosaurs were four to five times bigger than land mammals, we ask why dinosaurs grew a hundred times larger than land reptiles!

Our hypothesis centers around the logical argument that living in the high energy field produced by gravity is a hard and constant struggle that can only be won with the great strength and sustained power inherent to a high energy tachyaerobic system. The belief that low energy bradyaerobic forms can bear the burden of great bulk is naive. Being an aquatic giant is much easier because water is a low energy environment where buoyancy negates the effects of gravity, and swimming is five to twelve times more efficient than walking the same distance.

Avian-mammalian versus reptilian chauvinism and other matters. - Some accuse those who have restored dinosaurs with HiMRs of being biased in favor of bird- and mammal-like metabolic

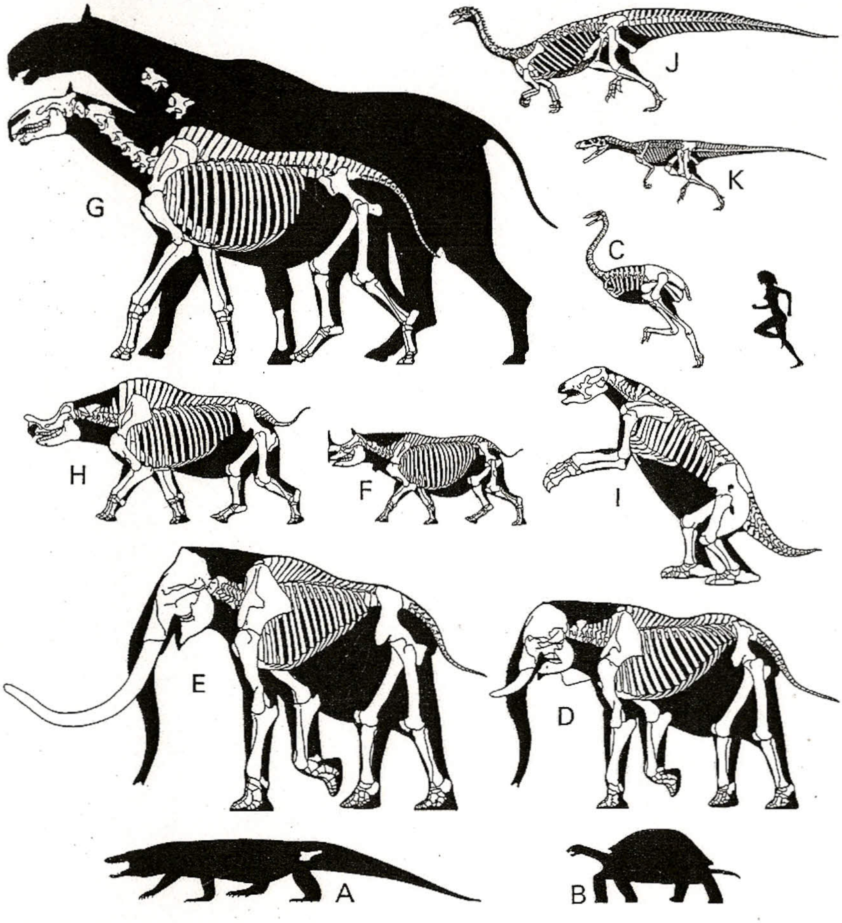
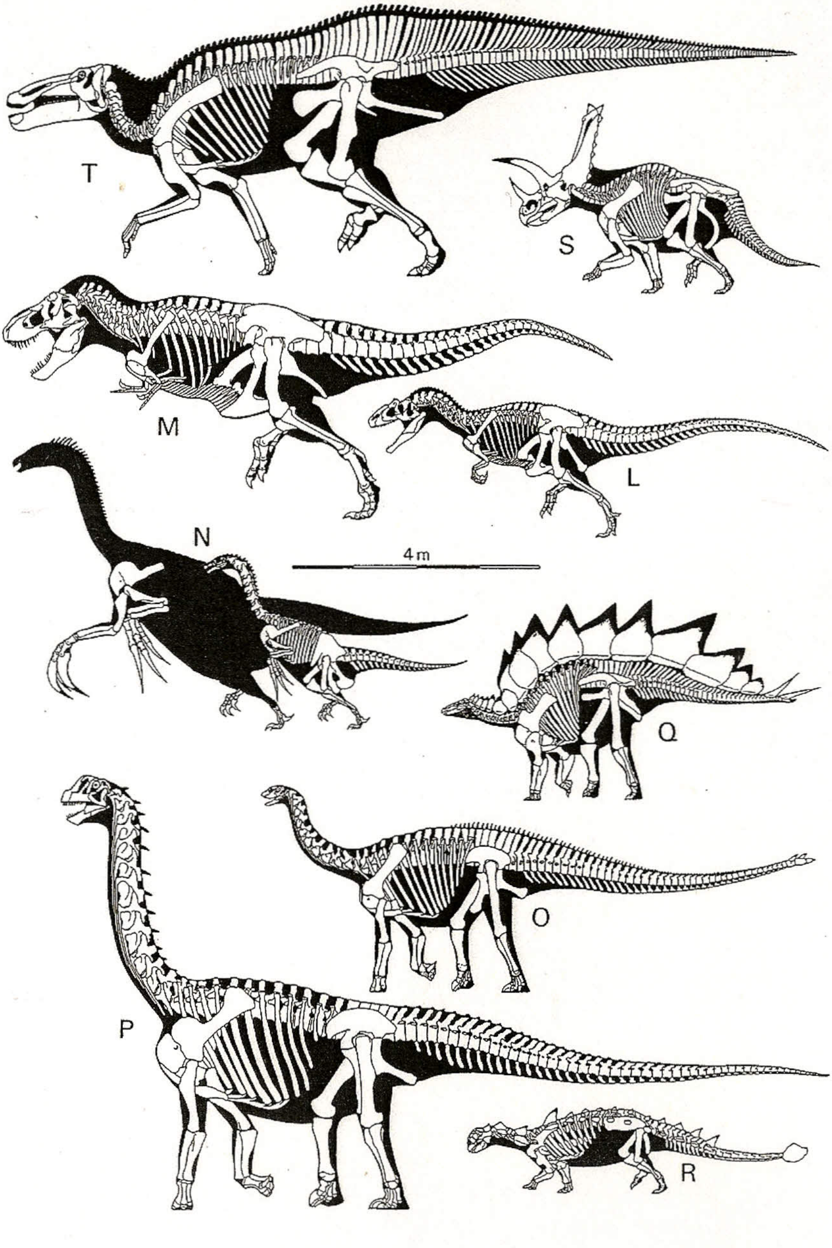


FIGURE 1 - Same scale figures of large land animals. A-B, largest extinct reptiles (0.8-1.0 tonnes), A, monitor Megalania (with preserved ilium), B, tortoise Geochelone atlas. C, elephant bird Aepyornis (0.4 t). D-H, megamammals, D, Loxodonta (6 t), E, Mammuthus (8 t), F, Rhinoceros (1.5 t), G, rhino Indricotherium (f 8 t, m 16 t), H, brontothere Brontops (3 t), I, sloth Eremotherium (4 t). J-K, brevischian dinosaurs, J, Herrerasaurus (0.2 t), K, Plateosaurus (0.8 t). L-T, megadinosaurs, theropods L, Allosaurus (1.3 t) and M, Tyrannosaurus (6 t), N, Therizinosaurus (6 t) and Nanshiungosaurus (1.2 t), sauropods O, Shunosaurus (3 t), and P, Camarasaurus (14 t), Q, Stegosaurus (2.2 t), R, ankylosaur Euoplocephalus (2.3 t), S, ceratopsid Pentaceratops (2.5 t), T, hadrosaur Shantungosaurus (10 t). Masses from volumetric models based on skeletal restorations.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systems. However, an equivalent charge can be leveled at some of those who favor some form of reptilian or "intermediate" energetics for dinosaurs. We have no inherent preference for any metabolic system over another, and are interested only in which system best explains the phenomenon of dinosaurian gigantism.

In order to objectively diagnose the metabolics of megadinosaurs, this study follows some logical and conservative premises. Restorations of dinosaur metabolics should not be driven by theoretical ideas - such as the supposed superiority of reptilian or avian-mammalian systems, or that dinosaurian metabolics should have followed an exponential growth curve. Instead, the anatomy and biology of dinosaurs must be used to restore their metabolics before the evolution of their energetics can be understood. In order to minimize speculation we prefer to fit dinosaurs with anatomico-metabolic systems that are known to work in living forms over theoretical models unless the latter are unavoidable. In choosing living analogs for megadinosaurs we prefer forms that are closest to them in form and habitat - so large terrestrial creatures living under natural conditions are considered better analogs than aquatic, legless forms, or those raised under artificial conditions.

Leatherbacks versus elephants as dinosaur analogs. - Are sea turtles or land giants better living analogs for dinosaurs? Leatherbacks are legless forms with low capacity and low pressure respiro-circulatory systems. They live in a low energy world where cruising at high speeds and migrating long distances costs six times less energy than walking the same distance. Heat generated by internally placed muscles during constant swimming and trapped by heavy fat insulation helps maintain moderate body core temperatures of ~30°C. Leatherbacks never experience severe heat or tissue freezing temperatures.

Elephants of the desert Skeleton Coast of southwest Africa have long striding limbs powered by large volumes of tachyaerobic muscles, high blood pressures, and high capacity respiratory tracts. These land giants do not cruise constantly, the leg muscles are placed away from the body core, and insulatory fat is absent (Haynes, 1991). Body core heat is generated largely by hard working internal organs. The Skeleton Coast elephants not only survive in a desert with limited resources by expending large amounts of energy as they wander long distances in search of food (Bartlett & Bartlett, 1992), they are unusually gigantic with world record weights up to 10 tonnes. Rather than going belly up when it gets hot, they use high body temperatures of 37°C and bulk to thermoregulate in extreme heat. Proboscideans have experienced frostbiting temperatures (Haynes, 1991).

The form and habitat of leatherbacks could hardly be more different from the dinosaur world. Acceptance of their use as primary models for dinosaurs is therefore surprising - imagine the reaction if whales were used as the primary analogs for dinosaurs! The structure and hot climates of elephants are very reminiscent of the dinosaur condition, and it is surprising how many reject their biology when restoring dinosaur thermodynamics.

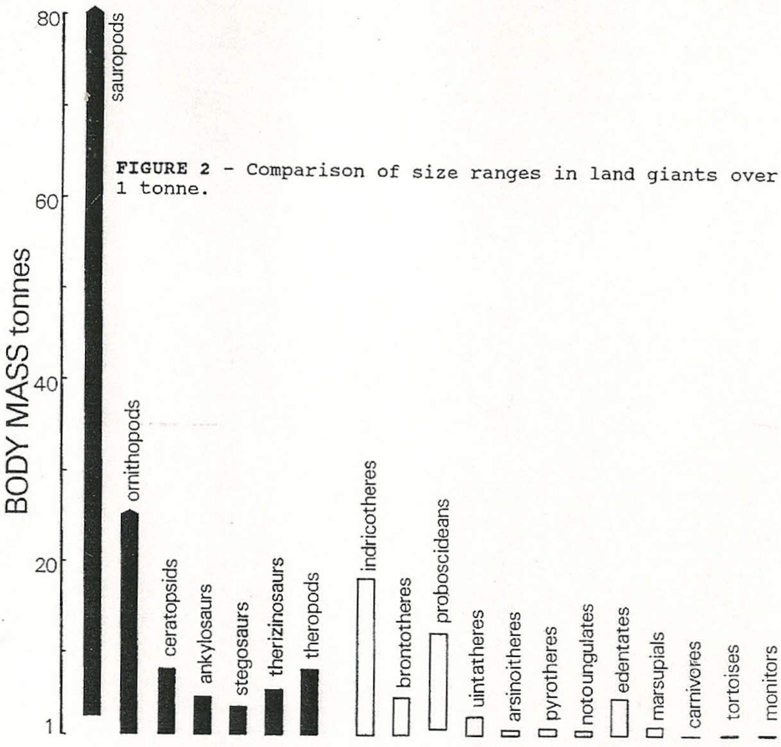

FIGURE 2 - Comparison of size ranges in land giants over 1 tonne.

METABOLIC CHARACTERISTICS OF LIVING GIANTS

Muscles, blood pressures and breathing. - The great strength and endurance needed to carry great bulk are provided by large muscles. The skeletal muscles of birds and mammals are about twice as large as those of reptiles at a given body size (Ruben, 1991). Reptiles, including the largest, have correspondingly small legs, with narrow thigh muscles that are anchored upon correspondingly small ilia (the upper pelvic bone, Fig. 1A). The large legs of birds and mammals, including slow gigantic elephants, have broad thigh muscles supported by large ilial plates (Fig. 1C-I). A plot comparing ilium length in land animals confirms that birds and mammals have much bigger pelvic bones than reptiles (Fig. 3; a comparison of ilium surface area is preferable but was not feasible). Are large ilial plates required to support great mass, for erect legs, or for bipedal posture? The connection between the vertebral column and pelvis in bipedal and in big mammals is much shorter than the ilium. Bipedal birds

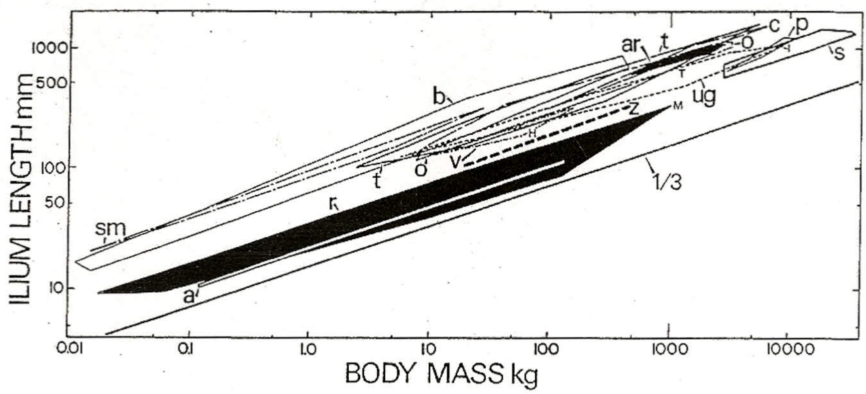

FIGURE 3 - Length of the ilium - the upper pelvic bone that anchors the thigh muscles - in land animals: r, reptiles; M, Megalania; a, alligator growth curve (courtesy P. Dodson); b, birds; sm; saltorial mammals; H, human; v, carnivores; ug, ungulates; I, indricothere; p, proboscideans; z, brevischian staurikosaur, herrerasaur, prosauropod; t, theropods; T, therizinosaur; s, sauropods; ar - stegosaurs and ankylosaurs; c - ceratopsids; o - ornithopods.

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and saltorial mammals have longer ilia than quadrupedal mammals, but the ilia of the latter are much longer than in reptiles. Some bipedal, erect-limbed dinosaurs had short ilia. The sole purpose of large ilia is to support large leg muscles.

Why do reptiles have such small leg muscles, and birds and mammals such large ones? One reason is that reptile muscles can produce twice as much anaerobic power as those of mammals and birds (Ruben, 1991), so even small legged lizards and crocodilians sprint at high speeds. However, hyperanaerobiosis is an inefficient process (that consumes ten times as much food as aerobiosis) that works for only a few minutes, and is followed by toxic effects (Bennett, 1991). For example, anaerobic power falls off so quickly that big crocs may be unable to drag smaller ungulates into deep water to drown them if they do not succeed with the first lunge (Deeble & Stone, 1993; contrary to the assertion of Bennett et al. (1985) that big reptiles can produce hyperanaerobic power for long periods). A croc or gator can outsprint a person, but loses speed after a few seconds (Grenard, 1991). Also, large reptiles are at high risk of death after long periods of intense exercise because large animals cannot quickly recover from the toxic effects of anaerobiosis (Bennett et al., 1985). The lower anaerobic power production of tachyaerobic muscles means that birds and mammals need larger leg muscles than reptiles to produce as much overall burst power. The inability to carry massive bulk with small anaerobic muscles helps explain why really gigantic reptiles have always been aquatic.

In addition to anaerobic factors, the aerobic capacity of the respiro-circulatory system determines the size of the leg musculature. The low capacity and low pressure respiro-circulatory system of reptiles can deliver only enough oxygen to supply small bradyaerobic muscles. The large, tachyaerobic muscles of exercising birds and mammals demand large amounts of oxygen. The only way the muscles can get so much oxygen delivered to them is via large volumes of blood that are driven by high circulatory pressures, and oxygenated by a high capacity respiratory system. The ability of mammals to oxygenate large sets of leg muscles helps explain why some became land giants.

There is another reason why giants need high blood pressures. Pumping blood up against the gravity well to the brain requires work. The higher the blood is pumped the harder the work must be - and following the adage that one cannot get something for nothing, we presume this is true even if special cardiovascular adaptations are present. It is not possible to pump blood more

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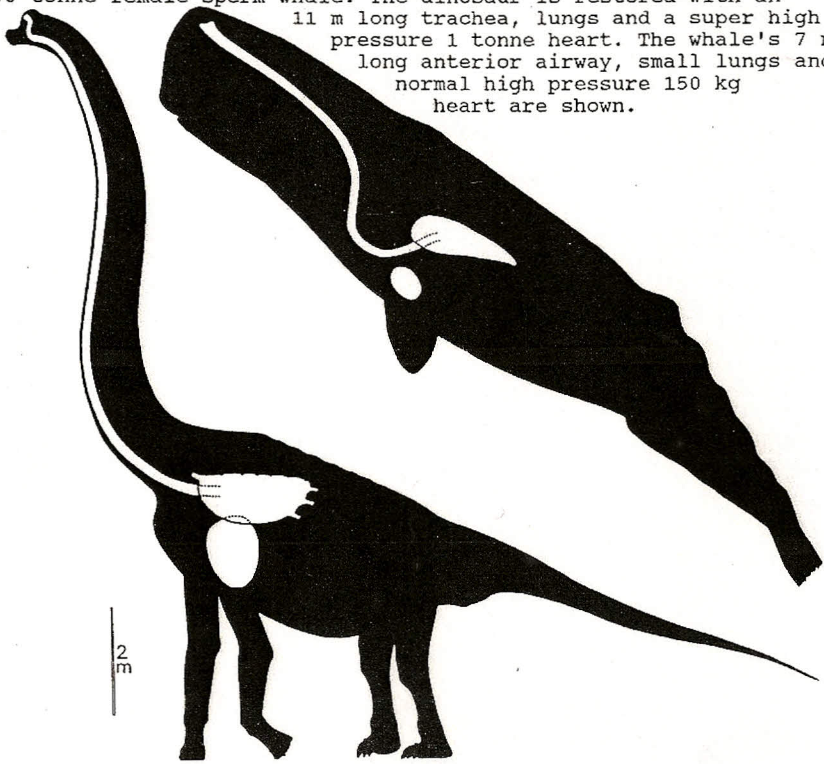
FIGURE 4 - Same scale figures of a 30 tonne Brachiosaurus and a 30 tonne female sperm whale. The dinosaur is restored with an 11 m long trachea, lungs and a super high pressure 1 tonne heart. The whale's 7 m long anterior airway, small lungs and normal high pressure 150 kg heart are shown.



than 0.5 m above heart level with low, reptilian circulatory pressures and bradycardiac work (Seymour, 1976), so no land reptile has a long erect neck. The high pressure hearts of most mammals, from mice to humans, elephants, and whales, make up about 0.6% of body mass (Fig. 4, Table 1). Long necked giraffes have oversized hearts that produce unusually high pressures (Table 1).

A consequence of high aerobic capacity and high circulatory pressures is high resting MRs. In order to process large volumes of oxygen when exercising, tachyaerobic muscle cells have "leaky" membranes that require that the cell consume large amounts of oxygen in order to resist osmotic flow and maintain a proper chemical balance with surrounding tissues (Else & Hulbert, 1987). Failure to properly oxygenate the tissues of tachyaerobic animals results in a shutdown of the system causing torpor, so failure to maintain high blood pressure even when resting results in torpor.

Maintaining high resting blood pressure requires that the heart work hard. The respiratory system must also work hard to supply the hard working heart and other tissues with large volumes of oxygen. The liver and kidneys must work hard to process the wastes produced by the hard working respiro-circulatory system. To supply the hard working organs with large volumes of food the digestive tract must work hard. The high oxygen consumption of tachyaerobic cells and the hard working internal organs adds up to a resting metabolic rate that is nearly as high as the entire oxygen consumption of active reptiles with low pressure circulatory systems (Jansky, 1965, who notes that cardiac work is an increasingly large part of the resting metabolism in larger mammals). This is why vertebrates always have low exercise/resting aerobic ratios.

Long anterior airways pose a respiratory problem because they hinder ventilation of the lungs. Even so, sperm whales (Fig. 4) inhale enough air through long anterior airways to sustain HiMRs with modern oxygen levels. This is true despite the small size of their lungs, the lack of respiratory air-sacs, and the need to respire during brief periods at the surface between long dives.

Cruising and migration. - In order to forage long distances on a daily basis, or to migrate very long distances on a yearly basis, sustained walking speeds should be above 2-3 km/h. Because moving on land is energy expensive, high aerobic capacity is needed to power such high cruising speeds for many hours (Bennett, 1991). This is true of large as well as small animals. The 2-7 km/h walking speeds observed in elephants for example (Fig. 5) are easily achieved aerobically. Although swimming leatherbacks cruise at 3-5 km/h, the sustainable aerobic capacity of leatherbacks can power walking speeds of only 0.5-0.8 km/h (Fig. 5). The long migrations of leatherbacks are possible only because they swim so cheaply, and exploit favorable currents - land does not convey animals in this manner. Anaerobiosis does not produce power long and efficiently enough to power high walking speeds, so calculations that bradyaerobes can migrate farther than tachyaerobes on land (Spotila et al. 1991) are incorrect, and no land reptile migrates.

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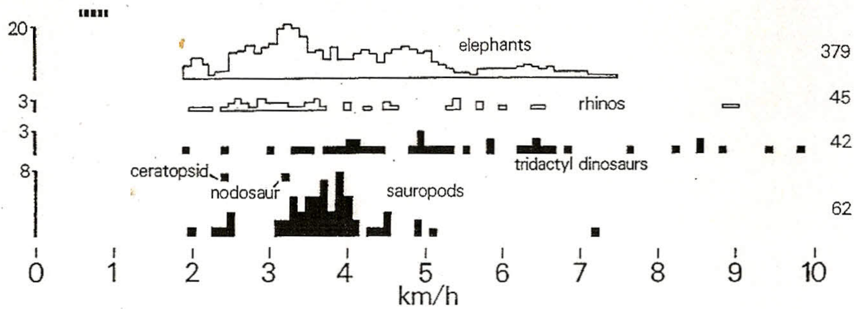

FIGURE 5 - High cruising speeds in megamammals and megadinosaurs over 1 tonne. Elephant and rhino speeds from videos, ornithopod, theropod, ceratopsid, ankylosaur and sauropod speeds estimated from trackways (incl. Currie, 1983; Lockley et al., 1986; sauropod data courtesy J. Farlow). Upper left bar indicates the low sustained walking speeds predicted by the reptilian aerobic metabolism of a cruising leatherback sea turtle.

Galloping rhinos do not have higher resting MRs than slower elephants, although their exercise MRs may be higher. The most gigantic extinct mammals were 10 to 20 tonne, HiMR proboscideans and indricotheres with long striding legs (Fig. 1D,E,G). Giant extinct edentates and marsupials with heavy awkward limbs never exceeded about 5 tonnes (Fig. 1I), and these rather sluggish beasts probably had InMRs like their living relatives (McNab, 1983). If so, land animals much over 5 tonnes may need HiMRs.

Heterometaboly. - Farlow (1990) suggested that nonmammalian giants may be able to save energy by sharply dropping their MRs from high to low levels on a seasonal basis, or when they complete growth. Birds and mammals can drop mass specific MRs by about a third under similar circumstances. Greater metabolic declines are probably not feasible in vertebrates because suppressing MRs strongly decreases cardiac work and circulatory pressures, resulting in impaired aerobic capacity and torpor.

Growth and reproduction. - Fig. 6 shows that land reptiles grow more slowly than birds and all but a few terrestrial HiMR mammals (Case, 1978). Note that the divergence between terrestrial reptilian and mammalian growth rates <u>increases with size</u>; this negates the premise of gigantothermy that the growth rates of land giants should converge towards a common level. The inability of bradyaerobic juveniles with low foraging speeds and ranges to gather enough food is one reason they grow slowly. It has been suggested that elevated growth rates of farm-raised alligators and captive leatherbacks show that reptiles can grow rapidly. Raising alligators is an energy expensive and labor intensive proposition that involves providing idle reptiles with large quantities of food (Grenard, 1991). The relevance of captive and or aquatic reptilian juveniles to natural land conditions is nil.

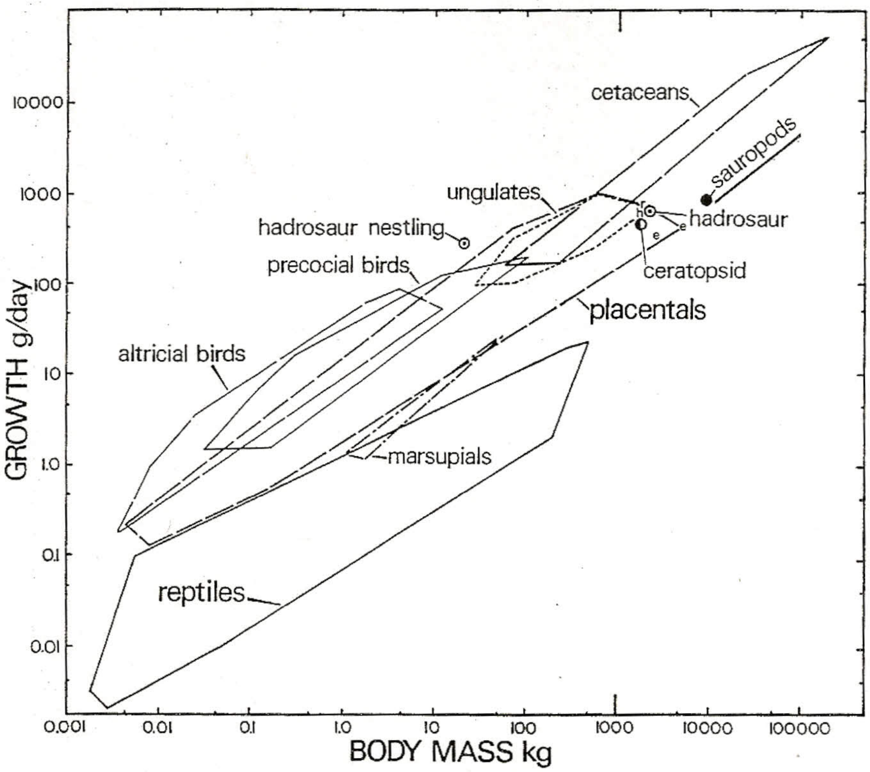

FIGURE 6 - Growth rates in land tetrapods and whales, r, white rhino, h, hippo, e, African elephants. Data for modern animals in part from Case (1978). Growth rates for megadinosaurs based on nesting periods and size distribution patterns in bonebeds (Currie & Dodson, 1984; Horner & Gorman, 1988) and bone rings (Reid, 1990). Minimum growth rates needed for giant sauropods to reach sexual maturity at 1/3 adult mass is indicated.

In order to maintain stable populations over time, generational turnover must be sufficiently rapid. Giants must therefore reach sexual maturity within about twenty years and their lifespans should not be much greater than a century (Dunham et al., 1989). Big ungulates, rhinos, elephants, and whales fit these characteristics (Owen-Smith, 1988). Note that the more gigantic an animal is, the higher the rate of growth must be in order to keep the juvenile stage and lifespan within reasonable limits. We conclude that HiMRs are necessary to grow more than 5 tonnes. The large size of some extinct marsupials and edentates suggests that InMRs are sufficient to grow to about 5 tonnes, and LoMRs can grow animals to only about 1 tonne.

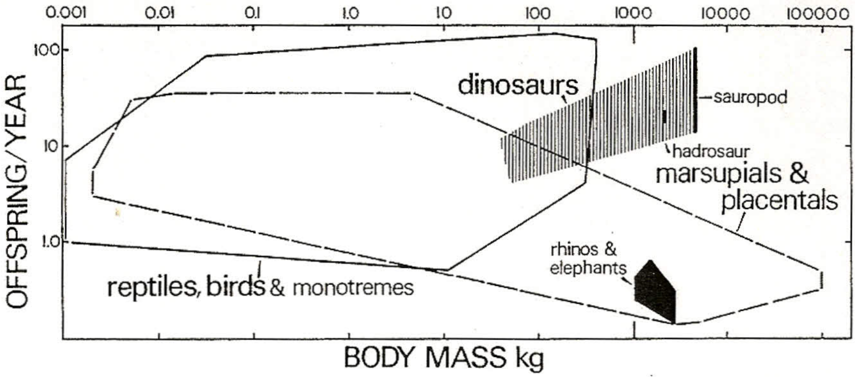

FIGURE 7 - Rates of reproduction in egg laying and live bearing tetrapods compared to dinosaurs, values for two megadinosaurs indicated with solid bars. For more details see Paul (1994).

A problem with being a tachyaerobic giant is that each adult consumes large amounts of food, so the total adult population size is rather small (Farlow, 1993; Paul, 1994). Small HiMR mammals and birds and LoMR reptiles can have much larger adult populations than megamammals. In general, small populations are less stable than larger ones over geological time. Big mammals produce a few (Fig. 7) fast growing calves that are highly dependent upon their parents for survival. Under optimal natural conditions megamammals can expand their populations about 6-12% per annum (Owen-Smith, 1988). These modest rates of population expansion have allowed megamammals to evolve moderately gigantic masses during the Cenozoic. Large reptiles lay large numbers of eggs, but their slow growth and generational turnover hinders their ability to exploit their rapid reproduction to evolve giant dimensions. We predict that if giants combine high rates of growth with high rates of reproduction, then the resulting high rates of population expansion - perhaps over 100% under optimal conditions even with high juvenile mortality - should allow them to survive as species even if the adult populations are so small that they are prone to periodic crashes. If so, then fast breeding tachyaerobic giants have the potential to have smaller populations of larger adults living off of the same resource base than observed among slow breeding big mammals (Paul, 1994).

Socialization and parenting. - The most parental of reptiles are semi-aquatic crocodilians that move only short distances around their nests and expend little energy as they swim after their charges in water. Crocodilians do not forage for their young, and they care for them only while they are very little. Terrestrial reptiles do not have the energy to care for their young, or to engage in the extended social activities associated with living in packs or herds. Extended parental care, foraging for the young, and organized groups are observed on land only in tachyaerobic birds and mammals.

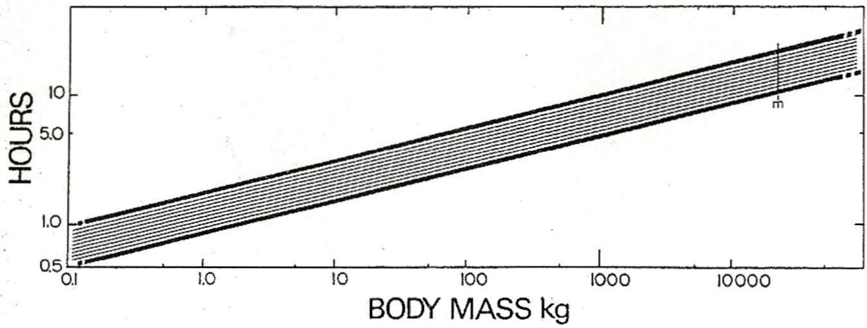

FIGURE 8 - This plot shows the time it takes for HiMR animals to overheat if they store all internally generated heat and exclude external heat with high body temperatures increasing to 46°C. The size of the largest mammals is indicated. For details of the calculations see Paul (1991).

The big overheating myth. - It is a nearly universal truism that giant HiMR endotherms are in danger of "frying" or "melting down" in hot climates. Spotila et al. (1991) calculate that an inactive 3.6 tonne tachyaerobe will have a body temperature of 53°C when the environmental temperature is 35°C. The reality is that desert elephants traverse shadeless land in the middle of hot days, and even when chased by helicopters elephants do not heat up to dangerous levels (Bartlett & Bartlett, 1992 and Osborn, 1992, pers comms.). In hot droughts the big bulls suffer the lowest mortality, and females and calves die largely from starvation (Owen-Smith, 1988; Haynes, 1993), there are no documented examples of elephants dying from heat stroke under natural conditions. Extinct elephants, mammoths and indricotheres of 10 to 20 tonnes thermoregulated in hot climates.

Giant tachyaerobes have relatively low MRs per unit body mass, enormous heat storage capacity, and high body temperatures of 36-39°C. A basic thermodynamic principle is that machines that operate in hot environments should be built to run at hot temperatures. An active tachyaerobe of 4 tonnes with a normal body temperature of 39°C can resist the inflow of an external heat load well over 40°C by raising its body temperature to 43-46°C. Internal heat is safely stored for about six hours (Fig. 8), and is later dumped into the night sky.

What it takes to be gigantic in 1 G. - The common idea that LoMRs are ideal for land giants fail in the absence of any living examples, and the success of HiMR megamammals. The inability of land reptiles to grow rapidly on land under natural conditions may be a critical failure that prevents them from being gigantic. If they did manage to grow much over a tonne, low circulatory pressures and small limb muscles would prevent them from functioning. The temperature stability of LoMR inertial homeothermy does not provide giants with the power they need to be so big. It is water giants that have no need for high blood pressures or large volumes of hard working limb muscles.

Owen-Smith (1988) described how land dwelling megamammals have thrived in the Cenozoic because of their rapid growth and good population recovery, ability to cope with climatic extremes, their powerful and nonselective feeding adaptations, slow rates of starvation, and their ability to wander far in search of the best conditions. This is the high energy system based on high aerobic power needed to be gigantic. Large tachyaerobic muscles support great bulk for long periods, and to move the bulk fast and far enough to find food during long droughts. Because land giants must have large tachyaerobic muscles, and often must pump blood far up to their brains, they are forced to have high circulatory pressures. The consequences of high blood pressures are high aerobic scopes and high resting metabolisms. The rapid growth sustained by HiMRs is necessary in order to reach adult size in a reasonable time. We predict that fast reproduction allows tachyaerobes to grow larger than terrestrial megamammals.

THE METABOLICS OF MEGADINOSAURS

Big sauropods (such as brachiosaurs, supersaurs and titanosaur: like new Argentinosaurus) reached 40 to 100 tonnes (Fig. 2). Skeletons and enormous footprints indicate that some bipedal ornithopods weighed as much as 10 to 30 tonnes (Fig. 1T). Predaceous theropods exceeded 5 tonnes. Bigger dinosaurs wait to be discovered, and rare "world record" individuals will never be found, so 100+ tonners are likely to have existed!

Hips, legs and cruising. - Early dinosaurs - eoraptors, staurikosaurs, herrerasaurs and prosauropods - had erect legs like birds and mammals, yet they retained short, reptile-like ilia (Figs. 1J,K & 3). These ilia could have only supported narrow thigh muscles like those of reptiles. The combination of erect limbs and reptile-like hips was an unusual and exotic combination that is now extinct. It suggests that these early "brevischian" dinosaurs had aerobic metabolics that were neither reptilian or avian-mammalian in nature, and that MRs, circulator pressures, cruising speeds and growth rates were insufficient to achieve great size - so it is not surprising that no small-hippe dinosaur became very big. These archaic dinosaurs may fit the definition of "damned good reptiles".

The early dinosaur condition was not a very satisfactory one because the full potential of the long erect legs could not be realized until the size of the ilium and the leg musculature expanded to avian-mammalian proportions. This is the condition observed in "longoschian" theropods, therizinosaurs, ornithischians and sauropods of all sizes (Figs. 1L-T & 3). Amon megadinosaurs, the ilial plates of tyrannosaurs are so large tha a high endurance limb musculature suitable for chasing down larg prey is indicated over ambush or scavenging habits. The prey of tyrannosaurs - hadrosaurs and especially the ceratopsids - also had long ilia that appear to have supported large sets of aerobically capable muscles suitable for running. Slower moving armored dinosaurs and sauropods are restored with large tachyaerobic limb muscles suitable for bearing great bulk. There is nothing reptilian about the hips and legs of longoschian megadinosaurs; instead, their form is bird- or mammal-like. The suggestion that the muscles of large dinosaurs were small and hyperanaerobic is therefore contra-indicated.

Most megadinosaurs had long striding limbs like those of fast cruising ungulates and elephants. Figure 5 shows that the estimated speeds of bipedal and quadrupedal dinosaurs are similar to those of elephants, and are much higher than those predicted in big reptiles. This proves that megadinosaurs walked in the same fast lane as HiMR megamammals, not in the reptilian slow lane. Only the bizarre advanced therizinosaurs (Fig. 1N) had awkward feet suggestive of InMRs like those of giant sloths. It is widely agreed that some megadinosaurs migrated long distances (Currie & Dodson, 1984; Horner & Gorman, 1988); such journeys demanded high aerobic capacity.

Circulatory pressures. - It has been widely accepted that big theropods had strongly S-curved necks that carried the brain well above heart level, and the same was true of the therizinosaurs (Fig. 1L-N). There has been much more controversy over the neck posture of sauropod dinosaurs. It has been argued that the long necks of sauropods evolved for high browsing and must have been held erect, or that circulatory pressure problems compelled them to carry their necks horizontally (Dodson, 1991), but no one has examined the articulation of sauropod necks in order to restore their true posture. Articulated specimens of Camarasaurus and Chinese sauropods consistently show an upward flexion at the base of the neck (Figs. 1,O,P & 9). The tall shoulders present in many sauropods (a cetiosaur, brachiosaurs, camarasaurs, omeisaurs, mamenchisaurs, euhelopids, many titanosaurs) favored an erect

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TABLE 1

Heart size and heat production in a 30 tonne Brachiosaurus

Resting MR in kcal/hour if it is.....
mammalian.................................**4000-8000**
reptilian.................................500-900

total heart tissue mass as % of total body mass	in kg	cardiac heat production kcal/hour
0.6% single normal (BP 100-130 mmHg)	180	1000
1.3% single giraffe oversized (BP 200 mmHg)	400	
2.0% multiple cervical (BP 200 mmHg)	700	**~2000**
3.3% single super oversized (BP 750 mmHg)	1000	**~3000**

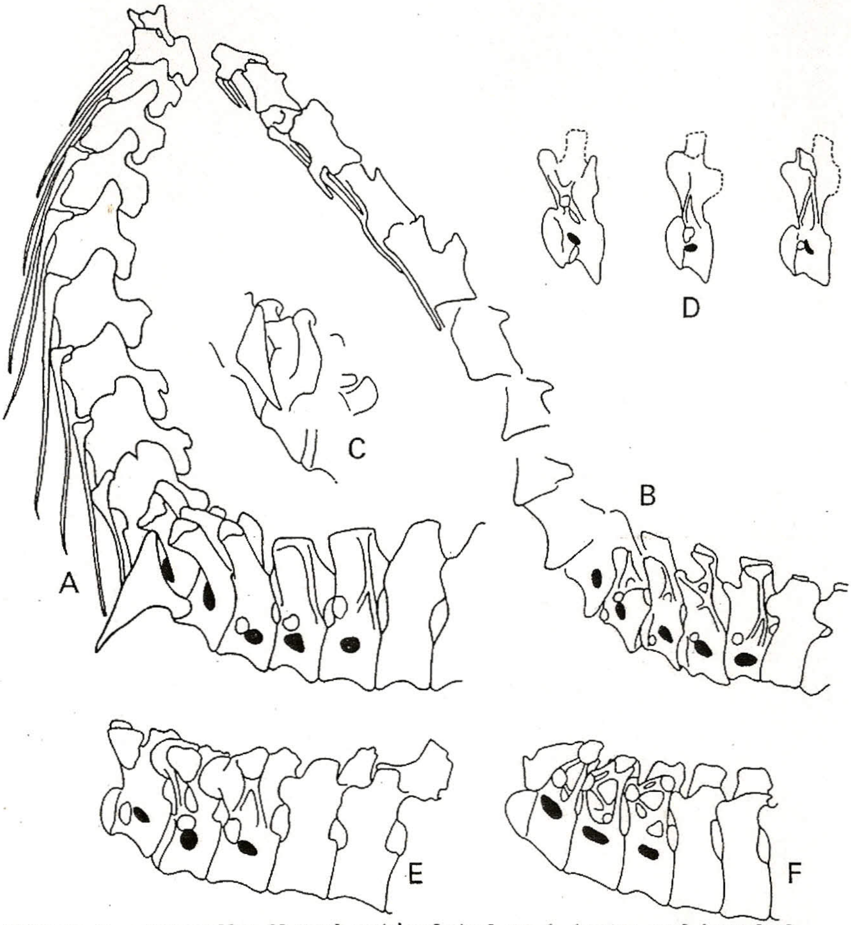

FIGURE 9 - Upwardly flexed articulated neck bases and beveled cervo-dorsals indicating habitually erect neck carriage in the sauropods A-D, Camarasaurus and E-F, Euhelopus.

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neck posture. Low shouldered diplodocids had horizontal necks, but large sacral complexes and heavy tails suggest they reared up to feed. Retroverted hips suggest that camarasaurs (Fig. 1P), mamenchisaurs and euhelopids also reared up often.

One way or another, sauropods had to pump blood all the way up their necks. Consider the problem faced by a 30 tonne Brachiosaurus (Fig. 4). We conservatively presume that even with special vascular adaptations a low power reptilian heart could not pump blood up 10 m. Even if the sauropod had a normal sized high pressure heart of 180 kg, the metabolic rate of the heart alone would be greater than that of the entire resting metabolism of a giant reptile (Table 1). If the heart had giraffe-like proportions it would have weighed 400 kg, but even this would not suffice to pump blood up over 30 ft. Seymour (1976) calculated that Brachiosaurus needed a supersized heart of over a tonne, and a one tonne heart is the largest that could fit into the sauropod's ribcage. Such a heart would be inefficient, and Choy & Altman (1992) made the interesting and controversial suggestion that sauropods had extra hearts in the neck so that the main heart would not need to be so huge. In either case, conservative calculations of cardiac heat production are many times higher than the resting metabolism of a reptile. When the heat production of the other internal organs is added in, it is clear that the resting MR of Brachiosaurus was as high as those of giant mammals, and many times higher than expected in a reptile of such size (Table 1).

It has been calculated that long necked sauropods could not draw enough air down their long trachea to sustain HiMRs (Daniels & Pratt, 1992). Alternately it has been calculated that elevated oxygen levels were necessary to sustain sauropods (Hengst, this volume). Although we take no particular position on Mesozoic oxygen levels, we strongly question whether the respiratory capacity of dinosaurs can be calculated accurately enough to estimate past oxygen levels. Nor do we predict that sauropods had any more trouble breathing large volumes of air with modern levels of oxygen than do sperm whales. The surface of sauropod trachea may have been aerodynamically configured to maximize airflow. Although sauropods probably lacked a mammalian diaphragm, thin walled, pneumatic vertebrae strongly suggest the presence of pulmonary air-sacs. Because sauropods were not close bird relatives, we predict that their air-sac/lung system operated in a different manner (note even some birds have sternal plates that are too small to ventilate abdominal air-sacs, Fig. 1C). Abdominal air-sacs operated by long posterior ribs probably improved pulmonary air exchange enough to oxygenate HiMRs.

Large theropods had pneumatic vertebrae that suggest a pre-avian air-sac system was being developed. Progressive elongation of posterior over anterior ribs suggest that ventilation of abdominal air-sacs became important in large theropods (Fig. 1L,M). Perry (1983) suggested that the prepubis and retroverted pubis/ischium of large ornithischians supported abdominal muscles that functioned like a diaphragm. Large ornithopods had a lumbar space that lacked long ribs, and was preceeded by long mid-dorsal ribs. This was a very mammal-like condition (compare Fig. 1D-H to 1T), and strongly suggests that ornithopods paralleled mammals in developing a vertical transverse diaphragm. Giant dinosaurs appear to have had high capacity respiratory systems designed to oxygenate their high capacity circulatory systems.

Growth and reproduction. - Estimated rates of growth for large duckbilled, horned, and ceratopsid dinosaurs suggest that giant dinosaurs grew as rapidly as rhinos and elephants of similar size (Fig. 6). MRs similar to those of big edentates, rhinos, elephants, and whales were necessary for big dinosaurs to grow up within reasonable time spans. Reptilian or intermediate metabolics would not have done the job under natural conditions. As the tallest and most massive sauropods grew, their increasing height and the very rapid growth needed to mature in due time are especially interesting. Even InMRs were probably not adequate for such fast growth, and the increasing cardiac work associated with increasing height suggests that mass specific MRs increased with maturity rather than falling off somewhat in the normal manner.

Why did some dinosaurs become bigger than land mammals? - Modern restorations (including the senior author's) that show dinosaur parents caring for a small number of youngsters in the manner of big mammals are not accurate. The egg laying megadinosaurs out-reproduced megamammals by a factor of dozens to hundreds (Fig. 7). Also, non-nursing, post-nestling juvenile dinosaurs were not as dependent upon adults for survival as are mammalian young. Megadinosaurs fit the ideal of being fast growing, fast reproducing forms that could achieve long term survivability with small, unstable populations of enormous adults - a feat attainable only with HiMRs (Paul, 1994).

Parenting and social organization. - The modern consensus is that megadinosaur socialization was highly variable and often well developed (Currie, 1983; Lockley et al., 1986; Horner & Gorman, 1988). Many examples lived in herds or packs and cared for their young, in some cases by foraging for nestlings. This was above the crocodilian level of socialization, and approaches the avian-mammalian condition. Only tachyaerobic dinosaurs could have sustained such intense social activity on land.

Megadinosaurs did not meltdown. - Tachyaerobic dinosaurs up to 20 tonnes would have had no more trouble thermoregulating in hot climates than have tropical mammals of the same size. A 40 tonne tachyaerobic sauropod with a high body temperature would have been able to safely store internally generated heat for 12 hours (Fig. 8). We restore tropical megadinosaurs with 2-7% body fat (as in tropical ungulates and proboscideans, Ledger, 1968; Haynes, 1991), rather than heavy domestic animal-like fat deposits postulated for gigantothermic dinosaurs (Spotila et al., 1991). Polar megadinosaurs probably built up fat deposits for winter use; whether they used it for insulation is more problematic (see Haynes, 1991).

Could tachyaerobic sauropods feed themselves? - Astute observers of <u>Jurassic Park</u> noticed that the brachiosaur's head was big enough to swallow the kids whole. A 30 tonne HiMR brachiosaur needed to eat about half a tonne of fodder/day, only 1.5% of its own mass. If the beast took six bites per minute for twelve hours per day (as per giraffes and elephants) each bite would be a mere four oz., hardly a problem for a mouth that was 42 cm broad. A 10 tonne HiMR diplodocid needed only 2 oz. bites.

Megadinosaurs were not weak. - Over the years it has been asserted that sauropods could not move on land, rear up, feed HiMRs, or pump blood up their long necks, that large dinosaurs had limited breathing capacity and moved slowly, and that big theropods were mere scavengers - it is amazing that the 1-100 tonne weaklings survived at all! Examining the structure of megadinosaurs reveals strong animals of high aerobic capacity and great athletic ability. Figure 1 shows that at any given size, megadinosaur skeletons (especially their vertebral columns) were more strongly built than those of megamammals.

SUMMARY AND CONCLUSIONS

Megadinosaurs grew two orders of magnitude larger than any LoMR land reptile. They also regularly exceeded the 5 tonne maximum of sluggish InMR mammals. Giant dinosaurs (except the awkward footed therizinosaurs) shared large hips and long striding legs with the biggest ungulates and proboscideans. These hindlimbs were probably operated by large volumes of muscles which required large amounts of oxygen during exercise and when at rest. High capacity respiratory systems were probably present to oxygenate the large volumes of blood pumped to oxygen-craving muscles and high held brains by high pressure circulatory systems. An unappreciated consequence of the modern consensus favoring high pressure double pump hearts in dinosaurs is that the hard working hearts and supporting organs produced high avian-mammalian levels of heat production. Failure to maintain high internal pressures and high resting MRs would have resulted in torpor. Because large amounts of heat were generated by the muscles and organs even at rest, megadinosaurs were HiMR endotherms (except that InMRs are possible in therizinosaurs). The giant dinosaurs' fast growth was possible only because the juveniles had fast running metabolisms, and dramatic fall offs in MRs with maturity are not only contra-indicated but may have been reversed in tall sauropods.

We do not assert that the physiology of megadinosaurs was identical to that of megamammals. The evolution of megadinosaurs in a warm Mesozoic world may have left low latitude examples with less well developed thermoregulatory controls and auxiliary heat production than is present in birds and mammals - but these features may have been present in polar dinosaurs. Smaller dinosaurs may have been more prone to entering daily torpor than modern birds and mammals. This may help explain why dinosaurs were more prone to laying down bone growth rings as they matured than are birds and mammals (Reid, 1990; Varricchio, 1992; but deep set postcranial rings are also observed in mammal bones [Leahy, 1991; Varricchio, [1992]). But, contrary to the argument that many dinosaurs had some form of transitional metabolics, the anatomical evidence shows that this condition was limited to early brevischian dinosaurs with their unusual combination of reptilian and avian features. There was little or nothing reptilian in the energetics of big bodied and/or big hipped dinosaurs. So reptiles with small muscles and low blood pressures are not good analogs for giant dinosaurs. Marine reptiles that live in a world that buffers them from gravity are even less so. We find the recent tendency to cite marine and captive reptiles as primary analogs for dinosaurs as unconvincing as it is perplexing. Giant dinosaurs were not good reptiles, or damned good reptiles. They were marvelous archosaurs whose anatomy and aerobics converged with megamammals. It is only logical that the closest living models for extinct land giants are living land

TABLE 2

Size ranges possible with various metabolic systems in water, land and air

Metabolic Condition & Habitat	Size Range
SEMI-AQUATIC - MARINE	
BRADYMETABOLIC, BRADYAEROBIC - invertebrates, fish, amphibians, reptiles	microscopic - 15 tonnes
TACHYMETABOLIC, TACHYAEROBIC some tuna, sharks, birds, mammals	10 g - 200 tonnes
TERRESTRIAL & AERIAL-	
BRADYMETABOLIC, BRADYAEROBIC - invertebrates, amphibians, reptiles	microscopic - 1 tonne
BRADYMETABOLIC, TACHYAEROBIC larger flying insects	0.2 g - 250 g
Marginal TACHYMETABOLIC, TACHYAEROBIC basal therapsids, brevischian dinosaurs	100 g - 1 tonne
Moderate TACHYMETABOLIC, TACHYAEROBIC derived therapsids, basal mammals, edentates, therizinosaurs? (examples over 1 tonne are TERRAMEGATHERMS)	10 g - 5 tonnes
High TACHYMETABOLIC, TACHYAEROBIC some marsupials, most eutherian mammals longoschian dinosaurs, birds	1.5 g - 100 tonnes

giants with aerobic metabolisms, circulatory systems, and growth patterns suitable for terrestrial gigantism under natural conditions. One way that megadinosaurs differed dramatically from megamammals was in their rapid oviparous reproduction. Combining the latter with HiMR rapid growth produced theropods and sauropods bigger than their mammalian counterparts.

Giant dinosaurs were no more gigantotherms than are elephants. Instead, land giants are "terramegatherms", animals that have or had HiMRs because high aerobic capacity is a prerequisite for evolving body masses over 1 tonne in 1 G. Table 2 outlines the size ranges that can be achieved with various metabolic systems. In water, either low or high MRs work in animals up to 15 tonnes. It is possible that only very fast growing tachyaerobes can become larger in the sea. On land, insects with high active MRs are small because of their decentralized respiratory systems (see Heinrich, 1993; tiny flying insects have adaptations that minimize oxygen consumption). Both low and high MRs work in tetrapods up to 1 tonne, elevated MRs are necessary in bigger forms, and high MRs are probably needed to exceed 10 tonnes.

The anatomical and other evidence indicates that dinosaurian aerobics evolved as follows. MRs started to be elevated above

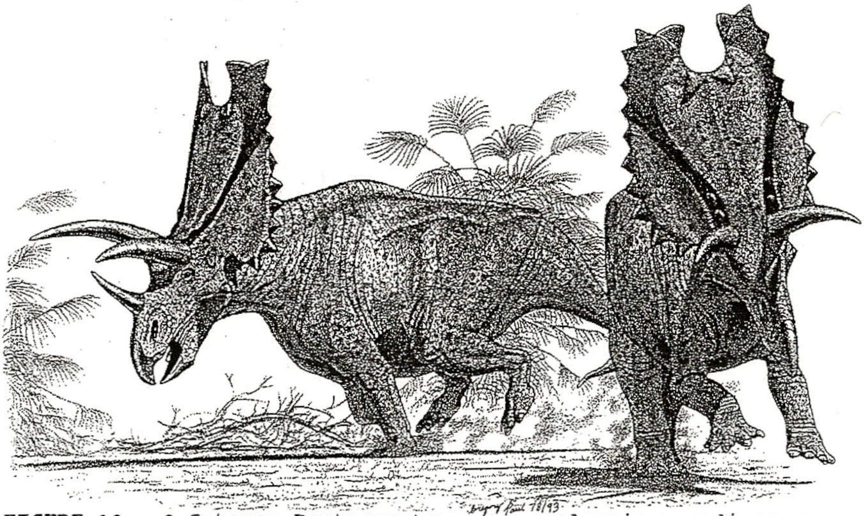

FIGURE 10 - 2.5 tonne Pentaceratops was a classic megadinosaur with long striding legs suitable for fast walking and running, powered by large volumes of tachyaerobic muscles that received oxygen via a high capacity respiro-circulatory system. High metabolic rates were the result of these anatomical features.

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reptilian levels in Triassic brevischian dinosaurs. Expansion of the leg muscles to avian-mammalian levels occurred in Late Triassic and Early Jurassic theropods, ornithischians and sauropods. Pneumatic vertebrae indicative of pulmonary air-sacs first appear in Late Triassic theropods and Early Jurassic sauropods. The ornithischian respiratory system evolved in the Late Triassic, and the mammal-like diaphragm of ornithopods evolved by the Middle Jurassic if not earlier. Trackways of fast cruising dinosaurs are imprinted on Late Triassic sediments. Terramegathermic sauropods appeared in the Early Jurassic, in the Late Jurassic sauropods reached 50 tonnes, the biggest 100 tonne examples are found in the Late Cretaceous. Other groups of predaceous and herbivorous dinosaurs also became terramegatherms in the Jurassic and stayed that way until the end. The combined evidence indicates that dinosaurs became tachyaerobic endotherms fairly early in the Mesozoic, and that the MRs of megadinosaurs flat-lined through the rest of the Era, except that the exercise metabolisms of big running tyrannosaurs, hadrosaurs and ceratopsids may have risen a modest amount in the Late Cretaceous. On the other hand, the MRs of ponderous Late Cretaceous therizinosaurs may have declined by a modest amount relative to the more normal Early Cretaceous alxasaurs.

Owen-Smith (1988) stressed the extinction resistance of slow breeding megamammals. It has been little appreciated that even the biggest dinosaurs were prolific "weed species" with much higher recovery potentials than mammals. It is very difficult to understand how a diverse array of thermally sophisticated Late Cretaceous dinosaurs adapted to living in climates ranging from tropical to polar could have been totally extinguished when environmentally sensitive birds and amphibians survived. This is true regardless of the proposed extinction agent - massive impacts, vulcanism, climatic shifts, marine regressions, oxygen declines, floral changes, etc. The loss of nonavian dinosaurs remains one of the most extraordinary and inexplicable events in Earth History, and may have as much to do with a bad roll of evolutionary chaos as with a specific cause or causes.

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APPENDIX 1: SOME DEFINITIONS

Bradyaerobic: Bradyaerobes have low rates of active oxygen consumption (the reptilian condition).
Bradymetabolic: Rates of oxygen consumption are low under resting conditions (the reptilian condition).
Ectothermic: In ectotherms the majority of body heat is acquired from the environment. These have LoMRs (reptilian condition).
Endothermic: In endotherms the majority of body heat is generated internally. Most examples have HiMRs (avian-mammalian condition), but LoMR giants like leatherback turtles can conserve enough body heat to be endothermic (McNab, 1983; Spotila et al., 1991).
Hyperanaerobic: The very high levels of anaerobic power generated by the muscles of many reptiles.
Tachyaerobic: Tachyaerobes have high rates of active oxygen consumption (the avian-mammalian condition).
Tachymetabolic: Rates of oxygen consumption are high under resting conditions (the avian-mammalian condition).