TERRAMEGATHERMY AND COPE'S RULE IN THE LAND OF TITANS

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The anatomy and biology of Morrison megadinosaurs is best explained by high aerobic exercise capacities that produced the power needed to pump blood in large volumes at high pressures. Such high levels of sustainable power generation may be a prerequisite for the evolution of great height and mass in 1G, a condition called terramegathermy. A causal link between limb posture, walking speeds and aerobic exercise capacity is demonstrated. The feeding posture and capacity of sauropods and stegosaurs is examined, and a new hunting strategy for Morrison theropods is suggested. Elephant- to whale-like growth rates and high metabolism were probably necessary for sauropods to achieve weights of 10–100 tonnes.

Keywords: Endothermy; Metabolism; Population

INTRODUCTION

When formulating the evolutionary rule that body size tends to increase in clades, Cope may have been influenced by the ultimate terrestrial example of his Rule, the Morrison megadinosaurs he described (Stanley, 1973). The Morrison Formation contains at least seven sauropod genera 10–100 + tonnes, as well as stegosaurs, theropods, and ornithopods that exceeded 1 tonne (Figs. 1(A)–(M) and 2(A); Table I). Although the majority of the Morrison dinosaur population was probably made up of small forms (< 1 tonne; Russell, 1989), it is the giants that capture our attention. Sauropods, stegosaurs and theropods include some of the most massive and tallest examples of each group, and they dominated the energy flow patterns in the Morrison.

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TABLE I Measurements of various Morrison megaherbivores

Length mm -	Brachiosaurus FMNH P25107	Brachiosaurus USNM 5730	Brachiosaurus BYU 5001	Haplocanthosaurus CMNH 10380	Haplocanthosaurus CM 572	Camarasaurus CM 11338	Camarasaurus USNM 13786	Camarasaurus CM 11393/120020	Camarasaurus AMNH 5761	Diplodocus CM 84	Diplodocus USNM 10865	Barosaurus CM 3542	Barosaurus AMNH 6341	Apatosaurus LACM 52844/CM 11162	Apatosaurus YPM 1860	Apatosaurus CM 3018	Apatosaurus FMNH 7163	Apatosaurus YPM 1980	Apatosaurus YPM 1840	Amphicoelias AMNH 5764	Amphicoelias AMNH 5777*	Supersaurus BYU 5501/5003	Supersaurus BYU 5500	Seismosaurus NMMNH 3690	Stegosaurus USNM 4934	Camptosaurus USNM 4937	Camptosaurus USNM 5818	Camptosaurus SMM P84.1
Skull		600				330	530	760p				440		650		(6507)									390			
Cervical Series	4750p			3140p		1004	2300	3660p		6520p	2450	~5225p	9830p			5410	2806		5400p	~2700p	~12000p			~3300p	870			
Dorsal Series	950			2990p		940	1750	2760p		2680			3160			2690			2790		~5500p				1540			
Sacrum				1090	795	420	620			765	760		950			1325	1260		1380						360			
Caudal Series						2440		7100p		~14100p			~13500p			12850p								~17000p	2850p			
Scapula-Coracoid	2250e		2690			650	1210	1950	1665	1600	1508		1730			2020		1975		~2100u	~4000e	2700	2440		930	609		468
Humerus	2040+		2420e			440	770	1175			1010		1090			1150		1121		~1000n					550	463		297
Radius						295	540	778			690					800		775							410			
Longest Metacarpal						140	272	340								285									120			
Ilium	1124			1315	872	540	782	1100e	1260	1089	945		960			1460	1210	1330		1170				~1500	980			
Pubis				1100	693	385	730	1055	1055	820	950		960			1190	1390	1122						1010	1020			
Femur	2030		2370e	1745	1275	567	1000	1525	1800	1542	1030		1510	~1550		1785	1830	1255	1950e	1770	~3800e				1050	580	805	~860e
Tibia-Astragalus						390	675	1000e	1265				1190			1270		1255							630			
Fibula							665	960			1055		1160			1175		1170							610			
Longest Metatarsal						90	165	217			205		200			238												
Flesh Hindfoot						-235		~680		620p			630			884								300	130e			
Height mm -																												
Hindlimb	760			1010	615	1010	500	2760	980	2850p	936		2930			3315	1340			1075	~2400e			~1400	1840			
Posterior Dorsal						280		670		1051			1110			1350									470			
Circumference mm -																												
Humerus	757						383	498			440					629		591										
Femur	876			755	518		481	672		581	584					845	754	740	755	735								
Breadth mm -																												
Mouth						104	180	265				148		255	~270p										53			
Meters -																												
Total Length	20-21e	~10	24-25e	14.15p	10-11e	5	~10	15.3p	~18e	24.8p	10	~6e	27.9p	~11e	~13e	22.8p				23-28e	40-60e	35-45e	30-40e	28-34e	6.1			
Total Height	12-13e		15-16e	10-11e		2.2		7.0p		11.7			15.5p			10.4												
Rearing Height	~16e		~18e	9.6p		3.0		8.9p														20-25e			4.0			
Shoulder Height	5.7p			3.6p		1.36		3.7		3.4p			~3.5p			3.9				4.2p	8-10e				1.5			
Hip Height	4.5p		~6.5e	4p		1.29		3.4		3.9p			4.1			4.6				4.4p					2.3			
Tonnes	~35p	~10	45-55e	12.7	~5	0.64	3.8	14.2	20-25p	11.4	10	~6e	11.6			17.5	18	19.1		11-12e	90-150e	45-55e	30-40e	25-30e	2.2	3-3.5e	0.51	1.7e

Notes: total lengths and vertebral series measured along centra spaced with intervertebral discs, skull length = tip of premaxilla to end of opisthotic wing, e = estimate, p = partial element/s and/or scaling in parts from other specimens allowed more precise estimate, t = length estimated from combined right and left element and left element is from same specimen, and radius length estimated from ulna length, * = number reserved for lost specimen.
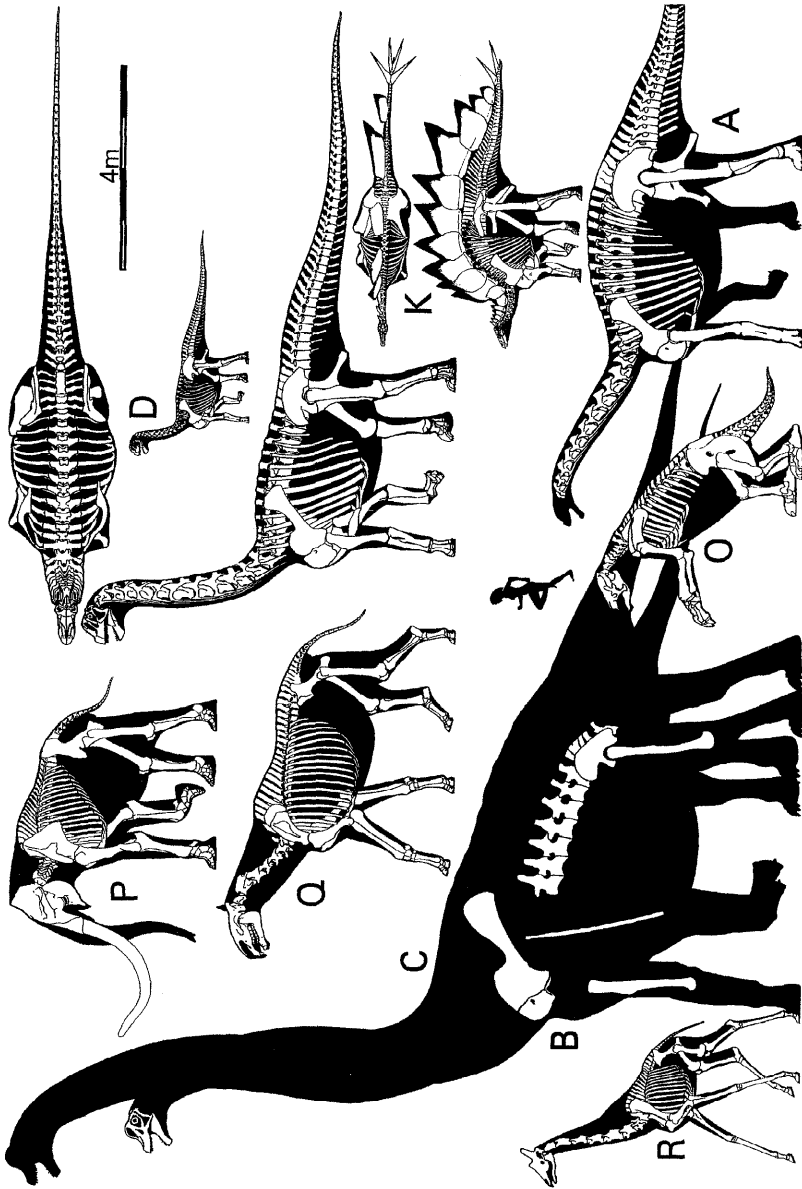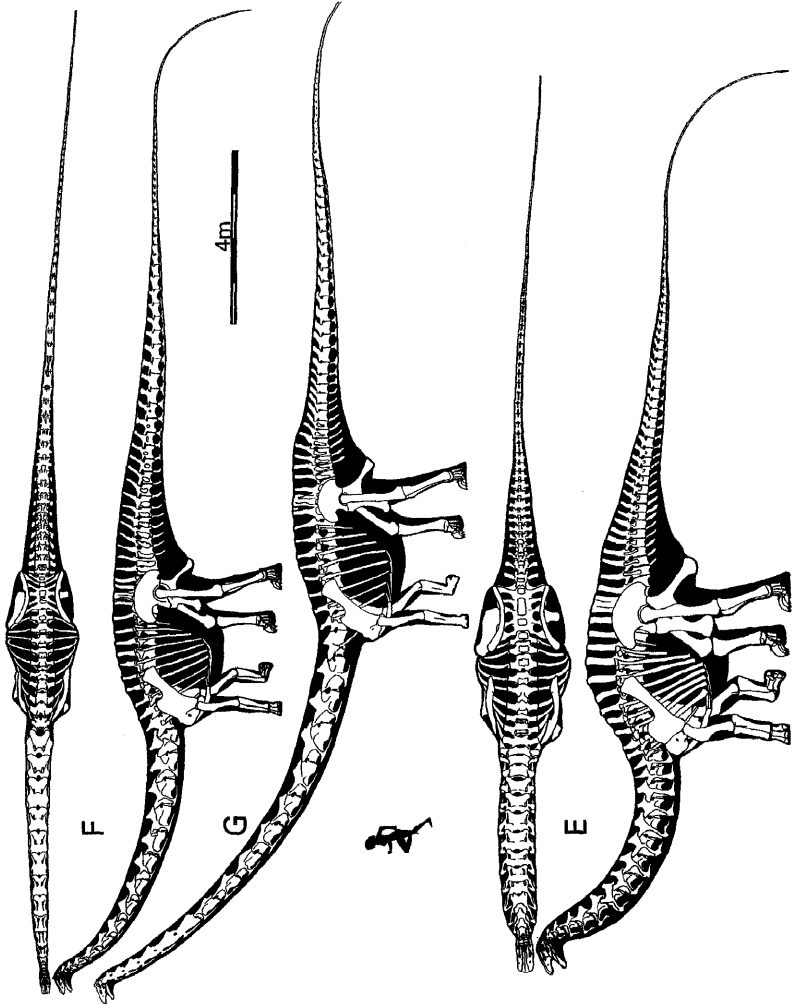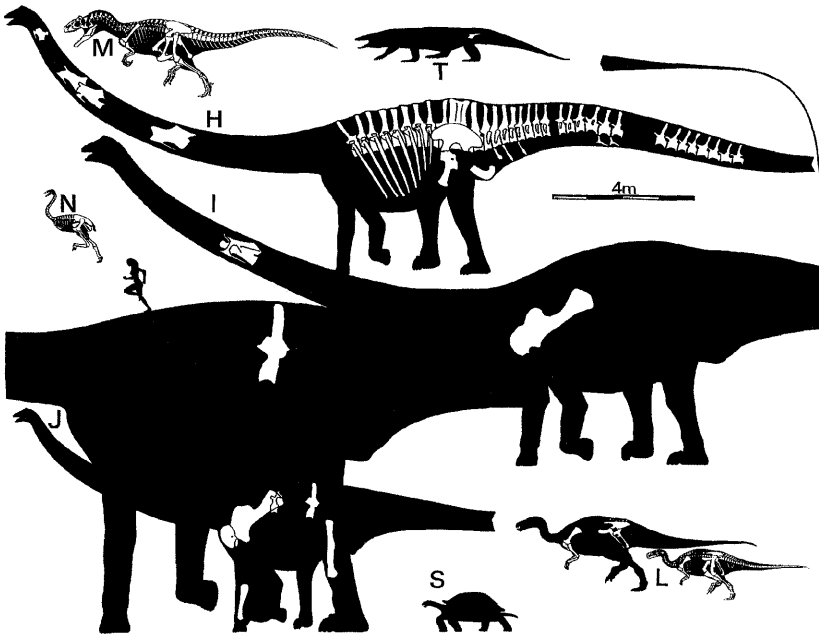
FIGURE 1(a)

FIGURE 1(b)

FIGURE 1(c)

FIGURE 1   Comparative skeletal restorations (all to scale). (A) *Haplocanthosaurus delfsi* (CMNH 10380), (B) *Brachiosaurus altithorax* (FMNH P25107 with skull USNM 5730 scaled to fit), (C) "*B. macintoshi*" (scaled to scapula-coracoid BYU 5001), (D) *Camarasaurus "lentus"* (CM 11393 and CM 11338), (E) *Apatosaurus louisae* (CM 3018, with skull CM 11162 scaled to fit), (F) *Diplodocus carnegii* (CM 84, with skull CM 3542 scaled to fit), (G) *Barosaurus lentus* (AMNH 6341), (H) *Supersaurus viviane* (BYU 5501 and 5003), (I) *Seismosaurus hallorum* (NMMNH 3690), (J) *Amphicoelias altus* (AMNH 5764) and *A. fragillimus* (AMNH 5777), (K) *Stegosaurus stenops* (USNM 4934), (L) *Camptosaurus dispar* (SMM P84.15.5 and USNM 5818), (M) *Allosaurus* (DINO 2850 [= UUVP 6000], 1.3 tonnes), (N) *Aepyornis* (0.4 t), (O) *Eremotherium* (USNM 20872, 6.5 t), (P) *Mammuthus* (DMNH 1359, 7.8 t), (Q) *Indricotherium* female? (AMNH 26387, 7.8 t), (R) *Giraffa* (1.5 t), (S) *Geochelone atlas* (1 t), (T) *Megalania* (1 t).

What are the energy requirements for terrestrial animals fulfilling Cope's Rule to such an extreme? Why did over half a dozen whale-sized, tree-height sauropods, which were preyed upon by rhino- to elephant-sized theropods, dwell in one region, a feat never matched before or since by terrestrial mammals, or reptiles? Many workers have argued that sauropods grew big by being energy efficient inertial homeotherms ("gigantotherms") that minimized demands upon their resource base (Coulson, 1979; Ricqles, 1980; Russell and others, 1980; McNab, 1983; Weaver, 1983; Coe and
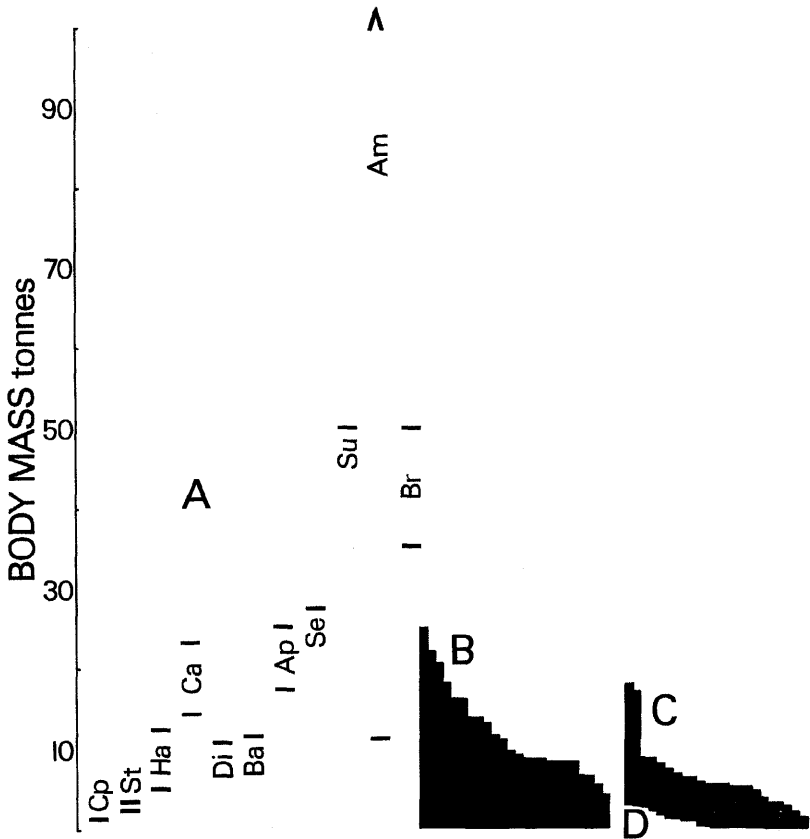
FIGURE 2   Comparisons of masses of megaherbivores. (A) Masses of Morrison sauropods, stegosaurs and ornithopods (from Table I); Am, *Amphicoelias*; Ap, *Apatosaurus*; Ba, *Barosaurus*; Br, *Brachiosaurus*; Ca, *Camarasaurus*; Cp, *Camptosaurus*; Di, *Diplodocus*; Ha, *Haplocanthosaurus*; Se, *Seismosaurus*; St, *Stegosaurus*; Su, *Supersaurus*. Sauropod size distribution recorded by trackway dimensions of (B) Morrison Purgatoire trackway site, (C) Glen Rose Limestone Davenport herd (data from Lockley and others, 1986; Lockley, 1987; Farlow and others, 1989: total mass 148 tonnes). (D) Size distribution in a typical female-juvenile African elephant herd (Laws and others, 1975; Owen-Smith, 1988: total mass 18.3 tonnes). Note that the larger number of individuals in the sauropod herd is due to many more juveniles, and that subadults dominated the elephant herd. Note also that the adult female elephants are juvenile size by sauropod standards.

others, 1987; Farlow, 1987; 1990; 1993; Dunham and others, 1989; Russell, 1989; Czerkas and Czerkas, 1990; Dodson, 1990; 1991; Reid, 1990; Spotila and others, 1991; Daniels and Pratt, 1992; Colbert, 1993; Farlow and others, 1995). Paul and Leahy (1994) hypothesized that megadinosaurs

and megamammals are "terramegatherms" that relied upon blood circula-
tion at high pressure and high levels of aerobic power production to carry
massive bulk and achieve great height in 1 Gravity.

MORRISON FLOODPLAIN: TOO HOT AND DRY
FOR TACHYAEROBIC GIANTS?

It is appropriate that the home of enormous terrestrial creatures is itself an
unusually large nonmarine formation that originally covered ~ 1.5 million
km^2 over 13 states. The Morrison Formation was deposited on a broad
floodplain in the mid-latitudes. The atmosphere may have been affected by
a CO_2 greenhouse, but whether the climate was highly seasonal or not is a
matter of dispute (Dodson and others, 1980; Coe et al., 1987; Peterson
and Turner-Peterson, 1987; Russell, 1989; Dodson, 1990; 1991; Retallack,
1990; 1996; Turner and Fishman, 1991; Moore and others, 1992; Wing and
Sues, 1992; Farlow, 1993; Demko and Parrish, this volume; Ash and others,
this volume). A north–south rainfall gradient may have existed, with harsh,
arid aeolian conditions and riverine vegetation in the south, moderate
rainfall in the central region with medium and/or short statured floodplain
flora, and water saturation and heavy vegetation in the north based on the
presence of coal. Trees included conifers, ginkoids, cycadeoids, and tree
ferns, so that fruits and large seeds were much less abundant than they are
today. Ground cover probably included rushes and ferns.

   The high temperatures and aridity of the southern and mid-parts of the
Morrison environment seems incompatible with giant animals that needed
large quantities of food and would have been subjected to heat stress.
However, unusually large elephants live in deserts today (McFarlan and
McWhirter, 1989; Bartlett and Bartlett, 1992; Viljoen, 1992). These desert
giants sometimes move all day across shadeless tracts under cloudless skies
when air temperatures exceed 40°C (Bartlett and Bartlett, 1992; personal
communication). Nevertheless, there are few if any documented cases of
elephants overheating under these conditions. Large bulls suffer lower
mortality rates than smaller elephants and ungulates during droughts. Nor
do elephants overheat after long chases on warm days (Owen-Smith, 1988;
Osborn, 1992; Viljoen, 1992).

   These examples of elephants surviving at elevated temperatures falsify
the calculations of Spotila and others (1991) that a 3.7 tonne dinosaur
with an elephant-like metabolism would overheat at only moderately hot
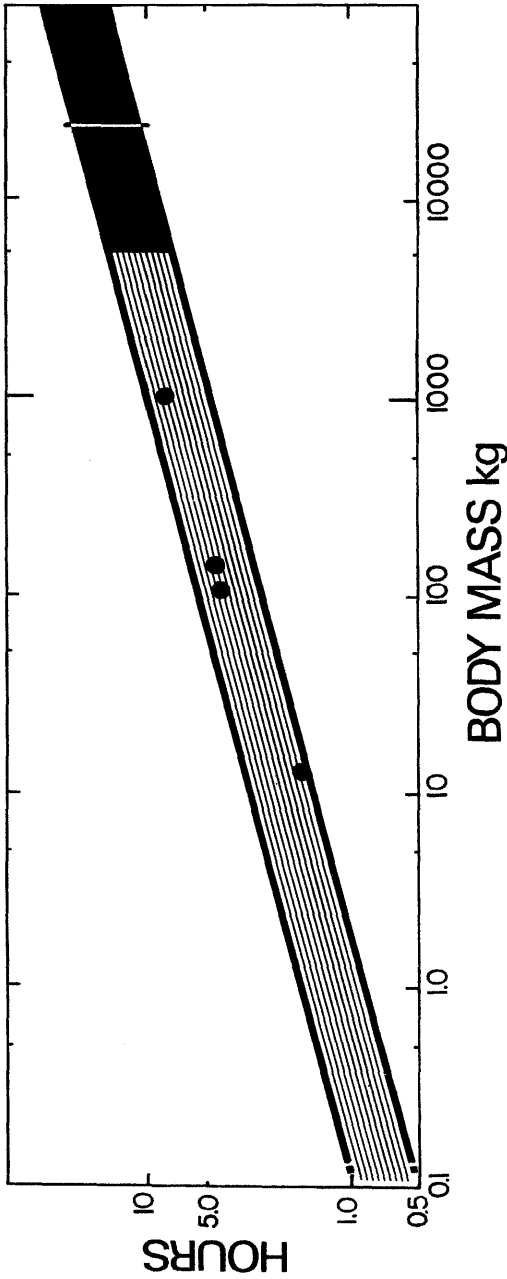temperatures. Large size actually confers protection against overheating

FIGURE 3   Estimates how long tachyaerobic tetrapods can store internal body heat before overheating. Assumption are: that a 6–8°C rise in body temperature (up to 46.5°C), 0.83 kcal is stored for each 1°C rise in body temperature, the total active energy budgets are 1.3 or 2 × mammalian resting metabolic rate, and that external heat is largely excluded by a combination of low surface areas and high rising body temperatures. The results are in agreement with heat storage times for ungulates (circles, from Taylor, 1970). Because resistence to overheating increases with size, tachyaerobic Morrison sauropods (solid black) should have been able to cope with hot, dry conditions, as well as, or better than giant land mammals (vertical slash). Modified from Paul (1991, fig. 5).
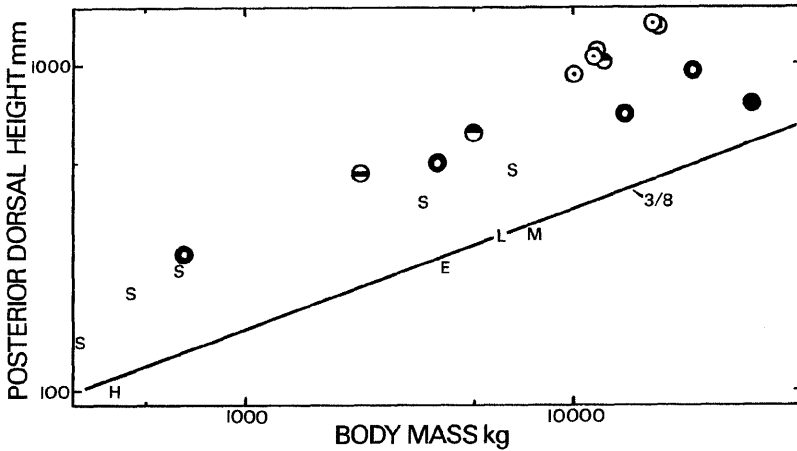
FIGURE 4   Height of the posterior dorsal vertebra as a function of body mass in Morrison haplocanthosaurs (circles with solid upper half), brachiosaur (solid circle), camarasaurs (hollow circles), diplodocids (circles with a dot), a stegosaur (circle with horizontal line) (data in Table I); S, ground sloths; L, *Loxodonta*; E, *Elephas*; M, *Mammuthus*; H, *Equus*. Slope line (3/8) projects a constant strength to mass relationship for elephant-like dorsal series if they act as a elastic beams (McMahon, 1984). Shifting the dinosaurs and sloths to the main mammal line would require increasing body mass estimates two to tenfold.

when ambient temperatures are too high to unload heat by convection and radiation. In addition, evaporative cooling is not viable because humidity may be high or pools of water for refuge scarce. External heat must then be excluded from the body while internal heat is stored in body water (Taylor, 1969; 1970; 1972; Finch and Robertshaw, 1979; Schmidt-Nielsen, 1984; Paul, 1991). Giant mammals can store their metabolic generated heat for many hours, and use increasingly high body temperatures and low surface areas to exclude external heat. In contrast smaller mammals quickly expire if shade or abundant water is not available (Fig. 3). In addition, the excess heat of large mammals is dumped at night (the steady-state thermal study presented in Spotila and others [1991] is inapplicable to terrestrial animals outside polar latitudes). The use of the long neck and tail of a sauropod as a heat radiator might have be ineffective at elevated temperatures; even elephants, which use their ears as radiators, cease flapping their ears to cool down when ambient temperatures are too high (Paul, 1991).

   Institutional abbreviations: AMNH, American Museum of Natural History; BYU, Brigham Young University, CM, Carnegie Museum; CMNH, Cleveland Museum of Natural History; DINO, Dinosaur National Monument; DMNH, Denver Museum of Natural History; FMNH, Field Museum

of Natural History; LACM, Los Angeles County Museum; NMMNH, New Mexico Museum of Natural History; SMM, Science Museum of Minnesota, USNM, United States National Museum of Natural History; UUVP, University of Utah, Vertebrate Paleontology.

FEEDING HABITS AND CAPACITY OF MORRISON MEGADINOSAURS

Predators: Did Morrison Theropods Nibble upon their Prey?

At ~ 1.5 tonnes, most Morrison allosaurs and ceratosaurs (megatheropods) are about one-tenth the mass of the average sauropod, whose tails alone weighed as much as an allosaur (Fig. 1). Although these theropods may have minimized risk of injury by using hit-and-run slashing attacks (Paul, 1988a), even these megatheropods would have been hard pressed to disable an adult sauropod. An alternative method of attack is suggested by a recently televised video showing small false orcas attacking a pod of sperm whales. None of the sperm whales were killed, instead chunks of flesh were extracted by the false orcas. This mode of attack suggests the possibility that theropod dashed in to slice a strip of flesh from tail, flank or leg of a big sauropods. A 1.5 tonne allosaur may have needed up to 15–27 kg of flesh per day (Paul, 1988a; less if reptilian energy budgets are assumed), which might have been about two or three large bites off a sauropod. Thus, a large sauropod herd, totaling 150 tonnes (Fig. 2(B)), need sacrifice only 0.12–0.2% of their flesh to satisfy the daily needs of a twelve pack of allosaurs.

Herbivores: A Tale of "Small" Heads and Long Necks

It has been argued that sauropods were low- to medium-level browsers with necks carried horizontal, or were unable to rear on their hind legs (Martin, 1987; Jensen, 1988; Czerkas and Czerkas, 1990; Dodson, 1990; 1991). It seems improbable that necks meters in length evolved in order to save a few steps towards a plant. The cost for 10–100 tonne animals to move 1 m would only be 1.5–10 kcal (Fedak and Seeherman, 1979; Langman and others, 1995), whereas 1 kg of fresh browse contains ~ 2000 kcal (see below). In fact, a long neck reduces over all energy efficiency because the large respiratory dead space of a long trachea increases the energy cost of breathing (Daniels and Pratt, 1992). On the other hand, sauropods could

fully exploit their energy expensive necks only if they regularly used them to reach plant energy found in tree crowns.

Although elephants do not have long necks, they occasionally rear to feed in the wild (Sikes, 1971, fig. 15). Even so, they are front heavy due to the lack of a large tail, and their hindlimbs are less strongly built than the forelimbs. One would predict that an animal that reared up more regularly than an elephant should have a heavy tail and semi-bipedal adaptations. These adaptations are seen in sauropods, as well as stegosaurs. As Alexander (1989) has observed, sauropods and stegosaurs bore a great deal of their mass on the hindlimbs. As a result, standing bipedal probably did not exceedingly increase the load on the hindlimbs. Certainly the femur was considerably more robust than the humerus, hence stronger (Table I). The dorsal vertebrae of all sauropods and stegosaurs are larger than those of quadrupedal mammals of similar mass, and usually matched or exceeded those of the semi-bipedal ground sloths (Figs. 1(A)–(J), (O)–(P) and 4). It is difficult to explain why sauropod dorsals were so extremely strong unless they were heavily loaded during bipedal stance, an act facilitated by the counterweight of the large tail. Also, the retroverted hips (Jensen, 1988) of camarasaurs are inexplicable unless they allowed hindlimb movement in a bipedal stance. Thus, camarasaurs may have been mobile during bipedal feeding with the tails kept clear of the ground, while stegosaurs and diplodocids were specialized for static tripodal feeding (Table II).

The rearing abilities, neck posture, and other browsing adaptations of Morrison megaherbivores are detailed in Table II. No other sauropod dominated formation produces such a diverse array of feeding types, includes so many low shouldered, semi-bipedal diplodocids and stegosaurs, or has so many sauropods with very long necks. The presence of so many large herbivores may have encouraged the diversity of feeding types in order to minimize competition. Haplocanthosaurs, suited for feeding at low- to medium-levels, are fairly common only in the lower Morrison; perhaps they were not able to compete with the more advanced camarasaurs. Giraffe-like brachiosaurs specialized for high level browsing may have been rare because they were ill suited for feeding on the shorter floodplain vegetation, and competed too directly with diplodocids for the limited supply of tall riverine trees. The high shoulders and erect necks of the camarasaurs (Fig. 5) were not well suited for feeding on ground cover, but were ideally suited to access the abundant mid-level vegetation below the level favored by longer necked diplodocids. Tooth wear patterns suggest *Diplodocus* spent most of its time feeding at higher levels than the shorter necked *Camarasaurus* (Fiorillo, 1991). The most diverse and abundant
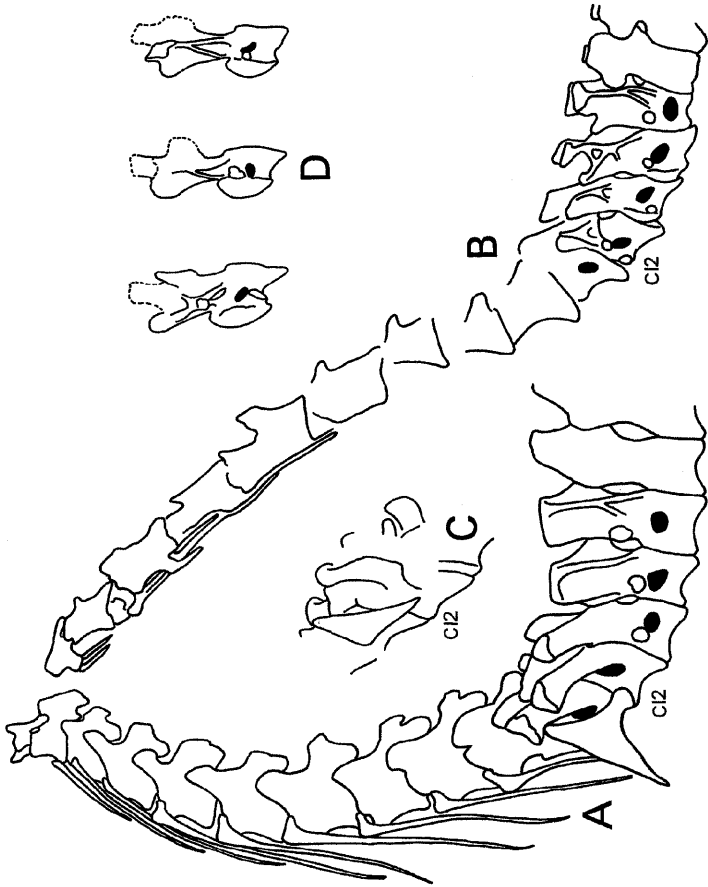
FIGURE 5 Upwardly flexed articulated neck bases and beveled cervo-dorsals indicating habitually erect neck carriage in *Camarasaurus*. (A) CM 11338 juvenile, (B) DINO 24 subadult (from a card photograph), (C) USNM 13786 subadult, (D) *C. supremus* adults (from Osborn and Mook, 1921). Not to scale. Note that flexion of the cervo-dorsals is present whether or not the articulated necks are dorso-flexed.

TABLE II   Restored browsing adaptations of Morrison megaherbivores

Haplocanthosaurus (Fig. 1(A)): Skull unknown. S-curved neck slender and rather short, could be moderately elevated. Shoulder/hip height subequal? Medium sized, nonretroverted sacro-pelvis and slender tail suggest rearing adaptations were not well developed. Abdomen moderately large. Overall build strong and heavy. Nonselective feeder, generalized browser at low to medium levels, least prone to rear to high browse up to 5 m.

Brachiosaurus (Fig. 1(B) and (C)): Skull large in absolute terms, mouth rounded, teeth large and spatulate. Cervo-dorsals poorly preserved, but upwards pitch of dorsal series suggests long S-curved necks were held erect; depressing neck to ground may have been difficult. Shoulder tall. Retroverted pelvis was a rearing adaptation. Thumb claw small. Abdomen very large. Overall build rather gracile. Nonselective feeder, but highly specialized for browsing at medium to very high levels up to 15 m, reach could be further increased by rearing when needed.

Camarasaurus (Fig. 1(D)): Skull large in absolute terms, mouth rounded, teeth large and spatulate, teeth worn by grit. S-curved neck stout, moderately long, habitually carried erect (Fig. 5), and could reach 7–8 m; depressing neck to low browse or drink was probably awkward and uncomfortable as per giraffes. Shoulder moderately elevated. Large posterior dorsals, a modest sized tail, and a large, retroverted pelvis that allowed the hindlimbs to function when bipedal suggest an ability to move about when rearing. Thumb claw large. Abdomen very large. Over all build fairly heavy. Nonselective feeder, specialized for browsing at medium to high levels, could readily reach 9–10 m when rearing, and use heavy build and clawed hands to fell trees.

Diplodocids (Fig. 1(E)–(J)): Skulls small in relative terms, mouth squared off, teeth narrow. U-curved necks articulated in a nearly straight line with anterior dorsals (possible erect neck in one apatosaur [Filla and Redman, 1994]). A progressive increase in the height of the dorsals posteriorly to very high values, very large posterior dorsals, massive but nonretroverted sacro-pelves, large tails, and sled-chevrons (similar to those of semi-bipedal ground slothes) suggest a regular, static tripodal posture in which the neck was used to move among tree crowns. Thumb claws large. Abdomen moderately large. Diplodocids were moderately selective feeders, flexible browsers of ground cover, middle levels and most often at very high levels when rearing, able to use strongly built skeletons and clawed hands to fell trees.

Diplodocus – Tooth wear moderate. Neck long and slender. Shoulder low. Could reach 12 m when rearing. Limbs gracile.

Barosaurus – Neck very long and slender. Shoulder not as low. Could reach 16 m when rearing, least prone to rearing among diplodocids. Limbs gracile.

Apatosaurus – Neck moderately long and very stout. Shoulder low. Could reach 11–12 m when rearing. Over all build very strong.

Supersaurus and *Amphicoelias* – Necks long? Able to reach up to 20–25? m when rearing. *Amphicoelias* shoulders moderately low?, limbs very long and gracile.

Stegosaurus (Fig. 1(K)): Skull small, mouth very narrow, beaked, dental battery poorly developed. U-curved neck short and slender, not strongly elevated. Shoulder low. A progressive increase in the height of the dorsals posteriorly to high values, large sacro-pelves, stout tail, and sled-chevrons suggest regular static tripodal posture. Abdomen moderately large. Over all build moderately heavy and strong. Selective feeders, flexible browsers at low to moderately high levels up to 4 m.

Camptosaurus (Fig. 1(L)): Skull relatively large, beaked rounded, dental battery well developed. S-curved neck short and slender. Normally bipedal, could move slowly on all fours. Abdomen moderately large. Feeding selectivity not clear, flexible browsers at low to moderately high levels up to 4 m.

Morrison sauropods were the advanced diplodocids, which were also the most trophically flexible members of the group. All sauropods could easily fell trees, but the unusually strongly built apatosaurs may have specialized in this task. The low shouldered diplodocids and stegosaurs, which could both rear, may have been common because they were able to feed on both trees and ground cover and even aquatic vegetation. Semi-bipedal campto-saurs could browse at many levels, and had sophisticated, tightly set denti-tion. However, it is not obvious why these seemingly trophically flexible forms were not more common in the Morrison.

Some workers assert that the small head size of the sauropods and stego-saurs were inadequate for high rates of food consumption based on mam-malian head size (Russell and others, 1980; Weaver, 1983; Coe and others, 1987; Farlow, 1987; Dodson, 1990; 1991; Russell, 1989; Colbert, 1993). However, such comparisons are misleading because mammalian heads are larger owing to the masticatory batteries and associated musculature, tusks (in elephants), and large brains. Instead, comparisons should be made between mouth size. As may be seen in Figs. 6 and 7, sauropods mouths were as wide or wider than those of ungulates and elephants relative to body mass (I follow Owen-Smith [1988] in comparing mouth width because it is not possible to estimate mouth cross sectional area in extinct forms). The mouth of many sauropods were broader than those of indri-cotheres, which had the same body mass!

It is easy to under appreciate the absolute size of sauropod heads and mouths. The head of a large *Brachiosaurus* had twice the mass of a human (Fig. 6(B)), and had about sixty stout teeth lining a mouth nearly half a meter wide capable of swallowing a 70 kg animal whole. Contrary to Weaver (1983) who stated that brachiosaur and giraffe heads were of simi-lar size and cropping capacity, the mouth of a very large brachiosaur could engulf the head of a giraffe (which incidently have a little arcade of six to eight cropping teeth) (Fig. 6). Even a *Diplodocus* mouth was two and a half times broader than a giraffe's, and contained four times as many teeth (Fig. 6(D)). Therefore, the feeding capacity of sauropods cannot be rated as inferior to that of mammals of equal mass.

Could the sauropod head–neck complex (Fig. 8) gather enough food to stoke a high metabolic rate? We can address the question by calculating food consumption on a per bite basis (this is intended to test sauropod feeding capacity, not to reconstruct sauropod feeding rates). A *Brachiosaurus* with a metabolism equal to that of a whale of the same mass, would have required about 500 kg of fresh browse per day (Weaver, 1983). Assuming 14 h of feeding, with one to six bites per minute (a fair assumption for a
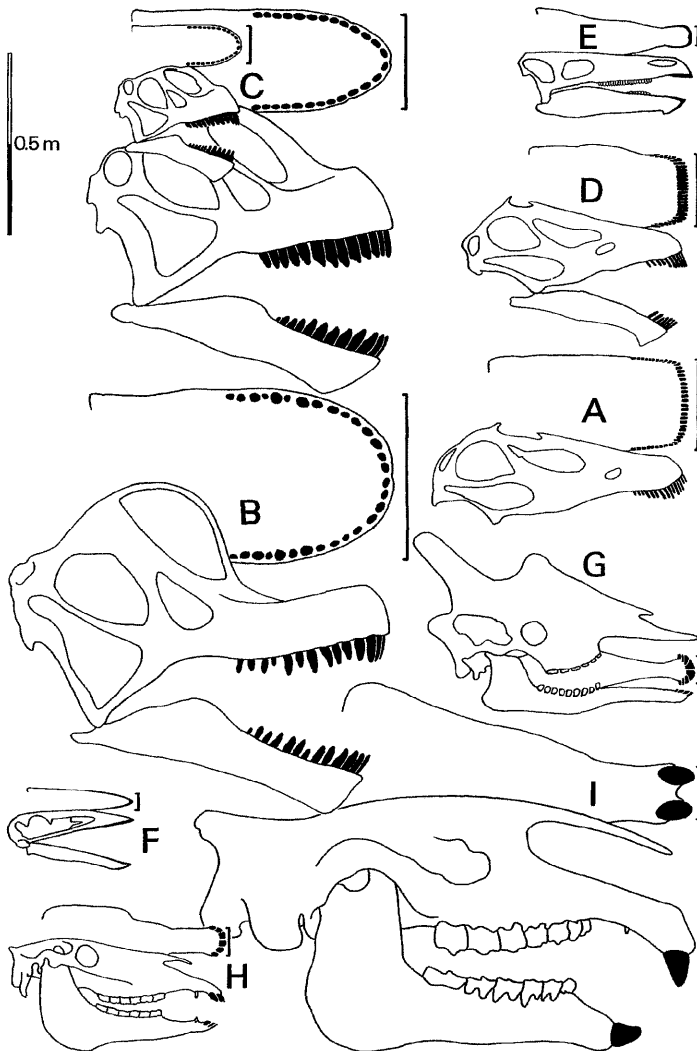
FIGURE 6 Skulls and cropping tooth arcades drawn to the same scale (see Table I). (A) *Apatosaurus* (CM 11162 belongs to LACM 52844, 11 tonnes, or CM 3018, 17.5 t), (B) cf. *Brachiosaurus* (150 kg [from a volumetric model] scaled to 45 t individual), (C) adult *Camarasaurus* (CM 12020/11393, 14.2 t) and juvenile (CM 11338, 640 kg), (D) *Diplodocus* (scaled to 12 t), (E) *Stegosaurus* (USNM 4934, 2.2 t), (F) *Aepyornis*, (400 kg), (G) *Giraffa* (1.1 t), (H) *Equus* (400 kg), (I) *Indricotherium* (AMNH 18650, 11 t). Cropping teeth are solid black, mouth widths are indicated by vertical bars. Note that mammals have proportionally larger skulls than dinosaurs, but dinosaurs have proportionally larger mouths. See text for discussion.
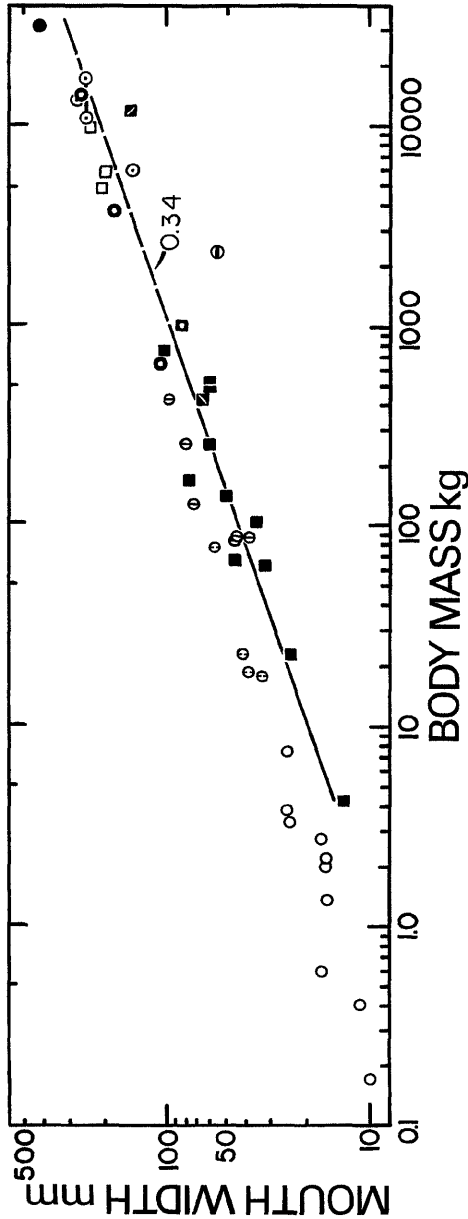
FIGURE 7 Comparison of mouth width as a function of body mass in Morrison sauropods and stegosaurs (symbols as per Fig. 4), herbivorous and omnivorous flying birds (open circles), living (circles with interrupted vertical lines) and extinct (circles with vertical lines) ratites, African bovids (solid squares), giraffe (square with an open dot), equid (square with diagonal bar), elephants (open squares), and indricothere (square with horizontal bar). Mouth width measured as in Fig. 6, data for Morrison dinosaurs is in Table I. Line is a linear regression for living ungulates, r = 0.86, showing that mouth width is essentially isometric as size changes. Note that mouth width is similar in small headed birds and bigger headed ungulates, that sauropods scale in the same manner as in ungulates, and that the mouths of giant mammals are no broader than those of sauropods. Doubling the estimated masses of the dinosaurs would not significantly alter the results.

megaherbivore; Dagg and Foster, 1976; Owen-Smith, 1988; Shipley and others, 1994), then each bite would only need to be about 0.01–0.66 kg. A 40 tonne sauropod should easily have taken such sized bites until the food equaled only 1.25% (500 kg) of its body mass. Russell and others (1980) suggested that the feeding capacity of the finger–trunk (proboscis) complex of an elephant was roughly equivalent to that of the head–neck complex of a sauropod. However, the head–neck combination of a sauropod was much larger and taller than the elephant proboscis (Fig. 8). The size and reach of the sauropod head–neck apparatus is difficult to explain if they only had a low, reptilian energy budget and were consuming only 0.2% of the body mass in food per day (the 5 kg of dry fodder per day for a 100 tonne sauropod suggested by Coulson [1979] would be a starvation diet amounting to just a few bites).

The head–neck complex of *Stegosaurus* is comparable to the trunk of a small elephant because its mouth was unusually small (Figs. 6(E), 7 and 8(F)). These features imply that stegosaurs consumed relatively less food than elephants and sauropods. Nevertheless, one to six 10–50 g/bites per minute over 14 hours/day would have been sufficient to sustain a moderately high metabolism.

METABOLIC IMPLICATIONS OF MEGADINOSAUR ANATOMY, LOCOMOTION, AND GROWTH

Reptiles are characterized by long periods of low level aerobic activity, punctuated by brief anaerobic bursts of high level activity (Bennett, 1983; 1991; 1994), so that food demands are low. The high levels of aerobic exercise capacity that can be sustained by most birds and mammals must be fueled by large amounts of food. Contrary to suggestions otherwise (Spotila and others, 1991), there is no strong metabolic convergence between giant reptiles and mammals (Paul, 1994b; Paul and Leahy, 1994; Ruben, 1995).

Were Morrison megadinosaurs fueling the low energy requirements of reptiles, or were they fueling the high energy requirement of a mammal like an elephant, or did they have an intermediate energy requirement like an edentate? Because animals are the sum of their many parts, it is unlikely that any single character is a "Rosetta stone" that can fully diagnose the metabolics of an extinct group, so a large number of characters is assessed in this section. Terminology used is defined in Appendix 1.
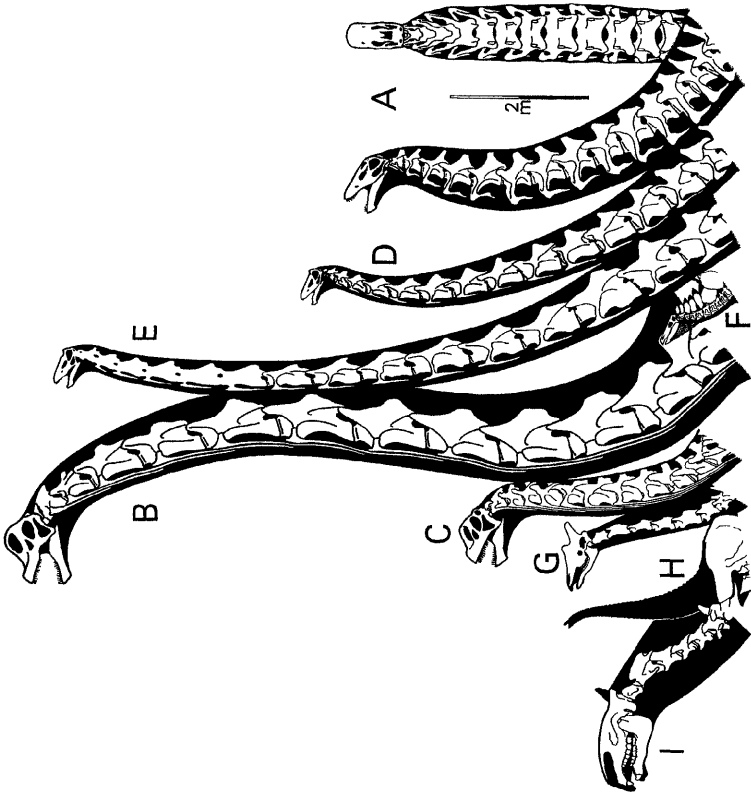
G.S. PAUL

FIGURE 8 Head–neck complexes and trunks drawn to same scale (see Table 1). (A) *Apatosaurus* (17.5 tonnes), (B) *Brachiosaurus* (45 t), (C) *Camarasaurus* (14.2 t), (D) *Diplodocus* (11.4 t), (E) *Barosaurus* (2.2 t), (F) *Stegosaurus* (1.5 t), (G) *Giraffa* (1.5 t), (H) *Loxodonta* (6 t), (I) *Indricotherium* (11 t).

Terramegathermy: Gigantic on Land More Energy
Demanding than Gigantic in the Ocean

It is often assumed that sauropods must have had low energy budgets in order to be so much larger than any terrestrial mammal. However, this argument is a logical non-sequitur, because such mammals have reached ten to twenty tonnes (Fig. 1(O)–(Q)), whereas fully terrestrial reptiles have reached only one tonne (Fig. 1(S) and (T); it is not yet certain that the largest monitor was not semi-aquatic). A more pertinent question is why did dinosaurs and tachyaerobic mammals achieved size superiority over bradyaerobic reptiles on land? In the oceans giant reptiles and fish are bradyaerobic poikilotherms with only a small fraction the energy turnover seen in big whales (Carey and others, 1971; Paul, 1994b; Paul and Leahy, 1994). Being a giant in the ocean is easy because buoyancy effectively eliminates gravity. The problem of pumping blood far above heart level does not exist, and skeletal muscles need not be extremely large and tachyaerobic because swimming is an order of magnitude more efficient than walking the same distance.

On land, 1 G imposes severe structural, internal fluid pressure, and transportation cost demands on large creatures. Domestic mammals and birds raised under 2.5 G have oversized limb bones and muscles, unusually powerful hearts, and elevated rates of food consumption (Smith and Kelly, 1963; Smith, 1976). A sharp decline in tolerance for high G forces as size increases shows that being gigantic in 1 G is similar to a small animal in high gravity (Smith, 1976; Economos, 1981; sauropods falsify the conclusion by Economos that terrestrial animals cannot exceed 20 tonnes). Terramegathermy therefore requires big terrestrial tetrapods to acquire enough food to produce high levels of power needed to survive and reproduce in 1 G. Terramegathermy predicts that a terrestrial giant must be an aerobically capable athlete (sensu Alexander, 1989). The prediction is supported by the observation that recent and living tetrapods become increasingly energetic as size increases (Table III).

Metabolism and the Gravity Well

Sustained power in large reptiles is grossly inferior to that of large mammals as shown by the inability of large reptiles to overpower or outrun large mammals after an initial burst of power (Auffenberg, 1981; Grenard, 1991; Deeble and Stone, 1993). The skeletal and leg muscles of small reptiles is 20–50% less than in mammals and birds of similar size (Else and Hulbert, 1985; Ruben, 1993). Bradyaerobic reptilian muscles cannot

TABLE III   Anatomical and metabolic characteristics of land giants

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Reptiles – Under ~ 1 tonne. Skeletal and leg muscle/body mass ratio low (ilia short and small). Muscle cells hyperanaerobic, bradyaerobic. Legs sprawling or semi-erect. Cruising speeds < 2 km/h, do not migrate. Heart–brain height differentials under 0.5 m (resting blood pressures < 95 mmHg). Airway short, respiratory capacity low. Brains small. Growth slow. Social and parenting activities minimal. Tachyfecund r-strategists. Aerobic exercise capacity low; resting metabolic rates low; overall energy budgets low; inertially semi-homeothermic, body temperatures 27–34°C.

Megamarsupials and megaedentates – Under ~ 7 tonnes. Skeletal and leg muscle/body mass ratio high (ilia large and plate-like). Muscle cells bradyanaerobic, tachyaerobic. Legs erect, stout, feet contorted. Heart–brain height differentials up to 1.5 m (restored resting blood pressure ~ 100 mmHg). Airway short, restored respiratory capacity moderately high. Brains moderately large. Growth rates probably moderate. Probably bradyfecund k-strategists. Restored thermo-energetics (extrapolated in part from smaller living relatives): aerobic exercise capacity moderate; resting metabolic rates moderate; overall energy budgets intermediate; automatically homeothermic, body temperatures 30–36°C.

Ground birds, carnivores, megaungulates and proboscideans – Birds and carnivores under ~ 1 tonne, megaherbivores over 20 tonnes. Skeletal and leg muscle/body mass ratio high (ilia large and plate-like). Muscle cells bradyanaerobic, tachyaerobic. Legs erect and long striding, feet symmetrical. Cruising speeds > 2–3 km/h, long migrations possible. Heart–brain height differentials up to 2.5 m (resting blood pressure > 100 mmHg). Anterior airway sometimes very long, respiratory capacity high. Brains moderately to very large. Growth rates rapid. Social and parenting activities extensive. Some large birds tachyfecund r-strategists, some large birds and megamammals bradyfecund K-strategists. Aerobic exercise capacity high, resting metabolic rates high; overall energy budgets high; automatically homeothermic, body temperatures 36–39°C.

Morrison megadinosaurs – Predators up to ~ 5 tonnes, sauropods over 100 tonnes. Ilia large and plate-like (restored skeletal and leg muscle/body mass ratio high). Restored muscle cells bradyanaerobic, tachyaerobic. Legs erect and long striding, digitigrade feet bird- or elephant-like. Estimated trackway cruising speeds above 2–3 km/h, long migrations probable in some cases. Heart–brain height differentials up to 10–15 m (restored resting blood pressure from 100 to at least 200 mmHg). Airway sometimes very long, respiratory capacity high. Brains small. Restored growth rates rapid. Restored social and parenting activities moderately extensive. Tachyfecund r-strategists. Restored thermo-energetics: aerobic exercise capacity moderate to high; resting metabolic rates uncertain; overall energy budgets high in sauropods, intermediate in stegosaurs, intermediate to high in theropods; at least partly homeothermic, body temperatures 36–39°C.

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sustain high levels of power, but do produce high levels of anaerobic power per unit muscle volume (Bennett, 1983; 1991). Reptile hearts only make up 0.1–0.5% of the total body mass and do not converge in size with those of mammals and birds as body size increases. In addition, the heart produces resting and exercise blood pressure up to 95 mmHg and 110 mmHg respectively (Fig. 10; White, 1976; Poupa and Ostadal, 1969; Schmidt-Nielsen, 1984; 1990; Else and Hulbert, 1985; Seymour, 1987; Grigg, 1992; Lillywhite and Donald, 1994). The four chambered hearts of crocodilians do not appear to be markedly superior to the three chambered heart of other reptiles in terms of blood flow, volume and pressure (White, 1976; Grigg, 1992). The other internal organs of reptiles tend to be smaller than those of birds and mammals (Else and Hulbert, 1985).

Skeletal muscles are about 40–45% of the body mass in small and large mammals (Schmidt-Nielsen, 1984; Else and Hulbert, 1985). The muscles of large mammals are tachyaerobic and are able to sustain high levels of work because the hearts make up 0.5–0.6% of the body mass, and produce resting and exercise blood pressures of 100–120 mmHg and 150 mmHg respectively (Fig. 10; Seymour, 1976; Prothero, 1979; Schmidt-Nielsen, 1984; 1990). The hypertensive hearts of giraffes and birds make up to 2.5% of body mass, and produce resting pressures as high as 200 mmHg (Fig. 9; Seymour, 1976; Dagg and Foster, 1976; Schmidt-Nielsen, 1984). The other internal organs of birds and mammals also make up a large portion of body mass and are tachyaerobic, in part so that they can support the operations of the large high pressure hearts (Schmidt-Nielsen, 1984; Else and Hulbert, 1985; Ruben, 1995).

In summary, at any given activity level and body size, reptile hearts consume an order of magnitude less oxygen than the larger hearts of mammals and birds, beat much more slowly, and pump a magnitude less blood per unit time (Seymour, 1976; Schmidt-Nielsen, 1984; 1990; Driedzic and others, 1987. The combined oxygen consumption of large, tachyaerobic muscles and central organs raises the over all aerobic budgets of birds and mammals above reptilian levels (Jansky, 1965; Else and Hulbert, 1985; Ruben, 1995).

Because a number of extinct and extant mammals exceed one tonne and are very tall, hypothetically there is no reason to doubt that mammalian energetics could power giant dinosaurs. More problematical would be powering megadinosaurs with a reptilian muscle-heart system. The ability of the largest and most powerful reptilian hearts to meet the minimal oxygen requirements of tachyaerobic muscles appears to be marginal, and would leave little or no reserve capacity for moderate aerobic exercise. This may explain why all animals with large, tachyaerobic muscles have larger, more energetic hearts than reptiles. Great height poses further problems for reptilian circulation and energetics. Pumping blood over one and a half meters against gravity requires hypertensive blood pressure above 120 mmHg, which is above those observed in any reptile (Dagg and Foster, 1976; Seymour, 1976; Choy and Altman, 1992). Failure to oxygenate either tachyaerobic muscle cells and/or highly held brains results in torpor and/or fainting. Bradycardia in terrestrial tachyaerobes is either a disabling pathology, or associated with hibernation (Schmidt-Nielsen, 1990).

Hyperanaerobic muscles found in many reptiles appear ill suited for carrying great bulk on a regular basis (contra Coulson [1979] who suggested that reptiles can power giant bodies with hyperanaerobiosis rather than

MR kcal/kg^0.75/day

80
T
d
—
60
m
—
40
T   w
d
m
—   4000
20   w   r
—
r

T
A   B   C   D
□   □

HM

8000
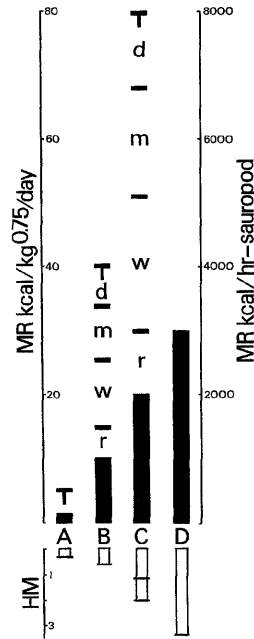
6000

MR kcal/hr–sauropod

4000

2000

FIGURE 9   Positive correlation between heart size, resting circulatory pressures needed to pump blood vertically, and metabolic rates observed in living tetrapods, and restored in dinosaurs. Lower range of white bars shows typical heart mass (HM) as a percentage of body mass: column (A) reptiles (blood pressure < 95 mmHg, heart–brain height differential values < 0.5 m); column (B) most mammals, plus allosaurs and stegosaurs (95–120 mmHg, < 1.5 m); and column (C) giraffes and many birds (blood pressure 120–200 mmHg, < 2.5 m). Upper range solid black bars indicate corresponding cardiac metabolisms, and heavy horizontal bars the metabolisms of other tissues; r, respiratory system; w, liver and kidneys; m, muscles, skin, bones, brain, etc.; d, digestive system; heavy T, total metabolic rate at rest (excluding auxiliary thermoregulatory heat); all in terms of mass specific metabolic rates as measured on the left. In general, as circulatory pressures rises to pump blood higher, the heart becomes larger, and the metabolic work of the heart and supporting organs increases. The result is that the cardiac work of a typical resting mammal equals the entire metabolism of a reptile (compare columns A and B). Columns A through D show the restored cardiac and total metabolism of a sauropod (30 tonnes, heart–brain height differential 10 m) assuming hearts of differing sizes. Heart mass as a percentage of body mass and in kg is as follows, Column (A) small reptilian sized organ, 0.3%, 90 kg, (B) single typical mammalian sized organ, 0.6%, 180 kg, (C) combined primary and cervical hearts, 1.2%, 600 kg, and (D) single oversized heart, 3%, 1000 kg (blood pressure >500 mmHg). The left axis continues to give mass specific metabolic rates for the sauropod, the right axis also gives metabolic rates in absolute terms for the sauropod only. Cardiac work provided by reptilian and normal mammalian sized hearts is considered inadequate to pump blood up 10 m, the work required for the single oversized heart is considered extreme, so the high metabolic rate restored in column C is preferred. All values are approximate, data sources (which provides typical total organ/cardiac metabolic rate ratios) include Jansky (1965), Poupa and Ostadal (1969), Bennett and Dawson (1976), Dagg and Foster (1976), Seymour (1976), McNab (1983, 1988), Schmidt-Nielsen (1984), Bennett and Harvey (1987), Driedzic and others (1987), Choy and Altman (1992), Paul and Leahy (1994).

tachyaerobiosis). Larger reptiles can sustain high levels of anaerobiosis longer than can smaller reptiles (Bennett and others, 1985), but anaerobiosis cannot regularly be used on a sustained basis because it is quickly exhausted and has toxic effects (mortality is high in large crocodilians after extended anaerobic exercise, Bennett and others, 1985). Small reptiles can stand and move for many hours/day (Bennett, 1983), but it would probably be difficult for the smaller and less tachyaerobic reptilian muscles to carry an elephantine body mass without frequent belly resting. Leg muscles of reptiles are equally energy efficient regardless of posture, so a switch from sprawling to erect limbs would not ease the energy burden of being a giant (Fedak and Seeherman, 1979; Bennett, 1994).

Finally, the lack of elephantine terrestrial reptiles supports my contention that reptilian musculature cannot adequately power animals of that size. That is because as the total body mass goes over the limit that the reptilian muscles can support, the percentage of the body made up of leg and other skeletal muscles increases above reptilian norms, and the cells become tachyaerobic. The work of the heart and other organs needs to increase correspondingly, with more oxygen consumption over reptilian levels. Beyond the threshold point, the animal is no longer a bradyaerobic reptile. In this model, the more gigantic and/or taller a terrestrial reptile is, the higher its muscle and organ generated metabolism must be. Future models of large tetrapod energetics may or may not confirm these metabolic size limits, but the hypothesis that reptilian circulation is workable in terrestrial giants has not yet been demonstrated, and will always be speculative.

The next question is whether the anatomy of Morrison megadinosaurs best fits the reptilian or avian–mammalian metabolic model. Sauropods and stegosaurs appear no better designed for frequent belly resting than elephants, suggesting they usually stood with large leg muscles. Support for this is seen in the ilia, which in terrestrial reptiles, including large ones, are short because of the relatively small muscle masses originating there. This is in contrast to the long, plate-like pelvis of birds and mammals of similar size, which have greater muscle mass (Fig. 10; Paul and Leahy, 1994). Figures 1 and 10 show that dinosaurs had plate-like ilia much longer than those of reptiles, indicating proportionally greater muscle mass. The length of sauropod ilia matches those of megaungulate and proboscidean pelves, stegosaurs have a long preacetabular blade of the ilia, ornithopod ilia are elongated fore and aft, and theropod ilia are bird-like in size and
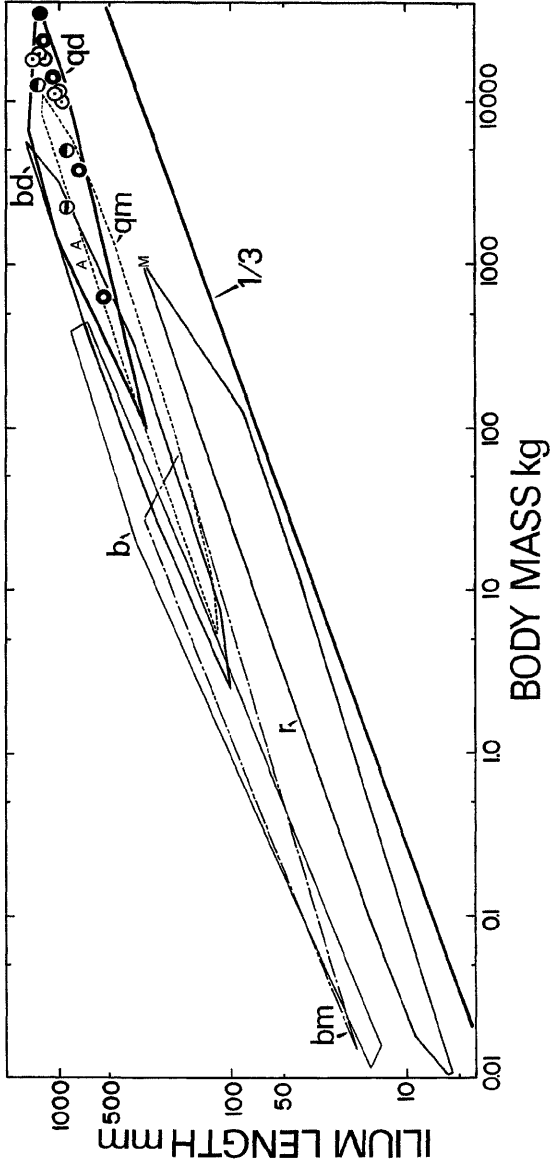
FIGURE 10 Relationship between ilium length and body mass in land tetrapods: r, reptiles; M, Megalania; b, birds; bm, bipedal mammals; qm, quadrupedal mammals; bd, bipedal dinosaurs; qd, quadrupedal dinosaurs; A, *Allosaurus*; symbols for sauropods and stegosaurs as in Fig. 7. The 1/3 slope line indicates isometric scaling, shifting the dinosaurs to the reptilian level would require increasing body mass estimates two to tenfold. Modified after Paul and Leahy (1994).

form. The combination of large muscles and great mass in megadinosaurs implies that cellular physiology had shifted from the hyperanaerobic of reptiles to the tachyaerobic of birds and mammals (Paul and Leahy, 1994). Such large muscles required their hearts to pump blood at high avian–mammalian flow rates, and pressures of at least 100 mmHg. In addition, the erect necks of the largest rearing stegosaurs and allosaurs required blood pressure of ~120 mmHg to cope with the ~1.5+ m heart–brain height differential. Gunga and others (1995) restored a tachyaerobic brachiosaur with an avian- or giraffe-like heart occupying 1.2% of body mass (corrected to 32 tonnes as per Appendix 1). Such a heart is assumed to have produced hypertensive blood pressures capable of megamammal-like levels of metabolic work. In contrast, Seymour (1976) suggested that brachiosaurs had super-sized hearts making up to 5% of body mass. He noted that such a big heart would have a high rate of oxygen consumption and that it might have been too inefficient to be practical (Fig. 9(D)). Also, it is questionable whether the blood pressure of 500+ mmHg proposed by Gunga and others and Seymour would be tolerable. Choy and Altman (1992) argued that such extreme blood pressures would promote disease, although this is disputed by Millard and others (1992). A smaller heart, occupying 3% of a brachiosaur's volume would get around some of these difficulties (Fig. 11).

Seymour (1976) and Millard and others (1992) proposed that sauropods avoided extreme tachycardia by living in water, whereas others have proposed that the necks were carried horizontally. Neither option appears tenable, especially for camarasaurs and brachiosaurs with erect necks (Table II). Choy and Altman (1992) suggested that sauropods had auxiliary cervical hearts that aided the primary heart in pumping blood upwards at less extreme, but still hypertensive, giraffe-like pressures of 200 mmHg (Fig. 9(C)). The need for and practicality of such extra hearts in tall sauropods is questioned by Millard and others (1992). Whether sauropod hearts were single or multiple, those species with necks proportionally taller than those of giraffes, probably needed more total cardiac tissues than in giraffes and the upper avian range, and probably 2–3% in a brachiosaur.

Reptilian levels of cardiac work appear grossly inadequate to pump blood up sauropod necks (Fig. 9(A)), and even normal mammalian levels may have been inadequate. A tall sauropod's expanded cardiac tissues are predicted to have produced much more heat than the entire resting metabolic rate of a reptile of equal size, and its over all energy budget is calculated to have been as high as in a whale (Fig. 9(C)).
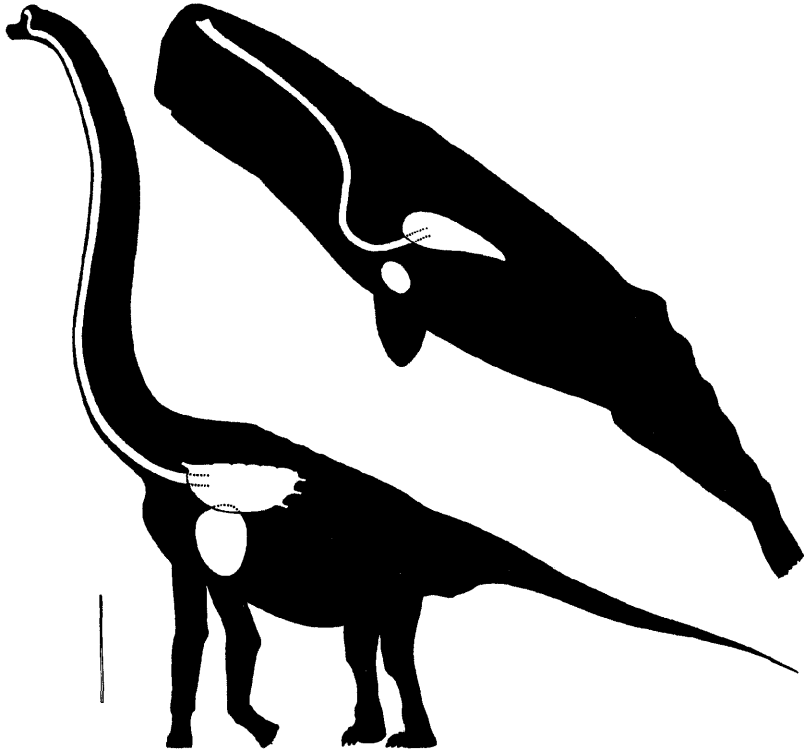
FIGURE 11   Same scale figures of a *Brachiosaurus* and female sperm whale of 30–32 tonnes, scale bar equals 2 m. The sauropod is restored with an 11 m long trachea, lungs and a super-high pressure 1 tonne heart that leaves just enough room for lungs. The whale's 7 m long anterior airway, small lungs and normal high pressure 150 kg heart are shown. After Paul and Leahy (1994).

Breathing

Reptilian lungs are probably able to oxygenate an avian/mammalian resting metabolism (Ruben, 1995), but higher capacity respiratory systems are needed to ventilate high aerobic exercise capacity and the elevated oxygen budgets to which they contribute. The lungs of nonavian dinosaurs may not have been as efficient as those of flying birds, but was more efficient than those of reptiles, and may have matched those of mammals. Birds dramatically improve the efficiency of their respiratory system with air-sacs (Perry, 1983; 1989). Analogous sacs may have been present in theropods and sauropods (Perry, 1983; 1989; Paul, 1988a; Daniels and Pratt,

1992; Britt, 1994; Filla and Redman, 1994). In both groups, bird-like respiratory features include pneumatic presacral vertebrae (nonpneumatic long bones are present in some birds as well as large dinosaurs), a shortened dorsal series (other terrestrial giants have long dorsal series), and long ribs with widely spaced double heads immediately anterior to the sacrum (increases antero-posterior rotation of the ribs while preventing latero-medial collapse of air-sacs [Duncker, 1978]).

The development of air sacs as a means of reducing skeletal mass in theropods and sauropods does not fully explain their development because they did not fly, and size analogous mammals do not have equivalent systems. The long sternal plates of sauropods operated by hinge jointed ribcages probably did not serve to ventilate abdominal air-sacs, because this arrangement is lacking in some flightless birds (Fig. 1(N)). These air-sacs were probably operated by the long, mobile posterior ribs. The air-sac lung ventilation systems of nonavian dinosaurs appear to have been well developed, albeit not as fully as in birds. Paul (1988a) restored a progressive evolution of air-sacs in theropods, with those of ceratosaurs being less developed than in allosaurs. In Morrison sauropods, the development of the air-sacs appears to increase through haplocanthosaurs, brachiosaurs, camarasaurs, and is highest in diplodocids.

With theropods and sauropods, the reasons for improved respiratory efficiency probably differed. In theropods the legs were adapted for high sustained speeds, hence the need for efficient lungs to ventilate high aerobic exercise capacity. In sauropods, Daniels and Pratt (1992) calculated that a sauropod with a long trachea would not have been able to achieve a high rate of oxygen consumption even with air-sacs. However, sperm whales have very long airways (Fig. 11). The ventilation problems faced by sauropods breathing continuously with high volume lungs and air-sac complexes should have been mild compared to the whales' need to oxygenate themselves with dead end lungs in just a few minutes between long dives (Ellis, 1980). Long airways are also observed in elephants, giraffes, long necked birds, and long necked reptiles, so there is no consistent correlation between airway length and metabolic rates. Sauropod air-sacs may have allowed them to evolve necks longer than the necks and prosci of terrestrial mammals, and at the same time oxygenate the oversized hearts that made the long necks possible. Calculations by Hengst and Rigby (1994) that sauropods required hyper-elevated levels of atmospheric oxygen are pessimistic because they assumed inefficient dead end lungs (and no gastralia). They also implied that the narrow nasal passages (average diameter 70 mm) inhibited the breathing of diplodocids, but elephants also

have narrow anterior nasal passages (40 mm in diameter). Narrow airways aid respiration by limiting the volume of long airways.

Perry (1983, 1989) suggested that the dead end lungs of most ornithischians were ventilated by diaphragm-like abdominal muscles supported by the prepubis and retroverted pubis. The oxygen capacity of this system may have been intermediate between reptilian and avian–mammalian levels, so modestly elevated aerobic exercise capacity and oxygen budgets are indicated. Paul and Leahy (1994) noted that ornithopods have a lumbar region of short ribs posterior to the long mid-thoracic ribs. This mammal-like arrangement may have been adapted for anchoring a vertical diaphragm to ventilate the lungs at mammalian exercise levels.

Cruising and Migrating in Herds

Walking on land is energy inefficient, and reptiles have such low aerobic exercise capacity, that large tortoises, crocodilians and even monitors regularly walk at speeds of only 0.1–2.0 km/h, even when body temperatures are high (Bennett, 1983; 1991; 1994; Paul, 1994b; Paul and Leahy, 1994). Slow walking speeds can be sustained for hours, but faster walking and running speeds are always limited in duration (timing of oras in videos reveals that the 4–5 km/h speeds cited by Auffenberg [1981], Farlow [1990] and Suzuki and Hamada [1992] represent individuals in pursuit of prey, or approaching or walking around a carcass). Because mammals and birds have a higher sustained aerobic capacity, their normal walking speed is above 2–3 km/h (Paul and Leahy, 1994).

Farlow (1990) hinted that a combination of large size, long erect legs, and rest-and-go tactics may allow animals with reptilian energetics to regularly make trackways at high walking speeds. However, limb posture has little effect upon locomotory energy efficiency (Fedak and Seeherman, 1979). Aerobic metabolic rates and the cost of locomotion scale to broadly similar exponents (Fedak and Seeherman, 1979; Jones and Lindstedt, 1993), so giant tetrapods walk cheaply (Langman and others, 1995). Even so, speeds above 2 km/h remain beyond the low sustainable aerobic exercise capacity of giant terrestrial reptiles (the energy cost for a 20 tonne animal walking 1 km is ~ 2500 kcal and the predicted maximum aerobic capacity of a reptile that size is ~ 5000 kcal/h).

The overall energy budget of a fast walking animal can be kept within a reptilian level only if it moves for just a brief period each day. For example, if a reptile moves at 1 km/h for 6 hours, keeping the daily oxygen consumption at the same level while walking at 4 km/h requires reducing

the time of movement to 1.5 h. Limited aerobics and energy budgets would probably force even giant, erect-limbed reptiles to make the great majority of their movements at very slow speeds, and daily range would be short even if the period of locomotion is extended. This conclusion contradicts Spotila and others (1991) who calculated that energy efficient terrestrial reptiles could migrate 50 km/day, and out range less efficient tachyaerobes. The pace required (3–4 km/h assuming at a few hours rest each day) is above that sustainable by a reptilian aerobic exercise capacity. Brady-aerobic sea turtles and fish migrate long distances at high speeds (Spotila and others, 1991) because they swim five to twelve times more efficiently than similar sized terrestrial animals walk (Seymour, 1982; Hill and Wyse, 1989; Bennett, 1991; Eckert, 1992; Paul, 1994b). Long land migrations are so arduous and dangerous that only ungulates with high aerobic capacity and uniquely energy efficient limbs engage in them (Meier and Fivizzani, 1980; Fancy and White, 1987).

Moving and interacting in organized herds is another form of sustained activity that requires high aerobic capacity. This activity is unlike the efficient turtle and fish swimmers which can form schools regardless of their aerobic exercise capacity. Therefore tetrapods with low aerobic capacity are not expected to form herds (Bennett, 1983).

The above observations reveal the causal link between limb posture and aerobic exercise capacity. Sprawling and semi-erect legs are well suited for reptiles because they allow the short stride, stable walking gait needed to move at slow, aerobically sustainable speeds. The legs can run the high speed bursts powered by brief anaerobiosis, and then set the body down for a much needed recovery. The higher aerobic speeds of tachyaerobes leaves them without the need for the slow speed potential of sprawling limbs. Instead, they need erect legs whose fore-and-aft pendulum effect promotes the longer strides and higher step frequencies that make a walk fast. Erect legs favor long strides so much that walking below 2 km/h is awkward and difficult. An erect limbed reptile would tend to walk too fast to avoid overuse of anaerobic power, yet would be unable to fully exploit the legs' full sustainable walking and running potential. The evolution of erect legs probably forces the elevation of aerobic exercise capacity.

Dodson (1991) suggested that sauropods lived in the "slow lane" compared to modern megamammals. The long striding, fully erect, digitigrade limbs of Morrison megadinosaurs were better suited for fast walking than the legs of reptiles, and the stout, awkward limbs of megaedentates (Fig. 2). This view is supported by the many trackways made by megadinosaurs, 98% of which record long stride, dynamic gaits made at estimated speeds

of 2−10+ km/h for tridactyl bipeds, and 2−7 km/h with a peak at almost 4 km/h for sauropods (sample size over 400, data in part from Lockley and others 1986; Fig. 2 in Paul, 1994b; Fig. 5 in Paul and Leahy, 1994). Sauropods therefore moved at the same speed as elephants, and theropods walked as fast as ground birds. The shoreline paralleling paths followed by many Morrison trackways are compatible with migratory activities (Cohen and others,· 1993), and it is widely agreed that sauropods probably moved long distances over the Morrison plain (Dodson and others, 1980; Lockley and others, 1986; Coe and others, 1987; Russell, 1989; Dodson, 1990; 1991). Multiple parallel-unidirectional Morrison sauropod trackways and bonebeds are suggestive of herding behavior (Lockley and others, 1986; Russell, 1989; Dodson, 1990; 1991; Farlow, 1992).

Megadinosaur activity patterns differed dramatically from the classic terrestrial reptilian pattern, and was most similar to that of walking birds and mammals. Morrison dinosaurs could have walked fast, yet had a reptilian aerobic exercise capacity and energy budgets only if they powered almost every step partially anaerobically, and if they moved for much shorter periods of time than extant reptiles. The evidence, however, suggests the opposite. The observed walking speeds from trackways required sustainable aerobic exercise capacity at least two to four times higher than the maximum expected in reptiles. The long distances that may have been walked by dinosaurs suggests their locomotory energy budgets were a magnitude greater than those predicted for reptiles. To put it more simply, a 10 tonne sauropod and proboscidean moving at a similar pace suggests they would consumed oxygen at similar rates that are well above that predicted for a megareptile. The link between locomotion and energetics can be falsified by a statistical demonstration that the regular walking speeds of tetrapods show much less disparity than presented here.

Growth and Changing Metabolic Rates

Does a combination of slow, indeterminate, reptilian growth and exceptionally great age explain the size of megadinosaurs, especially supersized-sauropods? Not necessarily, because indeterminate growth is not limited to reptiles. For example, some kangaroos never stop growing (Grigg and others, 1989), and cessation of growth and death are coincident in African elephant bulls (Laws and others, 1975; Haynes, 1991; Lindeque and Jaarsveld, 1993). The taxonomic distinctiveness of the largest Morrison theropod and supersized-sauropod remains indicates that they represent unusually large species, rather than rare statistical outliers of the smaller,

more common species. Incremental adult growth of less than 1 kg/day would take centuries to reach for the individual to reach the whale-like masses of supersized-sauropods. The odds of surviving disease, accident and predation decrease as life spans approach or exceed ~ 150 years (Hayflick, 1994). Thus, it is doubtful that sauropods that functioned as "meals on legs" for theropods would have reached ages of 150+ years. Dunham and others (1989) argued that large terrestrial animals must reach sexual maturity (which usually occurs when the individuals reach at least one-third the adult mass) within two or three decades in order to sustain sufficiently stable population dynamics. I therefore conclude that rapid growth was necessary for hatchlings to reach an adult mass that was thousands of times greater in a matter of a few decades (Paul, 1994a; Britt and Naylor, 1994). Such a feat exceeds that of megamammals weighing hundreds of kilograms upon birth.

Baby sauropods probably grew from a few kilograms at hatching to over a hundred kilograms in the first year, with a daily growth of a few hundred grams (a pace matching juvenile ostriches; Degen and others, 1991). Supersized sauropods probably grew as rapidly as extant whales, reaching 30–40 tonnes in twenty to thirty years, with a peak daily growth of a few kilograms. Growth during the following sixty to one hundred years reached 70–100 tonnes, with a daily growth rate of at least 2 kilograms (if so, truly slow adult growth never occurred). Alternately, supersized-sauropods may have reached full size by the onset of sexual maturity at age twenty to thirty by adding ten or more kg each day, followed by adult growth of a few grams/day. Smaller sauropods probably grew as fast as elephants by putting on a few hundred grams/day. Reid (1987) estimated that an 8 tonne (my estimate) sauropod died at age 28–29 (based on a possible annuli). The presence of extensive rapidly deposited plexiform fibrolamellar matrix in the deep cortex of the bones of sauropods and other megadinosaurs has been widely accepted as evidence for rapid growth (Ricqles, 1980; Dunham and others, 1989; Russell, 1989; Farlow, 1990; 1993; Reid, 1987; 1991; Janis and Carrano, 1992; Farlow and others, 1995).

Ostrich-, elephant- and whale-like growth rates are far above the tens of grams per day growth observed in the fastest growing large continental reptiles (McIlhenny, 1934; Case, 1978; Reid, 1987; Paul, 1994a; Ruben, 1995). Observations by Owerkowicz and Crompton (1995) confirm that juvenile reptiles can grow rapidly only when kept at elevated temperatures in the mammalian range. The boosted growth of reptiles in captivity requires high amounts of heat and food (Grenard, 1991; Paul, 1994a). In the wild, low sustained activity levels (see above) probably prevent reptiles

from gathering enough food to sustain high rates of growth (to the point that lush habitats increase the biomass density of reptiles, not their growth rates). It may be impossible for terrestrial reptiles to grow fast enough to exceed one tonne (Reid, 1987). Megamarsupials and megadentates suggest that moderate energy budgets are sufficient to grow to about 7 tonnes, but higher energy budgets may be necessary to regularly exceed this limit.

Horner and Gorman (1988), Farlow (1990) and Lambert (1991) suggested that dinosaur metabolisms were high during rapid growth and/or during optimal seasonal conditions, and dropped strongly when they matured or during poor seasons. Metabolic drops of 30–50% are observed in normally active mammals and birds (Taylor, 1972; Brody, 1974; Merkt and Taylor, 1994; Piersma and others, 1995). Greater metabolic declines were improbable because bradycardia would have severely suppress or shut down activity (so that migrating adults would be unable to keep up with juveniles), and a massive reconfiguration of cellular physiology would be needed (Ruben, 1995). As tall Morrison sauropods grew, increasing heart–brain height differentials probably forced the heart and supporting organs to increase in step. Resting metabolic rates may have increased relative to mass$^{0.75}$ with maturity, the reverse of the situation in most tetrapods.

Brain Size

Small, simple reptilian brains have been cited as evidence of low metabolic rates in allosaurs, stegosaurs and sauropods (Hopson, 1980). However, Farlow (1990) and Paul (1991) noted that the correlation between brain size and metabolic rates is weak. Some tachyaerobes have small simple brains and some bradyaerobes have large complex brains. Small brains were advantageous to sauropods allowing them to keep their heads small, and in minimizing the amount of blood pumped up long necks. Both adaptations allowed greater heart–brain height differentials than are possible in bigger brained forms, but small brains do not solve the pressure problems associated with extreme height. In addition, Martin (1981) has shown that allosaur brain/body mass ratios were marginally in the lower avian range.

Metabolism of Morrison Megadinosaurs

The restored energetics of dinosaurs are summarized in Table III (note that stegosaurs may have been somewhat less energetic than other dinosaurs).

This study concludes that the motive power systems of dinosaurs were probably similar to that of tachyaerobic birds and mammals. The situation with resting metabolic rates is less clear. In all reptiles, and most birds and mammals the maximal/minimal aerobic ratios are from ten to twenty, so high aerobic exercise capacities require a high resting metabolic rate (Bennett and Dawson, 1976; Bennett, 1983; 1991; Schmidt-Nielsen, 1984; Hill and Wyse, 1989; Jones and Lindstedt, 1993). However, some mammals have maximal/minimal aerobic ratios as high as 70 (Jones and Lindstedt, 1993). One can model a tetrapod with a resting metabolic rate that is reptilian, and with an aerobic exercise capacity that is in the avian–mammalian range because the maximal/minimal aerobic ratio is in the high range for vertebrates. Such a model would explain many of the characteristics of dinosaurs, especially their expanded musculature and high levels of sustained activity. However, bradymetabolic–tachyaerobic vertebrates are at best speculative because of the lack of any living examples. Nor would low resting metabolic rates give juvenile bradymetabolic–tachyaerobic megadinosaurs the thermal stability associated with rapid growth. The tachymetabolic–tachyaerobic model is therefore considered superior. As for adult herbivorous megadinosaurs, they may have moved constantly and rested so rarely that their overall energy budgets would have been almost as high as if they were bradymetabolic rather than tachymetabolic.

The thermoregulatory systems of megadinosaurs may have differed from those of mammals and birds. The evolution of most megadinosaurs in a warm Mesozoic world may have left them without the well developed thermoregulatory controls and auxiliary heat production needed to maintain body temperature at a set point (in this case, if the resting metabolisms of megadinosaurs was high, then it was generated in order to sustain elevated blood pressures, not for thermoregulation). If this hypothesis is correct, then the combination of high metabolic rates and large mass made megadinosaurs tachyaerobic inertial semi-homeotherms, with high body temperatures that varied less than in large reptiles, but fluctuated more than in automatically homeothermic birds and mammals. Weak thermal controls may explain why megadinosaurs appear prone to interruptions of bone growth.

If megadinosaurs had high aerobic exercise capacity and high energy budgets, then their energetics were sophisticated, very different from those of reptiles, and matched that of birds and mammals in a critical regard. This is true whether they had low or high resting metabolic rates, or if their thermoregulatory controls were poorly or well developed.

Acknowledgments

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APPENDIX 1: TERMINOLOGY

Bradyaerobic: Maximal aerobic exercise capacity is limited to reptilian levels, this applies at the level of cells, muscles, organs, or whole bodies.

Bradyanaerobic: Muscle mass specific anaerobic power generation is about half that common to reptiles.

Bradycardia: Cardiac work and output is limited to reptilian levels.

Bradyfecund: Rates of reproduction are low, as in large mammals.

Bradymetabolic: Minimal (resting, basal, standard, etc.) oxygen consumption is limited to reptilian levels, this applies at the level of cells, organs, or whole bodies.

Ectothermic: The majority of body heat is gained from the environment, no particular metabolic rate or thermoregulatory system is implied.

Endothermic: The majority of body heat is generated internally, no particular metabolic rate or thermoregulatory system is implied.

Hyperanaerobic: Muscle mass specific anaerobic power generation is as high as in reptiles.

Tachyaerobic: Maximal aerobic exercise capacity is above reptilian levels, this applies at the level of cells, organs, or whole bodies.

Tachycardia: Cardiac work and output is above reptilian levels.

Tachyfecund: Rates of reproduction are high, as in many reptiles, small mammals and large birds.

Tachymetabolic: Minimal oxygen consumption is above reptilian levels, this applies at the level of cells, muscles, organs, or whole bodies.