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Cardiovascular Physiology of Dinosaurs

Roger S. Seymour
School of Biological Sciences, University of Adelaide, Adelaide, Australia
roger.seymour@adelaide.edu.au

Cardiovascular function in dinosaurs can be inferred from fossil evidence with knowledge of how metabolic rate, blood flow rate, blood pressure, and heart size are related to body size in living animals. Skeletal stature and nutrient foramen size in fossil femora provide direct evidence of a high arterial blood pressure, a large four-chambered heart, a high aerobic metabolic rate, and intense locomotion. But was the heart of a huge, long-necked sauropod dinosaur able to pump blood up 9 m to its head?

Dinosaurs arouse the imagination because some fossil bones reveal huge vertebrates that dominated terrestrial ecosystems during the 186 million years of the Mesozoic Era. Dinosaurs are classified within the Archosauria, distinct from other Mesozoic reptiles such as ichthyosaurs, plesiosaurs, mosasaurs, synapsids (stem mammals), etc. The archosaurs evolved from captorhinids (stem reptiles) and gave rise to two lineages: dinosaur-avian and crocodylian. Birds are dinosaurs that survived the mass extinction event at the end of the Mesozoic, 66 million years ago, when the Cenozoic Era began and mammals became dominant. (In this review, the word *dinosaur* refers only to non-avian dinosaurs.) The crocodylians living today represent the other archosaur lineage. The dichotomous evolution of the archosaurs is physiologically important, because the two groups today have very different metabolic strategies that relate to the cardiovascular system. Birds are endotherms, with high metabolic rates, high aerobic capacity, and physiological body temperature regulation. Crocodylians are ectotherms, with low metabolic rates, low aerobic capacity, and behavioral thermoregulation. In view of the phylogenetic intermediate position of dinosaurs, there is much controversy about their metabolic and thermoregulatory status. Because the cardiovascular system is functionally related to aerobic metabolism and evidence concerning its structure can be seen directly in fossils, it is possible to make robust inferences about dinosaur physiology.

The cardiovascular system of vertebrates functions primarily to supply oxygen to the tissues fast enough to satisfy the metabolic rate of the animal. Once oxygen is adequately supplied, the numerous other functions of the system are largely taken care of without cost. The allometric (disproportionate) scaling of metabolic rate with body size is well recognized, although there is disagreement about its causes and statistical analyses (18, 121). In broad terms, however, there is a close relationship between cardiovascular function, metabolic rate, and body size (120). This review deals with the relationships between these factors, with particular reference to dinosaurs, because some of them were extremely large. Of course we cannot measure physiological functions directly in extinct dinosaurs, but we can study living animals and apply solid biophysical concepts to dinosaurs with some confidence.

Living Animals: Metabolic Rate, Blood Pressure, and Heart Size

Metabolic rate is functionally associated with cardiac output ($\dot{Q}$), mean systemic arterial blood pressure (MAP), and heart mass (M_h) in living vertebrates (FIGURE 1, A AND B). In general, endotherms have MAP more than three times higher than ectotherms. The hearts of a few reptiles can separate systemic and pulmonary pressures to generate MAP that approaches the lower range of mammals, but they are exceptional (118). The connection is that high metabolic rate (tachymetabolism) requires a high $\dot{Q}$ for adequate oxygenation, and this is associated with high MAP, thicker cardiac muscle, and larger hearts. According to the principle of Laplace, left ventricular wall thickness is approximately proportional to the pressure exerted and chamber radius (31). The principle is apparent in ontogenetic and phylogenetic contexts. Ontogenetically, the right and left ventricles are similar before birth of mammals but begin to differ after birth when pressure differences develop between the pulmonary and systemic circulations (29). After the switch from placental to pulmonary gas exchange, the relative ventricular thicknesses are constant during growth (32). In systemic hypertensive disease, the left ventricular wall thickens (33, 57). This also occurs in response to increased radius during athletic training (125). Phylogenetically, higher MAP is associated with thicker hearts in mammals vs. birds (7, 34), in hypertensive giraffes (68), and even among mammals of different sizes (99).

Although most textbooks say that mammalian MAP is independent of body mass (M), and heart

mass (M_h) scales with body size directly, this is approximately true only for small species (124). MAP increases with body size in 47 mammalian species, described by a three-parameter equation: MAP = $aM^b + c$, where a and b are values for the standard allometric power equation relating MAP to body mass M, and c is a constant (FIGURE 1D). The phylogenetically informed analysis shows that MAP increases from 93 mmHg in a 10-g mouse to 156 mmHg in a 4-tonne elephant. The increase in MAP accounts for most of the vertical distance between the heart and the top of the animal, but not completely (73); whereas MAP at the top of a mouse is ~90 mmHg, it is ~50 mmHg in the elephant. In giraffes, MAP at heart level is ~200-250 mmHg and ~50 mmHg in the head (8, 37, 68). Increasing MAP is matched by increasing M_h; in the same 24 species of mammal, MAP increases with an exponent of 0.05 above independence, and M_h increases with an exponent of 1.06 above isometry, according to the principle of Laplace (99) (FIGURE 1C).

MAP and M_h in snakes are also significantly related to body size and habitat (95). MAP in terrestrial species increases with body size and in parallel with the hydrostatic component of blood pressure due to heart-head distance (95), and also increases ontogenetically in pythons, but less than in proportion to heart-head distance (21). The cardiovascular system of snakes is clearly related to gravitational habitat, categorized as tree-climbing (scansorial), terrestrial, and aquatic. Scansorial species show the highest MAP, greatest ability to regulate MAP with postural changes, hearts positioned relatively closer to the head, and short vascular lungs. In contrast, aquatic species have the lowest MAP, poor regulation, hearts nearer the mid-body, and long vascular lungs, all factors related to the gravitational environment (55, 97, 100). If MAP at the heart of head-up-tilted snakes falls below the pressure of the blood column, flow ceases entirely in the carotid artery (56).

Archosaurs: Metabolic Rate, Blood Pressure, and Heart Size

The size range of dinosaurs was very large, and the vertical distance from heart level (anterior ventral

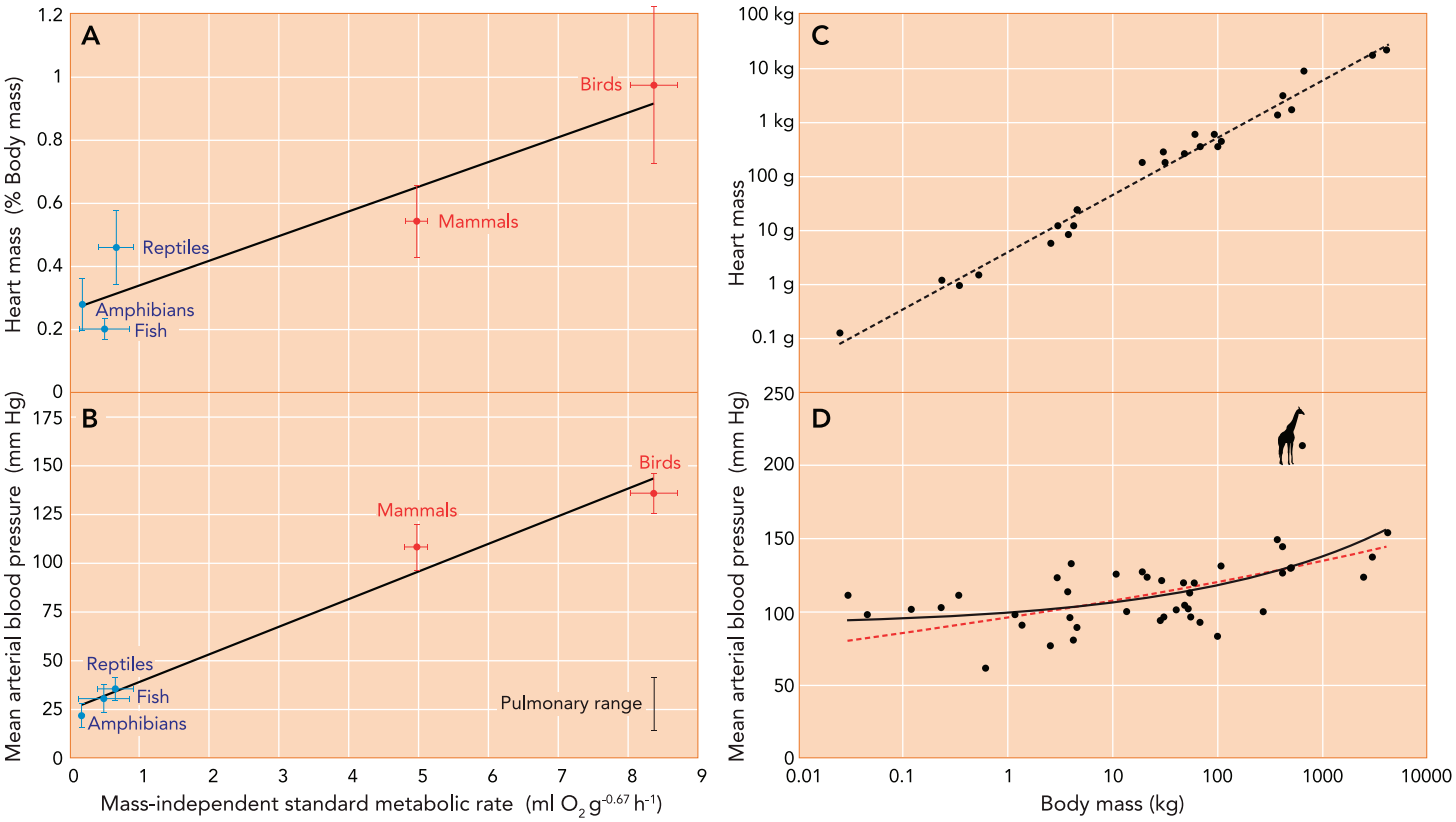


FIGURE 1. **Heart mass (M_h) and mean systemic arterial blood pressure in vertebrate animals in relation to metabolic rate and body mass (M)**
A and *B*: metabolic rate is expressed on a mass-independent basis (assuming a scaling exponent of 0.67; other exponents do not change the relationship significantly). The range of data for pulmonary blood pressure in air-breathing endotherms and ectotherms overlaps systemic blood pressure in ectotherms but not in endotherms. Mean data include 95% confidence intervals and come from Refs. 40, 50, 98, and unpublished collections of the author. *C*: heart mass for 24 species of mammal that also have mean systemic arterial blood pressure (MAP) measured (99). The allometric equation is $M_h = 4.0\ M^{1.06}$. *D*: MAP at heart level in 47 species of mammal (124). The curve (black) is a three-parameter nonlinear equation: $MAP = 9.8\ M^{0.23} + 90$. The dashed curve (red) is a two-parameter equation: $MAP = 96\ M^{0.05}$ for the 24 species for which M_h is known. The highest point is the giraffe; the increase in MAP is still significant if the giraffe datum is excluded.

rib cage) to the top of the body can be measured in reconstructed fossils to estimate the gravitational hydrostatic blood column according to the equation $P_g = \rho gh$, in which P_g is the increase in pressure at the bottom of the blood column due to gravity, ρ is the density of blood, g is the acceleration due to gravity, and h is the vertical height. The largest bipedal ornithopods (herbivores including hadrosaurs) and theropods (carnivores including tyrannosaurs) had 90- to 240-cm heart-head distances (P_g = 70–185 mmHg) (91). In addition to P_g, a perfusion pressure of perhaps 50 mmHg was required to move the blood. MAP typical of modern ectotherms could not support the blood column, let alone perfuse the head, but MAP of modern endotherms clearly could (FIGURE 1B). Tall blood columns are therefore consistent with high metabolic rates of endothermic dinosaurs. Small dinosaurs probably had high MAP too, just as birds do today. It is proposed that the evolution of endothermy in archosaurs was associated with high MAP in short animals, which in turn permitted some dinosaurs to become large and erect. The earliest archosauroforms were short, but some of their skeletons appear adapted to a highly active lifestyle, including obligatory bipedalism. It is significant that the highest P_g of any captorhinid (Permian stem reptiles that gave rise to archosaurs) occurred in *Moradisaurus grandis*, which had vertical heart-head distance of <30 cm (P_g = 23 mmHg), suggesting that this group was ectothermic (69). Conversely, some Permian synapsid reptiles that gave rise to mammals were tall; the top of the neural spine of the eupelycosaur *Dimetrodon grandis* reached 1.5 m above the heart (114), equivalent to P_g = 115 mmHg and clearly in the endothermic range.

The appearance of endothermy in basal archosaurs is supported by the fact that both groups of extant archosaurs (birds and crocodylians) have a completely separated, four-chambered heart. Although usually thought to separate oxygenation states of the blood, a four-chambered heart also separates systemic and pulmonary blood pressures. This is vital, because high pulmonary blood pressure can cause potentially fatal pulmonary edema, in which alveoli fill with water and reduce diffusive gas exchange (108). Modern crocodylians have both low systemic and low pulmonary pressures like other ectothermic reptiles (3) but have the same four-chambered heart of an endotherm. However, the arrangement of the outflow arteries of the crocodylian heart is unique, involving one pulmonary artery (that has both leaf valves and a "cog-tooth" valve), two aortas (one from the right ventricle and the other from the left ventricle), and the Foramen of Panizza that connects the two aortae outside of the valves. These curious features have been enigmatic for over a century but are now known to control pulmonary bypass shunting possibly associated with diving and digestion (2, 40). Embryological development of the crocodylian heart shows that the features are evolutionary novelties derived secondarily from a completely divided heart with no capacity for shunting, i.e., an endothermic heart (98). The lungs of living crocodylians are also very complex, with anatomic flow-through ventilation (23, 85), a feature typical for highly aerobic birds but oddly present in crocodylians that show very low maximal rates of oxygen consumption (92). Several other features involving anatomy, behavior, and molecular biology of living crocodylians indicate an endothermic heritage (11, 98). If the stem of archosaur evolution was indeed endothermic, why did the crocodylian lineage become ectothermic?

The crocodylian lineage is characterized by over 400 genera that occupied wholly terrestrial, marine, and freshwater environments throughout the Mesozoic Era. The eusuchians, appearing in the Cretaceous (last third of the Mesozoic), apparently abandoned the active predatory lifestyle of their endothermic ancestors and began a sit-and-wait lifestyle in water, where they probably preyed on terrestrial dinosaurs coming to drink (89). In water, the high aerobic metabolic rates of endothermy would be selected against, whereas long breath-holding capacity of ectothermy would be favored, and predatory events powered by powerful anaerobic metabolism would be valuable. The results today are crocodylians with little aerobic capacity and a moderately high capacity for anaerobic metabolism (92).

Further Cardiovascular Evidence from Fossils

Although we know that dinosaurs had high MAP, it was not clear if they had high cardiac outputs ($\dot{Q}$). If we had a fossil heart from a dinosaur, we could estimate $\dot{Q}$ from heart size (FIGURE 1A). If we had an aorta, we could estimate it from the well known cardiovascular relationship, the Poiseuille-Hagen equation: $\dot{Q} = (\Delta P \pi r^4)/(8L\eta)$, which relates $\dot{Q}$ to the pressure difference (ΔP) along a segment of a vessel of length (L) and radius (r), and to the blood viscosity (η). An apparently fossilized heart of an ornithischian dinosaur, *Thescelosaurus*, was estimated to weigh ~0.58% of the 300-kg body (24). The fossil also revealed a single aorta of 27-mm diameter, which, assuming that the dinosaur was fossilized without blood pressure, could be about the 32-mm predicted size of a 300-kg mammal under normal pressure (45). Together, these sizes are consistent with an endothermic animal. However, the dimensions may be simply coincidental,

because gross and microstructural analyses of the fossil do not confirm that it was actually a heart (14, 80). Other than apparent red blood cells, no soft tissues of the cardiovascular system of dinosaurs have been found (87), although there is a fossil turtle with blood vessels and osteocytes (9).

Nevertheless, some fossil bones reveal foramina where blood vessels once passed through, and the size of these holes provides a measure of blood flow rate. In particular, the long bones have nutrient foramina that are intimately related to the metabolic rate of the bone and the locomotor intensity of the animal. Long bones used in locomotion are particularly metabolically active because of the requirement for remodeling to repair micro-fractures that would otherwise accumulate to cause a catastrophic bone fracture (79). The mechanism involving capillary loops that literally bore through Haversian bone, dissolving old bone and laying down new bone, is increasingly well known (20, 105). Increased loading or exercise increases the frequency of micro-fractures and stimulates bone remodeling (16, 54). The vessels that supply blood to the long bones often enter and leave the bone cavity through a single nutrient foramen on the shaft. The size of this foramen can provide an index of blood flow derived from the Poiseuille-Hagen equation (103). The index, Q_i, is not a flow rate but is proportional to it, because it considers only radius and a length (derived from the length of the bone), and assumes that MAP and viscosity are approximately constant. In any case, the radius is the main determinate of Q_i, because it is raised to the fourth power. We have measured the nutrient foramina of the femur because it has a consistent blood supply, usually has a single foramen, and is involved in locomotion (103).

Q_i increases with body mass in mammals, from rat to elephant (FIGURE 2). The exponent of the allometric relationship of Q_i on body mass is 0.86, almost identical to the exponent of 0.87 for maximum aerobic metabolic rate for mammals on treadmills (123). Q_i is better correlated with maximum metabolic rate than it is with body mass in 12 mammal species for which data are available (exponent = 0.99) [(103), supplementary data]. This is consistent with the idea that bone blood flow is associated with bone remodeling as a result of micro-fractures due to locomotion stresses: the more locomotion, the higher frequency of micro-fractures and the greater requirement for remodeling. Q_i measured for 24 species of primarily cursorial birds produce an allometric exponent of 0.89, similar to mammals, but when differences in blood pressure are taken into account, bipedal cursorial birds have 1.9 times the femoral blood flow compared with quadrupedal mammals, in line with expectations based on number of legs (1).

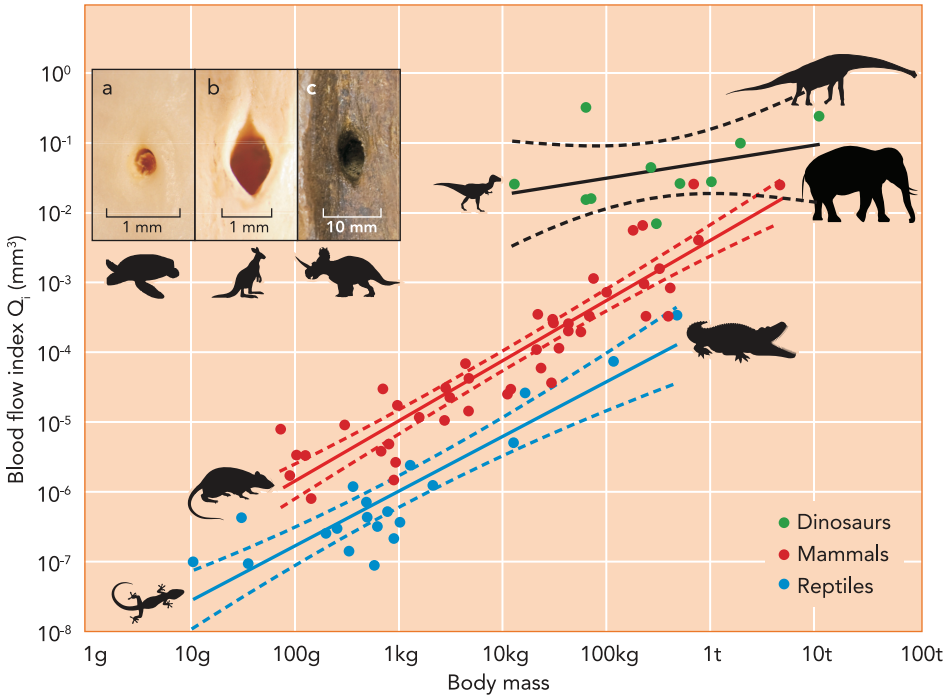
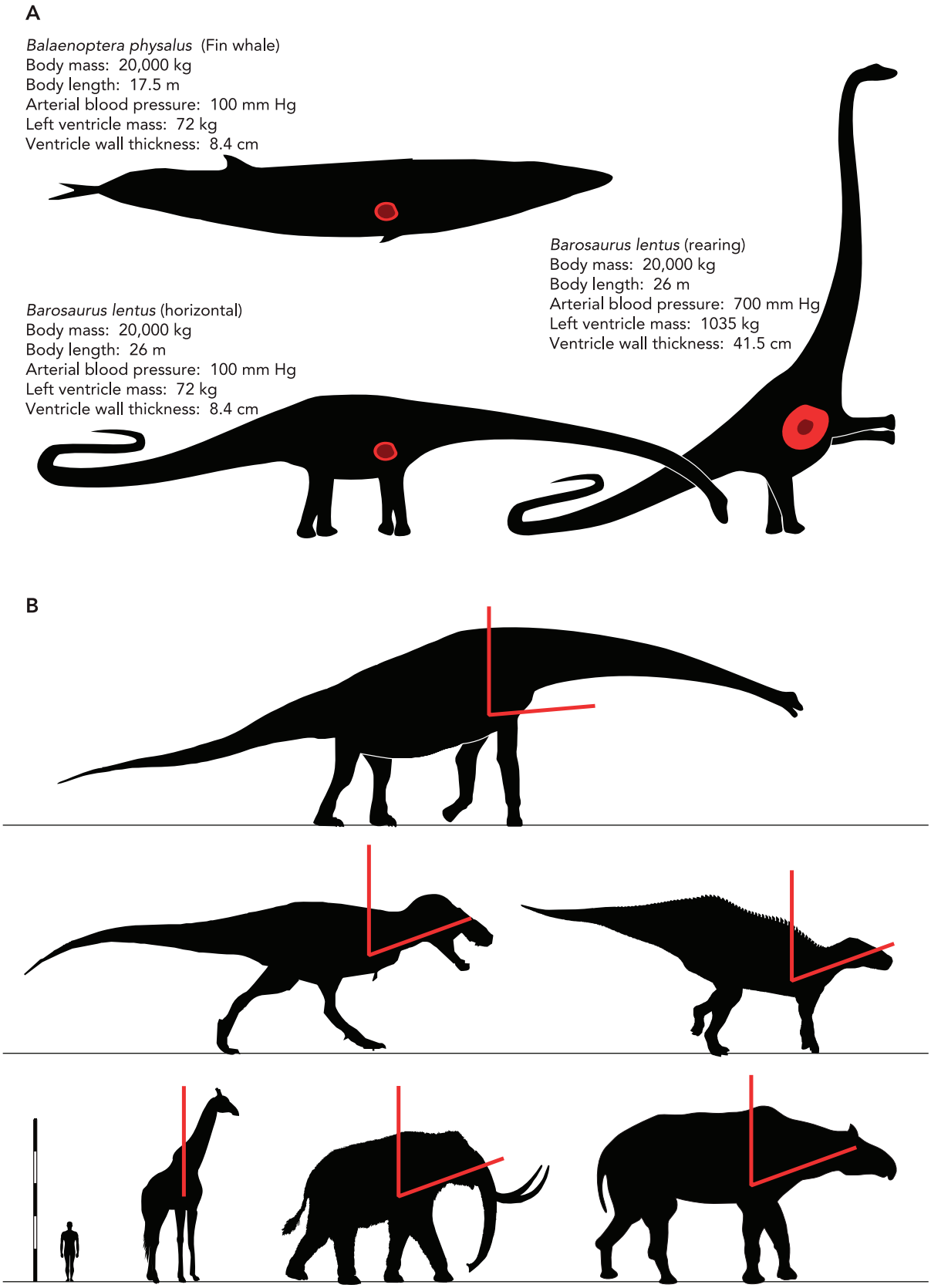


FIGURE 2. **Blood flow index derived from the size of the nutrient foramina of the femora of individual species of mammals, reptiles, and dinosaurs (103)**
Regressions are plotted on logarithmic axes with 95% confidence bands for the regression means. *Inset*: femoral nutrient foramina of a reptile, *Lepidochelys olivacea* (a); a mammal, *Macropus robustus* (b); and a ceratopsian dinosaur, *Centrosaurus apertus* (c) (*photo c* is courtesy of Don Henderson, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada, and used with permission).

Cursorial birds have about twice the femoral blood flow as do volant birds, again related to relative loading. In constrast, Q_i in reptile femora is ~10 times lower than mammals but with a similar exponent (FIGURE 2); however, given that MAP is lower in reptiles, actual blood flow rates are ~50 times lower (103). This is consistent with the fact that reptiles do not remodel their bones in re-



sponse to exercise, with the exception of varanid lizards, which have Q_i values that overlap mammals (71, 72).

Measuring Q_i from fossil bones appears to be a good indication of aerobic activity levels of the original owners. Q_i data from fossils of eight species of extinct giant birds of New Zealand (the moa) fall on the extrapolated curve for cursorial birds (1). So far, we have data from fossil femora of only 10 species of dinosaur, which nevertheless represent four major groups: theropods, ornithopods, ceratopsians, and sauropods (103) (FIGURE 2). It is clear that dinosaurs were highly active animals with substantial requirements for bone remodeling, as also evident by the presence of Haversian bone (46). However, it is not clear why their data are much higher than mammals or birds. Blood flow to long bones is essential for growth, but the growth rates of dinosaurs, as evident from rings in long bones, appear to be lower than those for mammals and birds (30). Mobilization of calcium for egg-laying cannot explain it, because foramen data from all fossil birds are lower than dinosaurs (1).

Cardiovascular Problems of Sauropod Dinosaurs

Sauropods are a major group of dinosaurs that are characterized by species with exceptionally long necks and huge body size. The recently discovered titanosaur, *Dreadnoughtus schrani*, is estimated to have weighed 59 tonnes with a 12.2-m neck and head (52). Neck lengths in complete sauropod skeletons are up to 9.5 m and are estimated to reach 15 m in incomplete skeletons (112). Many palaeontologists now believe that sauropods were terrestrial and used their necks to browse in tall trees (82, 84).

We can gain insight to the cardiovascular problems of sauropods by examining giraffes. Giraffes have been interesting to cardiovascular physiologists precisely because of their long necks (68). The measured MAP at heart level in adult giraffes is ~200–250 mmHg (8, 28, 107, 115), much higher than the mean of 100 mmHg expected in most mammals. These values are reasonable for an animal with a 2-m neck to produce a perfusion pressure of ~50 mmHg in the head, because the gravitational hydrostatic pressure of the blood column is ~150–200 mmHg. The left ventricular wall of the giraffe is grossly thickened such that the cross-sectional stress is normal for mammals, although total heart mass is a similar fraction of body mass (0.5%) as in other mammals (68, 107). Because the stroke volume is small compared with other mammals, the $\dot{Q}$ would also be lower if not compensated by high heart rate (99, 107). Because giraffes are skittish and difficult to study without restraint or anaesthesia, values of $\dot{Q}$ and heart rate are quite variable. One review of the literature concludes that giraffes tend to have higher than expected heart rates and normal $\dot{Q}$ for a mammal of their body mass (68), but another study of anaesthetized giraffes indicates low $\dot{Q}$ (107). The giraffe's long neck imposes a high MAP at heart level, which is transmitted throughout the arterial system of the entire body. The peripheral resistance throughout the body is therefore high and probably occurs mainly at the arteriole level as it does in other mammals. MAP is highest at the feet, reaching over 400 mmHg in tall individuals. Giraffe legs are characterized by hypertrophic arterial walls, arterial vasoconstriction to limit blood flow downward, lymph vessels and veins with valves to push fluids upward during locomotion, and tight skin, fascia, and capillary membranes to prevent edema (38, 70, 76).

The heart-head vertical distance is ~3.4 m (P_g = 260 mmHg) in the tallest (5.88 m) giraffe on record, requiring a MAP of ~310 mmHg at the heart. The distance is ~9 m (P_g = 700 mmHg) in the rearing *Barosaurus* in the American Museum of Natural History or *Brachiosaurus* (= *Giraffatitan*) in the Museum für Naturkunde in Berlin, requiring ~750 mmHg at the heart to achieve 50 mmHg in the upright head (35, 44, 91). The size of the left ventricle necessary to produce such pressures can be calculated from ventricular stress in relation to heart and body size in mammals and birds (99, 101). To put it in perspective, a fin whale's heart weighs ~0.5% of the body, which is 100 kg in a 20-tonne animal (64), and the left ventricle comprises ~72% of total heart mass (99). Thus 72 kg of muscle is required to work at normal mammalian blood pressure of ~100 mmHg (124) (FIGURE 3A). Unfortunately, there appears to be no direct measurements of MAP in whales, but 100 mmHg is con-

FIGURE 3. **Comparison of end-diastolic left ventricle size**
A: comparison of end-diastolic left ventricle size, scaled accurately to body size, in a fin whale and a sauropod dinosaur in different poses. Body mass and end-diastolic blood volume are assumed to be the same in both species, and mean arterial blood pressure is assumed to be either 100 or 700 mmHg. Calculations are according to a model in Ref. 101, except that the body mass is assumed to be 20 tonnes (88) instead of 40 tonnes. *B*: silhouettes of the largest known megafauna to the same scale (see human and 5-m scale). Superimposed are 3.4-m red bars, representing the heart-head distance in the tallest giraffe known. All animals could support this vertical blood column with blood pressures of the giraffe, including the sauropod with its neck held horizontally. If these animals reared to take the head directly above the heart (indicated by the lower 3.4-m bars), they could probably perfuse the brain, except for the sauropod. Genera illustrated in *B* are (from *top*, *left* to *right*): sauropod dinosaur (*Brachiosaurus*), theropod dinosaur (*Tyrannosaurus*), ornithopod dinosaur (*Shantungosaurus*), mammals (*Homo*, *Giraffa*, *Mammuthus*, *Paraceratherium*).

sistent with arterial wall mechanics (104). Although a whale would have a MAP of 202 mmHg according to the terrestrial equation (FIGURE 1D), the hydrostatic column of water nearly balances the blood column, so P_g is negligible. We assume that a 72-kg ventricle could service a *Barosaurus* of the same body mass and a MAP of 100 mmHg (FIGURE 3A). However, if the MAP were a conservative 700 mmHg in a rearing animal, the ventricle would have to be 15 times heavier, with a wall 5 times thicker, weighing >1 tonne (5% of the body). In diastole, the ventricle would measure 1.25 m across, which fills the chest between the ends of the ribs and the dorsal vertebral column (FIGURE 3A). Aside from being too large to fit easily, a thicker-walled ventricle becomes progressively inefficient in pumping blood due to interfascicular tension. It is estimated that ~10% of the total energy consumed by the human heart is used to overcome ventricular wall stiffness, whereas 25% is involved with external work moving the blood (116). This effect has been demonstrated in hypertrophic hearts of laboratory animals (36). With a wall five times thicker, the cost of deformation of sauropod ventricles could reach twice that of moving the blood. It is important to realize that these problems would exist regardless of the rate of blood flow up the neck. As in giraffes, the neck imposes the MAP at the heart level, and that pressure must be delivered to the entire body.

How high could a sauropod lift its neck? Osteological evidence indicates that some sauropods had rather straight, horizontal necks, but others had enough cervical vertical flexion to raise the head a few meters above the shoulders (109). With the same fossils, and ignoring blood pressure problems, other estimates lift the head nearly vertical, with extreme flexibility, including an S-shaped neck (13, 77, 113). Because MAP is related proportionally to vertical height, there is no discreet limit. However, 9 m is clearly improbable, and 3.4 m is probably close to the limit of vertical distance between the heart and the top of the animal. This distance is similar to the head of the tallest living mammal (giraffe), to the shoulders of the largest extinct mammal (*Paraceratherium*), and to the shoulders of the largest sauropods (*Giraffatitan* and *Argentinosaurus*) (FIGURE 3B). All of these animals could have been perfused by a heart 3.4 m below the highest part and producing ~300 mmHg MAP, whether in normal pose or rearing up, with the obvious exception of sauropods.

Independent of any considerations of heart size or performance, it is possible to evaluate the energy cost of the circulation by examining the scaling relationships between metabolic rate, blood flow rate, blood pressure, and cardiac work rate (94). The external energy cost of the circulation is directly related to the product of $\dot{Q}$ and MAP. In mammals, $\dot{Q}$ (liter/h) scales with body mass (M, kg) according to $\dot{Q} = 11.2\ M^{0.81}$ (10). MAP (mmHg) increases with body mass in 47 species of mammals, from mice to elephants, according to the relationship $MAP = 9.8\ M^{0.23} + 90$ (124) (FIGURE 1D). When $\dot{Q}$ is converted to liter/s and MAP to J/liter and multiplied, the product (Watts) is the raw external work. However, because the heart is only ~30% efficient (6), the total work of the heart (E_h; Watts) is greater (FIGURE 4A). Basal metabolic rate (E_b; Watts) scales according to $E_b = 2.29\ M^{0.71}$ (122) (FIGURE 4A). Because both $\dot{Q}$ and MAP increase with M faster than E_b, their product increases even faster, and the result is an increasing ratio E_h/E_b (FIGURE 4B). According to this allometric analysis, the human heart uses ~10.7% of the metabolic rate. The percentage cost has been analyzed independently from isolated papillary muscles in six species of mammal, also showing an increasing relative cost, from rats (3.6%) to humans (9.6%, similar to 10.7% estimated above) (59). The allometric equation of these six species is $E_h/E_b \times 100 = 4.0\ M^{0.21}$.

E_h/E_b in adult giraffes can be estimated from the literature, but unfortunately the results vary widely. The upper value of E_h calculated from data from conscious but frightened giraffes (M = 455 kg) yields MAP = 265 mmHg and $\dot{Q}$ = 1,920 l/h (28). The lower value of E_h from anaesthetized giraffes (M = 495 kg) yields MAP = 229 mmHg and $\dot{Q}$ = 980 l/h (107). E_b can be derived from the metabolic rate of conscious giraffe (53, 123), which is 2.4 times higher than allometric analysis of BMR in mammals in general (53, 123). With different combinations of these data, E_h ranges from 6.1 to 35.5% of E_b (FIGURE 4B). The lowest value represents reduced $\dot{Q}$ from anaesthetized giraffes (58, 107) in relation to metabolic rate from conscious giraffes. The highest value represents $\dot{Q}$ from conscious, but stressed, giraffes in relation to BMR from a mammal of giraffe body mass. These results are therefore equivocal about the cost of the circulation in relation to high MAP in the giraffe. Measurements of all variables in the same animal are clearly needed. The cost of the circulation in terrestrial sauropods with mammalian MAP and $\dot{Q}$ would be expected to fall on the mammal line. However, if MAP was 750 mmHg, E_h/E_b would reach 1.3, indicating that the left ventricular energy consumption would exceed the entire rest of the body (FIGURE 4B).

The high cardiac costs associated with the upright neck of sauropods are also unreasonable from a cost/benefit standpoint (94). The neck of a stationary animal can reach points within part of a semi-spherical feeding envelope. The volume of the envelope is maximal at shoulder level, but it decreases as the animal raises its head (the volume

of a sphere decreases as the perimeter is approached), so the volume of available food decreases while the cost of the circulation increases. It would be energetically better to use the neck as a vacuum cleaner hose near the ground and not move the bulk of the body (81). The problems of heart size and circulatory cost associated with an upright neck are independent of the metabolic status of the animal; whether endothermic or ectothermic, the left ventricle would be relatively thick-walled, inefficient, and extremely costly relative to the animal's total metabolic rate. Keeping the neck low is consistent with the limitations of actual fossil vertebrae, not imagined reconstructions necessary to raise the head (109).

Undaunted by skeletal rigidity or blood pressure problems, some paleobiologists still reconstruct sauropods in a rearing pose (61) or even a sitting pose (106) to get the head up in the trees. The famous *Brachiosaurus brancai* in the Museum für Naturkunde of Berlin, previously 11.87 m high (49), was recently raised to over 13 m at a cost of ~18 million Euros (78) and is now unfortunately called *Giraffatitan brancai* (74, 110). The giraffe model is so compelling that there have been several attempts to solve the blood pressure problem.

Accessory hearts in the neck have been proposed (5, 12, 19, 106), in which one heart pumps to the next, and so on, right up to the head. The advantage of this is that the rest of the body and the tissues between the accessory hearts can be at reasonable pressures. However, such hearts are unknown in the arterial system of any vertebrate animal. They are unlikely to have evolved from the circulatory systems of smaller reptiles because pulsatile arterial walls would not be advantageous without valves, and valves would not be valuable in a pressurized arterial system that normally has no retrograde flow. Furthermore, the carotid arteries are not the only arteries that run up the neck. In birds, the closest relatives to dinosaur ancestors today, there are at least four other arteries in addition to the carotids (27). Accessory hearts would also have to occur in each of these. There are further issues involving the coordination of multiple hearts (65).

A siphon mechanism is another attractive solution to the blood pressure problems in tall, long-necked animals, because the circulation to the neck is a loop. In a siphon, the potential energy used by raising the blood in one arm of the loop is reclaimed by the descending blood in the other arm, so the pressure at the heart does not have to be high. This has been proposed specifically for the sauropods, including estimates that the MAP within the head could have been −500 mmHg sub-atmospheric (4, 41, 48, 117). However, there are several fatal problems with this reoccurring idea (101, 102). Foremost is the fact that every vessel in the neck and head has to be protected from collapse, including those outside of the skull and vertebral column. Even if soft structures of the face, mouth, eyes, and ears could be protected, severely sub-atmospheric pressures in the head are impossible. If the vessels were effectively rigid, even a tiny wound would aspirate air, filling the upper circulation with gas. Wounds would not bleed or clot. In addition, sub-atmospheric blood pressure would cause degassing of the blood in the head (102). Blood equilibrating with the atmosphere in the lungs would load hemoglobin with O_2 and equilibrate with atmospheric N_2. These gases would then come out of the blood as bubbles when exposed to sub-atmospheric blood pressure, potentially reaching a volume of gas exceeding that of the volume of blood. Even if O_2 remained bound until consumed by tissues, N_2 is not consumed and would certainly build up to the point of bubble

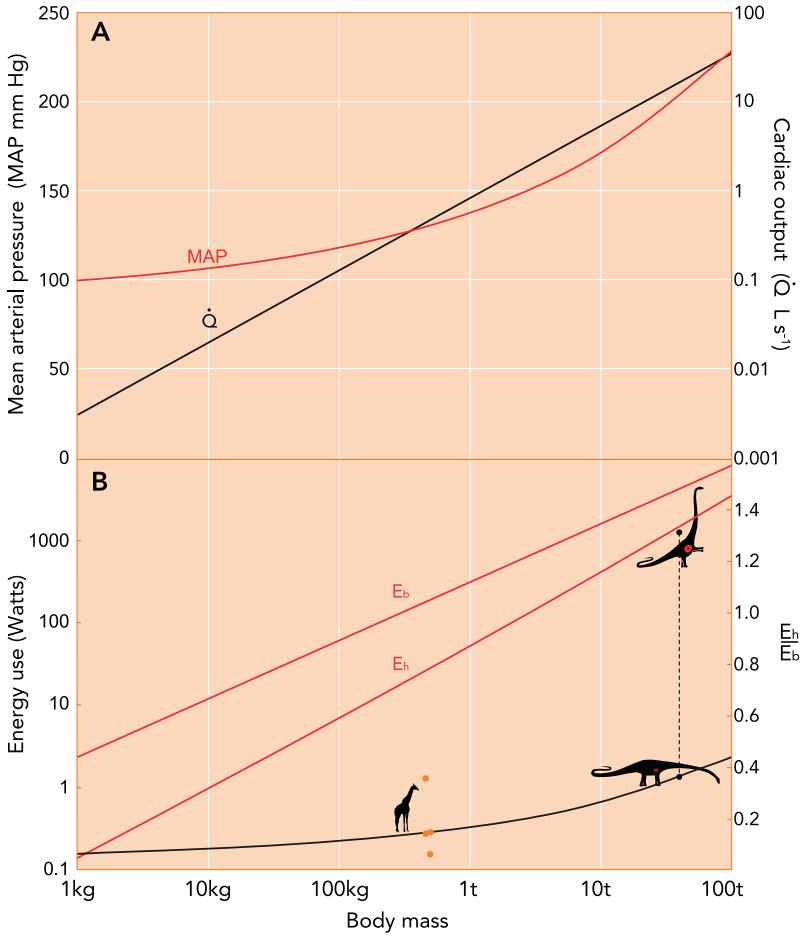


FIGURE 4. **Effect of body size on the scaling of MAP and $\dot{Q}$ in mammals**

A: effect of body size on the scaling of MAP and $\dot{Q}$ in mammals. Equations are $\dot{Q}$ (l/h) = 11.2 $M^{0.81}$ (10) and MAP = 9.8 $M^{0.23}$ + 90 (124). *B*: left ventricular work [E_h = ($\dot{Q}$ × MAP)/0.3] and basal metabolic rate (E_b = 2.29 $M^{0.71}$) (122) in relation to body mass. The percentage ventricular work [100 × (E_h/E_b)] is given on the *right* axis. Data points for the giraffe (orange) and sauropod (black) are given in relation to E_h/E_b. Points for the giraffe represent the range of values from the literature. Lower and upper points for the sauropod assume MAP of 100 and 750 mmHg, respectively.

formation (decompression sickness). N_2 bubbles have been produced in humans and animals during slow aircraft ascents to altitudes that produce much less severe sub-atmospheric pressure as would occur in sauropod siphons (42, 43). Finally, the siphon effect is not evident in any living animal, including giraffes that have positive cranial blood pressures and no evidence of gravitational pressure gradients in the jugular veins (8, 28, 38), or in realistic laboratory models (66, 67, 93), or according to hemodynamic modeling of collapsible vessels (75).

Other explanations to justify vertical sauropod necks are doubtful. Some palaeontologists suggest that the neck could be kept low normally to save cardiac energy but could be raised during food shortages (13, 83). If this were true, then the animal would have had to maintain a huge ventricle all of the time, have a circulatory system capable of regulating within a sevenfold range of MAP, and have organs such as the kidney that could deal with such changes. No living animal does this, not even giraffes that maintain MAP above 130 mmHg when recumbent or anesthetized with their heads down (8, 28), although giraffes have an unusually robust renal capsule (17). Others propose that sauropods had edema-preventing mechanisms like the giraffe, different blood viscosity or a rete mirable in their heads that allowed them to raise their necks high (25), but none of these would affect the arterial blood pressure at the heart.

Another suggestion to permit upright necks is to surround the vasculature with a column of fluid that has a hydrostatic gradient that matches that of the blood column (47, 48). This idea is similar to the water-filled "G-suit" that protects aviators from syncope by facilitating venous return. The effect of this is to raise the hydrostatic indifferent point (HIP), which is the point in the circulatory system where blood pressure does not change with postural change (26). If the HIP is higher in the body, then it could reduce the arterial pressure necessary to raise the blood to the head. The fatal problem with this idea is that the HIP in real animals is near the heart and the lungs, and for good reason. Because the HIP would have to be in the neck of an erect sauropod to do any good, the extravascular pressure below the HIP would bear on the systemic venous return to the heart, which in turn would be transferred through the right ventricle to the lungs, causing edema or rupture. Only if both the heart and the lungs moved with the HIP into the neck would the sauropod G-suit function (101).

Blood flow in the sauropod's body could occur without difficulty if gravity were eliminated by immersion of the whole body in water. Here, gravity has almost no effect, because the internal and external hydrostatic pressures due to the blood and water columns are balanced, except for a slight difference in fluid density. Aquatic or amphibious habits of sauropods were generally accepted throughout most of the 20th century, with some depictions of them on the bottom of water bodies and using their neck as a snorkel (111). However, after the 1970s (5, 15), most palaeontologists consider that sauropods were primarily terrestrial (111). Kermack provided a physiological reason for rejecting the snorkel idea (51). Because air pressures in the lungs are necessarily slightly sub-atmospheric during inspiration, it would be difficult to expand the lungs against the hydrostatic pressure of 9 m of water (ca. 700 mmHg). In addition, the water pressure could be transmitted through the body to the vascular system, with the consequence that blood pressure would greatly exceed that of the pulmonary gas during inspiration and

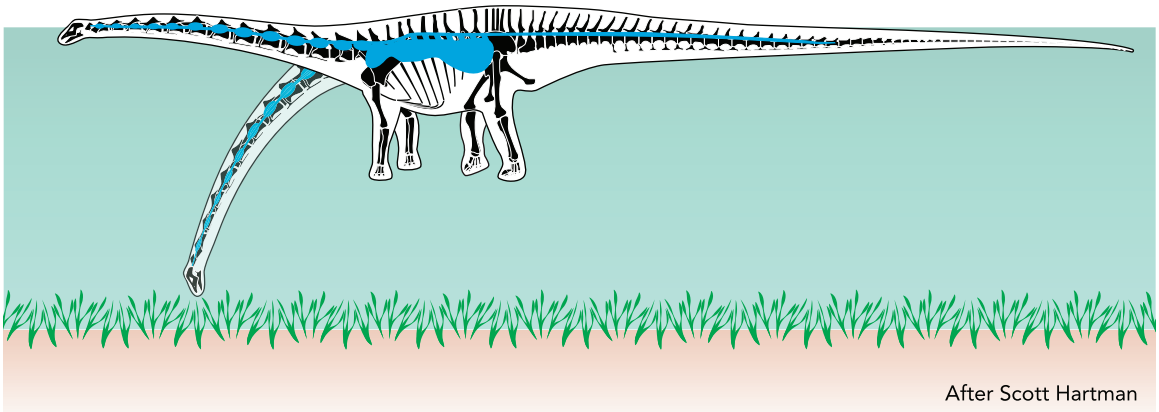


FIGURE 5. **Breathing at the surface and feeding at depth could have been the use of a sauropod's long neck without blood pressure problems**
Pneumatized cervical, dorsal, sacral, and caudal vertebrae, and presumed lungs and cervical and abdominal air sacs (blue) are thought to have been present in *Diplodocus* (119), and they would have been near the water line in a floating animal, making inspiration easy and preventing high blood pressures in the pulmonary vessels.

potentially cause capillary rupture or edema. The assumption that Kermack and many subsequent palaeontologists made is that the animal walked on the bottom; however, we know that sauropods were highly buoyant (39), with air-filled vertebrae and heavy legs (63). They could have floated in the water with the lungs, neck, and nostrils at the surface where lung inflation would not be a problem (FIGURE 5). It is certainly not a problem in whales, where the distance from the blow-hole to the mid lungs can exceed 6 m, but they bring the lungs close to the surface during inspiration. The sauropod neck could be used to reach deep aquatic vegetation without any problems involving blood pressure. In fact, this lifestyle is consistent with the limited upward flexion of sauropod necks, but ability to flex it down well below the level of the feet (109). It explains many anatomical features, including dorsal nares, pneumatic vertebrae, and weak dentition (15), manus-only or pes-only trackways most straightforwardly, in contrast to explanations involving differential preservation (22), and close association of many sauropod fossils with coastal estuarine and lacustrine environments (62). All terrestrial features of the sauropod skeleton can be explained by the requirement of all dinosaurs to lay eggs on land, because the eggshell pores had to be air-filled (90). Breath-holding duration provides a strong selective pressure for larger body size, which can explain sauropod gigantism very simply. As in marine mammals and birds (86), the stores of oxygen are approximately proportional to body mass, but the rate of oxygen use during the breath-hold scales with mass to the ~2/3-3/4 power. The result of this scaling is that dive duration increases with body mass to the 1/4-1/3 power (10). Freed from the energy required to support a large body against gravity, and freed from the requirement to support a high column of blood, the sauropods were able to attain large size.

Conclusions

Because of the nexus between cardiovascular function, metabolic rate, and body size, it is possible to convert direct measurements of fossil bones into solid inferences about the physiology of dinosaurs. In future studies, levels of locomotor stress on bone could be measured from bone foramina in more dinosaur species of different locomotor patterns (bipedal vs. quadrupedal, terrestrial vs. aquatic). The technique could be applied to key species of both archosaur lineages to see whether large nutrient foramina are more widely distributed among the dinosaur-avian lineage, and where in the crocodilian lineage the transition from highly aerobic basal archosaurs to anaerobic sit-and-wait eusuchians occurred. Of course, nutrient foramen size could be measured in other long bones of dinosaurs and from any other extinct group of reptiles or mammals. Foramen size is easier to measure and less destructive than bone histology, and it can be applied correctly to animals of different size. Fossil foramina in the skull have been used to quantify brain perfusion in primates and marsupials (96), and if the pattern of circulation to the brain of archosaurs can be determined, it might be possible to apply the technique to them. The use of the circulatory system for temperature regulation may also appear in fossil bones. For example, the role of vascular indents on the surface of stegosaur dorsal plates may be determined (60). It is hoped that more cardiovascular evidence from fossils can clarify the paleobiology of other vertebrates. ■

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