Donald F Egan Scientific Memorial Lecture

The Physiology of Dinosaurs: Circulatory and Respiratory Function in the Largest Animals Ever to Walk the Earth

David J Pierson MD FAARC

The cardiopulmonary physiology of dinosaurs—and especially of the long-necked sauropods, which grew much larger than any land animals before or since—should be inherently fascinating to anyone involved in respiratory care. What would the blood pressure be in an animal 12 m (40 ft) tall? How could airway resistance and dead space be overcome while breathing through a trachea 9 m (30 ft) long? The last decade has seen a dramatic increase in evidence bearing on these questions. Insight has come not only from new fossil discoveries but also from comparative studies of living species, clarification of evolutionary relationships, new evaluation techniques, computer modeling, and discoveries about the earth's ancient atmosphere. Pumping a vertical column of blood 8 m (26 ft) above the heart would probably require an arterial blood pressure > 600 mm Hg, and the implications of this for cardiac size and function have led to the proposal of several alternative cardiopulmonary designs. Diverse lines of evidence suggest that the giant sauropods were probably warm-blooded and metabolically active when young, but slowed their metabolism as they approached adult size, which diminished the load on the circulatory system. Circulatory considerations leave little doubt that the dinosaurs had 4-chambered hearts. Birds evolved from dinosaurs, and the avian-type air-sac respiratory system, which is more efficient than its mammalian counterpart, may hold the answer to the breathing problems posed by the sauropods' very long necks. Geochemical and other data indicate that, at the time the dinosaurs first appeared, the atmospheric oxygen concentration was only about half of what it is today, and development of the avian-type respiratory system may have been key in the dinosaurs' evolutionary success, enabling them to out-compete the mammals and dominate the land for 150 million years. *Key words: dinosaurs, sauropods, circulation, blood pressure, respiration, evolution, comparative physiology, endothermy, avian respiration, air sacs, dead space, trachea, gas exchange.* [Respir Care 2009;54(7):887–911. © 2009 Daedalus Enterprises]

Introduction: Why Dinosaurs?

Being asked to present the 35th Donald F Egan Memorial Lecture is a distinct honor, considering not only Dr Egan's contributions to education and clinical excellence in the field of respiratory care, but also the eminence of the previous presenters. I was thus deeply honored by the Program Committee's invitation, although their request that the topic be the physiology of dinosaurs initially gave me pause. This lecture typically acknowledges the career contributions of a leading researcher or clinician whose work has influenced respiratory care both as a field of endeavor and as a profession. It therefore usually consists of a review of those contributions in the context of the subject area in which the presenter has worked. That description would not apply this year if my topic was truly to be the cardiopulmonary physiology of dinosaurs. On reflection, though, I understood the Committee's intent. Several of its members knew of my longstanding involvement in the teaching of comparative respiratory physiology,[1-8] and of my interest in the largest dinosaurs as challenges to known physiologic principles and limits. In this context the assignment fits with Dr Egan's role in education—in expanding the scope of respiratory care, and in both broadening and stimulating the interests of its practitioners—and also with the purposes of the lectureship that honors him.

No members of the animal kingdom are as often or as prominently in the public eye as dinosaurs.[9] Whether in books, movies, the comics, video games, or advertisements in media of every type, dinosaurs remain more or less continually in our consciousness. This applies both to children—many of whom can reel off the names of a dozen different dinosaurs before they can name the street on which they live[9]—and to adults, thanks to the Discovery Channel, *National Geographic*, and other popular media. A *Google Books* search under "dinosaurs" in March 2009 retrieved nearly 5,000 citations, and there are currently several excellent books on dinosaurs for educated lay readers as well as for scientists working in this field.[10-12] And

David J Pierson MD FAARC is affiliated with the Division of Pulmonary and Critical Care Medicine, Harborview Medical Center, and with the Division of Pulmonary and Critical Care Medicine, Department of Medicine, University of Washington, Seattle, Washington.

Correspondence: David J Pierson MD FAARC, 325 Ninth Avenue, Box 359762, Seattle WA 98104. E-mail: djp@u.washington.edu.

the study of dinosaurs is as active as any field of scientific endeavor; seldom does a month pass without a news report about some new discovery or insight into dinosaurs and the world in which they lived.

Given their size, their status as real-life "monsters," and their mysteriousness—having been extinct for 65 million years—it is no wonder that dinosaurs continue to fascinate many of us throughout our lives. However, for those of us involved in health care there are additional motivations for such interest. Respiratory therapists, nurses, physicians, and other health-care professionals are all biologists, in the sense that their work requires knowledge of the laws of the natural world and of the structure and function of living things. Respiratory care, especially, relies heavily on an understanding of physiology, and the areas in which the relevance of that understanding is most apparent are respiration and the circulation. It is also in these areas that the physiology of dinosaurs is most intriguing, particularly when one considers their physical dimensions.

Figure 1 illustrates the relative sizes of 2 well-known dinosaurs, *Brachiosaurus* and *Mamenchisaurus*. Given our understanding of the physiology of humans and other living animals, the implications of the sheer size of these creatures with respect to circulatory and respiratory function are truly staggering: what would the systemic blood pressure have to be in an animal standing 40 feet tall, and how could a creature breathe through a 30-foot neck? I will consider these questions in the context of present-day knowledge about dinosaurs and the physiology of different living animal groups, from the perspective of a clinician-educator interested in cardiorespiratory function.

How Can We Know Anything About the Physiology of Dinosaurs?

That we could know anything for certain about the physiology of dinosaurs seems at first a dubious proposition, given that physiology deals with soft tissues and organ function that can be observed, and that such knowledge would have to be generated many millions of years after the last dinosaur died. To place the challenge of studying dinosaur physiology into perspective, it is helpful to consider when in life's history they lived.[13] Geologists divide earth history into eons—extremely long intervals of time—and subdivide the eons into eras, which are in turn broken down into periods (Fig. 2).[14] Periods are subdivided into epochs (eg, late, middle, and early), and these epochs are further divided into ages. The oldest rocks that survive to the present day are about 4 billion (4,000 million) years old, and the oldest fossils date from roughly that time. Animals with sophisticated internal or external skeletons first appeared about 570 million years ago, at the beginning of the Phanerozoic eon, which continues today. Dinosaurs lived during the Mesozoic era, which began ap-
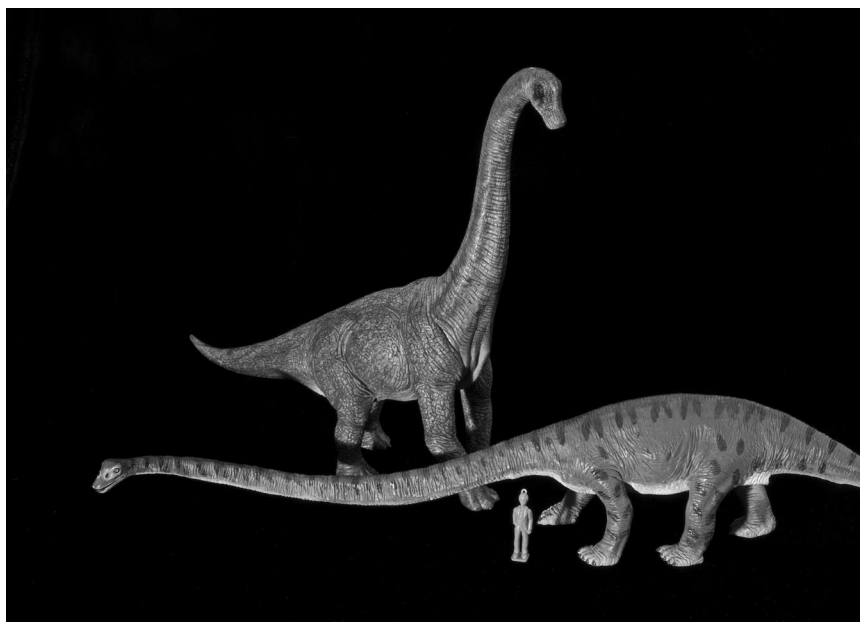
Fig. 1. 1:40 scale models of 2 sauropod dinosaurs and an adult human, to illustrate the physiologic challenges of sauropod circulation and respiration. *Brachiosaurus* (rear), was 12 m (40 ft) tall, and *Mamenchisaurus* (front), had a neck more than 9.2 m (30 ft) long.
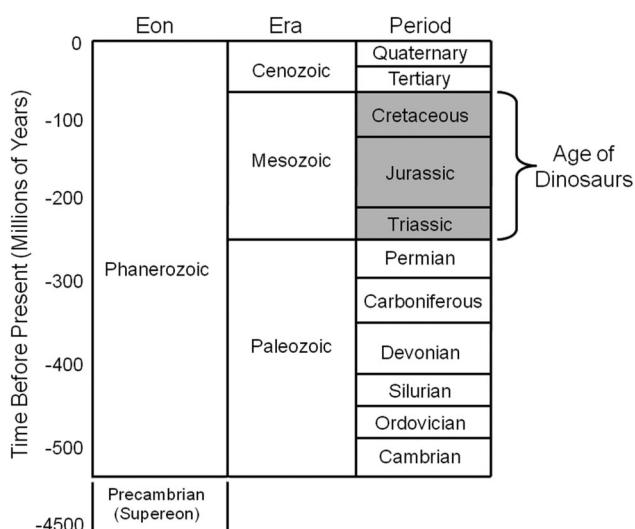

Fig. 2. The geologic time scale, showing the age of dinosaurs, which lasted more than 180 million years, starting in the early Triassic period. The time scale shown is approximate.

Table 1. Increased Interest in Dinosaur Physiology Since 1965, as Reflected in *Index Medicus* Citations

Publication Interval	Total Citations Found With These Search Terms	
	Dinosaurs	Dinosaurs and Physiology
1965–1979	11	1
1980–1989	33	4
1990–1999	73	13
2000–2008	436	213

proximately 250 million years ago and ended at the time of their disappearance, about 65 million years ago. The Mesozoic era is divided into the Triassic, Jurassic, and Cretaceous periods, which together lasted about 185 million years and can be thought of as the age of dinosaurs.

When I was first given the task of teaching comparative respiratory physiology to pulmonary fellows in the late 1970s, that field had essentially no overlap with paleontology. This was understandable, given that the latter was based on the study of the fossil record while the former relied on investigation of living animal species in the laboratory. A PubMed search for the word "dinosaur" retrieved only 11 citations to publications between 1965 and 1980, and only 1 when "dinosaur" and "physiology" were combined (Table 1). Somewhat more articles appeared during the 1980s, and more still during the 1990s. However, interest in dinosaur physiology among paleontologists and physiologists has mushroomed during the present decade, and PubMed returned 213 citations with the 2 search terms "dinosaurs" and "physiology" for the years 2000 through 2008. Table 1 gives only a partial view of the increased scientific activity in this interdisciplinary field; during the present decade, hundreds of other relevant articles have been published in paleontology, zoology, and earth-sciences journals, and other sources not included in *Index Medicus*.

While our knowledge of dinosaurs a half-century ago was based on the fossil record—primarily dinosaur bones—
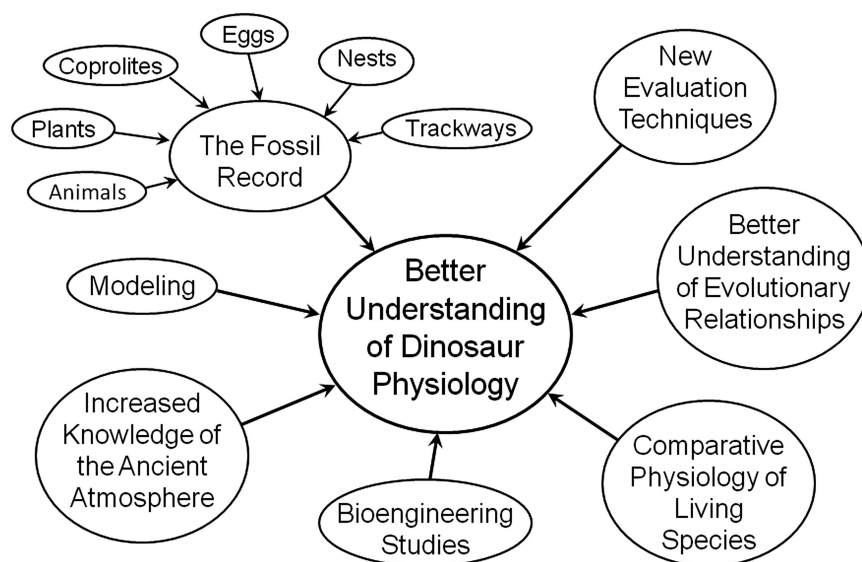
Fig. 3. Sources of present-day knowledge about dinosaurs.

today the study of dinosaur physiology draws on many more information sources (Fig. 3). The fossil record is now much larger, thanks to new and better dinosaur discoveries on every continent, and to greatly expanded capabilities for studying them. Dinosaur fossils now include not only bones and teeth but also skin (and skin appendages, such as feathers) and perhaps even DNA[15] and soft tissues[16]—although these last two are controversial. The fossil record has yielded information not only about the dinosaurs themselves, but also about the plants they ate and other aspects of their environment.[17-21] The study of coprolites (fossilized feces) has generated an abundance of data about dinosaur diets and feeding habits.[19,22] Fossilized dinosaur eggs, some of them with embryos,[23-25] and well-preserved dinosaur nesting grounds[26,27] have greatly expanded our understanding of their reproduction and behavior.

Preserved footprints left in soft mud or clay as dinosaurs went about their daily lives, while not fossils in the usual sense, can provide information unavailable from the other sources described, and their study has become a whole subspecialty within dinosaur paleontology.[28-32] Some trackways contain thousands of individual footprints made by dozens or even hundreds of individuals. From such sources can be derived insights not only into the dimensions and biomechanics of the animals that made them, but also about aspects of their lifestyles and behavior. For example, some trackways contain the footprints of large groups of herbivorous dinosaurs moving together across the landscape—and in a few cases also those of predators apparently stalking them.

Another area in which great advances have led to increased understanding of dinosaurs in general and also of their physiology is the study of evolutionary relationships

among different groups of animals.[33-36] Several technical terms apply to this area, and not everyone working in the relevant fields agrees on how these should be used. *Phylogeny* refers to the evolution of genetically related groups of organisms, as distinguished from *ontogeny*, which is the development of the individual organism. *Systematics* is the scientific study of the diversity of organisms within and among genetically related groups, or *clades*. The related term *taxonomy* refers to the scientific practice and study of naming and ordering like groups of organisms. Systematics thus deals with understanding the relationships among different animal groups, and taxonomy deals with labeling them. Unfortunately, several approaches to the classification, description, and naming of individual species and groups of organisms are currently used, and this can make reading the relevant literature confusing. The approach used by most vertebrate paleontologists today is called *phylogenetic systematics*, or *cladistics*, which emphasizes the recency of common ancestry and the relationships among different clades. A *cladogram* is a graphical representation of the evolutionary relationships among groups of organisms. Figure 4 is a cladogram of our current understanding of the evolutionary relationships of dinosaurs, as constructed by Sereno.[37]

As technology has advanced in other areas of science and engineering, the application of emerging techniques to the study of dinosaurs has yielded important information about both recently discovered fossils and specimens already in museum collections. Paleontologists still do field work, and still spend time meticulously studying and describing specimens. However, they also rely heavily on mathematical and computer techniques, phylogenetics (the study of the relationships among organisms), taphonomy (the study of the process of fossilization),[38] paleoecol-
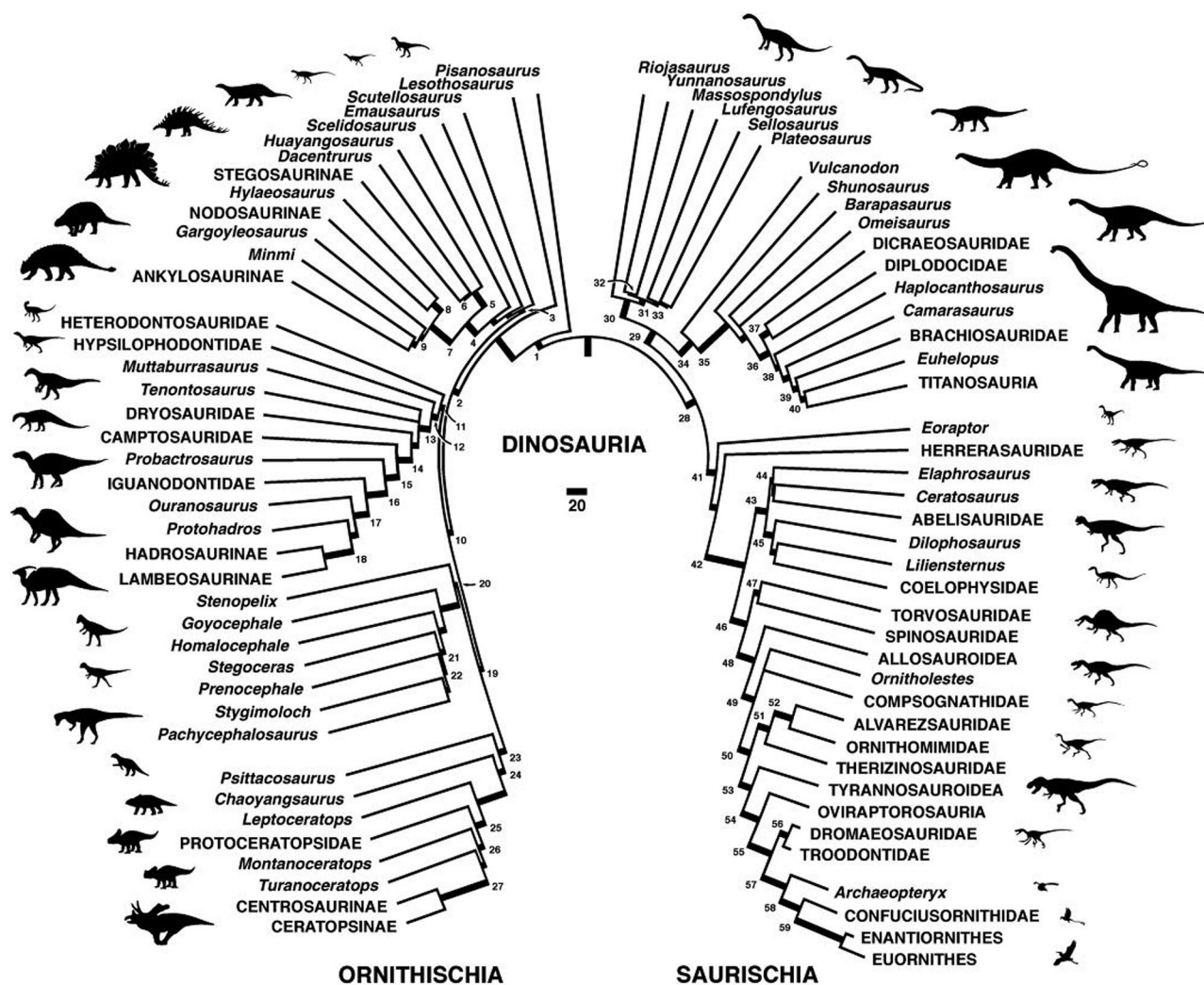
Fig. 4. Phylogeny (evolutionary development and history) of the Dinosauria, as depicted in a cladogram (hierarchical classification of species based on evolutionary ancestry) by Sereno.[37] The names of individual genera are italicized, and those of larger groups such as families are shown in upper case. The 2 dinosaur orders, Ornithischia and Saurischia, are shown on the left and right sides of the cladogram, respectively. Within the Saurischia, the suborder Sauropoda, which includes the largest dinosaurs, such as *Brachiosaurus*, is shown in the upper right, and the suborder Theropoda, which includes *Tyrannosaurus* and the direct ancestors of modern birds, is shown on the lower right. The numbers represent individual evolutionary branch points or nodes, as discussed in more detail by Sereno. (From Reference 37, with permission.)

ogy,[20] and many other techniques unavailable to the early dinosaur hunters.[39] Technologies familiar in health care, such as computed tomography and magnetic resonance imaging, have yielded important information about such previously inaccessible areas as the internal structures of fossilized animal bodies[40] and the contents of dinosaur eggs.[24] Increasingly sophisticated modeling techniques are being applied to the biomechanics and physiologic capabilities of the dinosaurs.[41-47]

As mentioned earlier, historically, comparative physiologists had little to do with the study of dinosaurs. However, this has changed in the last 20 years. During this time, numerous investigators have sought insight into the physiology and behavior of dinosaurs by comparison with

living species,[48-56] especially with respect to respiration in birds.[53-56]

Current concepts of dinosaur physiology have also been influenced by an increased understanding of the history of the earth's atmosphere, particularly with respect to the concentration of oxygen (O_2) in the air over geologic time. The atmosphere has not always had an O_2 concentration of 21% (160 mm Hg at sea level). Evidence of long-term change in the atmosphere's O_2 concentration has come mainly from the study of rocks, particularly as they reveal the geochemical cycles of carbon and sulfur during the last 550 million years.[57-59] Weathering of organic carbon and pyrite sulfur results in net O_2 consumption, whereas burial of organic carbon and pyrite sulfur in sediment (which

indicates an excess of global photosynthesis over global respiration) results in net O_2 production.[59] Several computer models have been developed for estimating atmospheric O_2 (and CO_2) at different times in earth's geologic history. These models employ different factors, such as the amount of reduced carbon and sulfur in sediment samples, the ratio of the carbon isotopes ^{13}C and ^{12}C, and the ratio of the sulfur isotopes ^{34}S and ^{32}S in rock samples.[58,60,61]

While the different models yield different estimates for O_2 and CO_2 concentrations during the last 200 million years, there is agreement that atmospheric O_2 has varied substantially during the Phanerozoic eon, with a maximum of 30–35% about 300 million years ago. Estimates of the nadir atmospheric O_2 concentration, approximately 200 million years ago, range from 10%[62,63] to 15%.[58,60] Later in this paper I will discuss how the much lower atmospheric O_2 concentration at the beginning of the age of dinosaurs may have influenced the evolution of their respiratory systems.

Circulation: How Could the Tallest Dinosaurs Have Perfused Their Brains?

The dinosaurs that raise the most fascinating questions with respect to circulatory physiology are the sauropods[64-66] (Fig. 4, upper-right quadrant), because this group includes the largest creatures ever to have lived on land.[67] Although there has been increasing evidence that the cardiovascular and respiratory systems of the sauropods and the theropods (Fig. 4, lower-right quadrant) were very similar, this discussion will concentrate on the sauropods, simply because of the hemodynamic implications of their enormous size and the fact that most of the existing data and published speculation relate to the sauropods.

Just how big some of the sauropods were is dramatically evident to anyone who has passed through Concourse B of the United Airlines terminal at Chicago's O'Hare Airport, where the Field Museum's renowned *Brachiosaurus* skeleton stands amid the throng of human travelers (Fig. 5). Stopping for a moment beneath the thorax of this monster, a traveler familiar with the blood pressures and other aspects of circulatory dynamics encountered in clinical medicine might well wonder how it could have been possible for this creature to pump blood all the way up to a head nearly 40 feet above the floor—and, if so, what the pressures involved would have to have been. These questions have intrigued both paleontologists and physiologists in recent decades, and, despite the impossibility of direct measurements, a number of lines of evidence (or at least reasoning) have been offered in the literature.

Systemic Blood Pressures in the Largest Sauropods

Of the 121 known sauropod species,[68] most were much bigger than terrestrial mammals, and at least a dozen were

Fig. 5. The *Brachiosaurus* in Concourse B. In 2000, after Chicago's Field Museum acquired "Sue," the largest *Tyrannosaurus rex* specimen yet discovered, its famous *Brachiosaurus* (actually a model made from casts of the actual bones) was moved to United Airlines Terminal 1 at O'Hare Airport. There, thousands of passengers each week can gain a first-hand appreciation of just how enormous a creature it was.

truly enormous—an order of magnitude larger than the ornithischian dinosaurs and any land mammal that ever lived.[68] Familiar species, such as the slender *Diplodocus* and stockier *Apatosaurus* ("Brontosaurus"), known from multiple well-studied specimens and thus of the most confidently known size, were 22–25 m (74–82 ft) in length, and *Brachiosaurus* stood as tall as 13 m (43 ft).[41,65] Although they are known only from very incomplete skeletons, several other, more recently described sauropod species can confidently be said to have been substantially larger, although precisely how large cannot be known until more complete specimens are found. *Supersaurus*, *Seismosaurus*, and *Amphicoelias*, all from the same fossil beds in the western United States, were similar to *Diplodocus* but larger, and may have reached lengths of 40 m (132 ft) and heights of 17 m (56 ft).[65,67] Another species, *Paralititan*, discovered more recently in Egypt, was a giant in the same size range.[69] Although body weights cannot be determined as precisely as lengths, the current estimates are that these largest sauropods weighed as much as 50–80 tons[67,70]—and perhaps even more in the case of *Argentinosaurus*, a member of the recently discovered Titanosauria from South America.[70]

By simple proportionality, the systemic arterial blood pressures in the tallest sauropods would have to have been several-fold greater than that of the giraffe, the tallest living mammal—at least if they stood erect, perfused their brains continuously, and had circulatory systems similar to those of living vertebrates (Table 2). Blood pressures in the giraffe have been measured in several studies,[71,72] and

Table 2. Hypothetical Arterial Blood Pressures in the Giant Sauropods, Based on Measured Blood Pressures in Living Mammals*

Species	Height of Head Above Heart (m)	Arterial Blood Pressure (mm Hg)
Human	0.5	120
Giraffe	2.8	280
Brachiosaurus	8.3	680
Largest sauropods	~12.6	~1,000

* The estimated pressures for the sauropods are based on their height and assume a perfusion pressure entering the head of about 70 mm Hg. The heights of the largest sauropods (see text) are speculative, given that complete skeletons have not yet been found.

a systolic pressure in the carotid artery of 260–300 mm Hg has been taken as representative. Calculated blood pressures for the tallest sauropods, based on the height of the presumed column of blood that would have to be pumped to the brain, approach 1,000 mm Hg, a value that begs credibility in terms of the strength and pressure-generating capabilities of known animal tissues. Putting aside the largest giants, whose height is admittedly speculative, pressures in the well-studied *Brachiosaurus*, in which a standing height of at least 12 m is accepted, the pressures involved—well over 600 mm Hg[73]—are so much greater than any ever measured in living animals as to make one wonder whether a circulatory system like that of the giraffe would have been possible in such animals.

Discussions of the potential magnitude of sauropod blood pressure spilled over into the clinical literature soon after the American Museum of Natural History installed a new exhibit in its main atrium in 1991. This exhibit contains the mounted skeleton of an adult *Barosaurus* (a slender sauropod similar to *Diplodocus*), rearing up on hind legs to protect her calf from a menacing *Allosaurus*, a theropod predator related to *Tyrannosaurus*. The head of the adult *Barosaurus* in this dramatic display is 12 m above its thorax, prompting Choy and Altman at the investigative cardiology laboratory at St Luke's Roosevelt Hospital in New York to question the feasibility of the blood pressures that would have been required with a conventional mammalian-type cardiovascular system.[74] They estimated that *Barosaurus* would have had an arterial blood pressure of 880 mm Hg leaving the heart, and that its heart rate would have had to be very slow, which would mandate a series of one-way valves in its carotid arteries to prevent blood from falling back into the chest between contractions. In association with these valves, Choy and Altman further proposed that *Barosaurus* may have had several localized concentrations of muscular tissue—essentially a series of auxiliary hearts—to pump the blood up to the head (Fig. 6).[74] Each "heart" in this series, located 2.44 m below the one above, would therefore have to generate a pressure
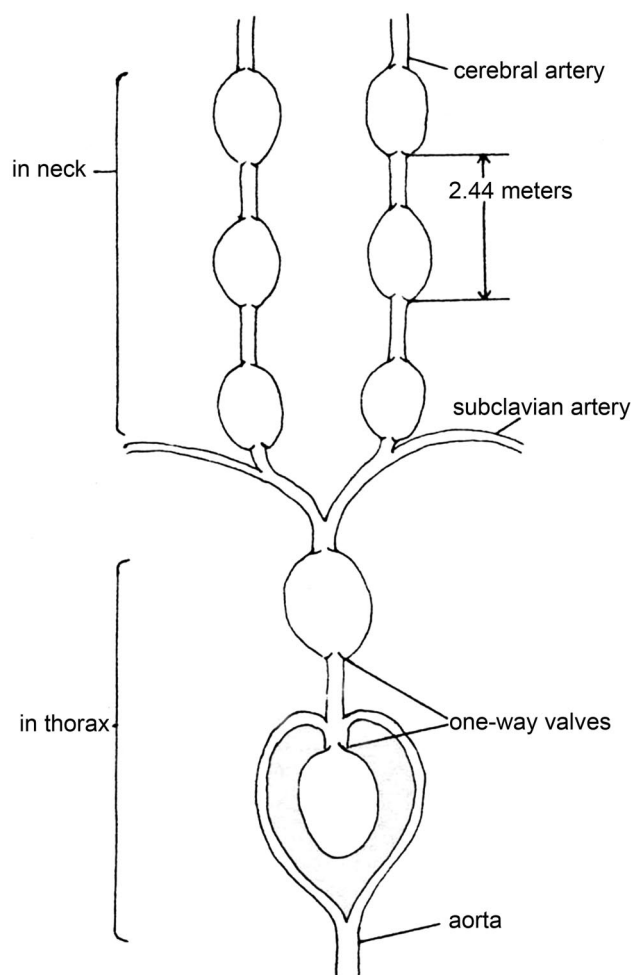

Fig. 6. System of "auxiliary pumping stations" postulated for the circulatory system of *Barosaurus* by Choy and Altman in 1992. (From Reference 74, with permission.)

of only 200–250 mm Hg. Bakker[75] had previously speculated that the long-necked sauropods might have used cervical muscular contractions of some sort to augment circulation to their heads, but the construct of Choy and Altman was unique in suggesting that the augmentation was provided by the cardiovascular system itself.

Publication of Choy and Altman's multiple-hearts proposal in *The Lancet*[74] drew attention from the comparative-physiology community and was shortly followed by 5 letters to the editor.[76-80] These mostly disparaged the idea, and more than one subtly questioned whether medical researchers should be venturing into speculations about dinosaurs. After first pointing out technical mistakes in Choy and Altman's argument (eg, based on height, the *Barosaurus* blood pressure would have been 740 mm Hg, not 880 mm Hg; and valves on both sides of each auxiliary heart would have been unnecessary), and noting that multiple cervical vascular pumps might cause discontinuous blood flow to the brain and predispose the animal to a

variety of injuries, Millard et al argued that because *Barosaurus* was most likely amphibious, its neck would have been supported by water most of the time.[76] This latter assertion had previously been made by others,[81] based on theoretical calculations of sauropod hemodynamics in the erect posture.

Choy and Altman speculated that *Barosaurus* would be subject to frequent fainting as it moved from the head-down to the head-up position.[74] Rewell[77] expressed doubt about this, pointing out that if a standing giraffe were to lose consciousness, it would probably sustain a spectacular cervical dislocation. In a letter published the following month, Dennis[78] supported the multiple-hearts hypothesis, and agreed with Rewell's observation about the unlikelihood of frequent syncope in sauropods. Dennis also calculated that, according to the law of Laplace (which says that the pressure generated by the heart is directly proportional to the ventricular-wall thickness), in order to generate 740 mm Hg (per Millard et al),[76] *Barosaurus* would have had to have a ventricular wall 90 cm thick and a heart weighing 7.3 tons[78]—which he considered highly unlikely. Taylor[79] took issue with Millard's proposal that *Barosaurus* was semi-aquatic, pointing out several structural features in favor of a terrestrial lifestyle and doubting that it could have breathed snorkel-fashion while submerged.

Hicks and Badeer wrote that multiple hearts would not have been necessary, because circulation in the neck of *Barosaurus* most likely functioned as a siphon.[80] These investigators noted that fluid flow in a siphon depends not on the height of the loop but on the relative levels of its 2 ends, as well as on overcoming the resistance of the system. Hicks and Badeer had previously published a study on circulation in the giraffe,[82] and subsequently elaborated on the siphon hypothesis as applied both to giraffe[83] and to *Barosaurus*.[84] However, Dennis[78] noted that the pressure at the top of a siphon tends to be sub-atmospheric, and argued that the net flow of blood out of the carotid artery and into the brain would be impossible under such circumstances, as was pointed out subsequently by others.[85]

Another way the sauropods might have avoided having to generate extremely high arterial pressure is not to have raised their heads much above the horizontal position. This possibility was mentioned in passing by Seymour in 1976,[81] and has since been explored by several investigators. In fact, many sauropods may not have been *capable* of raising their necks to the full vertical position. Stevens and Parrish[86] used an interactive software package to construct and manipulate detailed 3-dimensional digital models of *Diplodocus* and *Apatosaurus*, and attempted to reconstruct the limits of deflection attainable with each neck vertebra and hence the range of motion and likely posture assumed by these dinosaurs during life. They found that the necks of both genera were straight (horizontal) in the neutral position, and that neither had as much flexibility (particu-

larly for raising the head) as has been depicted in many reconstructions. These investigators concluded that the maximum feeding height for *Diplodocus* would have been about 4 m, barely above the level of its back; maximum dorsiflexion in *Apatosaurus* was somewhat greater, with an upper feeding height of approximately 6 m. Thus, "rather than flexing their necks like dinosaurian counterparts of giraffes or swans, [*Diplodocus* and *Apatosaurus*] appear to have fed more like giant, longer-necked bovids [such as cattle]."[86]

From other computer-modeling studies, those same investigators concluded that *Brachiosaurus* also held its head closer to horizontal than to vertical, and had a maximum browsing height similar to that of *Apatosaurus* (about 6 m).[43] Recent work with ostriches, which combined dissection of fresh neck specimens, experiments with neck vertebrae, photography of living birds, and computer modeling, supports the findings of Stevens and Parrish: studies that used fossilized neck vertebrae of *Diplodocus carnegii* and compared those data to data from ostriches indicated that the sauropod's neck positions of rest and maximum dorsiflexion were considerably more restricted than those of the ostrich.[52]

Perhaps, even if the sauropods were able to raise their heads to the heights assumed in Table 2, they did so only intermittently and did not perfuse their brains continuously as they did so. Given that a loss of cerebral blood flow during cardiac arrest in humans results in brain injury within a very few minutes, followed by death if it is not quickly restored, it seems counterintuitive to propose that animals as active as the giant sauropods could have survived with only intermittent perfusion to the head. However, recent evidence from several areas of investigation supports the concept that several vertebrate groups exhibit remarkable tolerance of brain hypoxia,[87-89] and it is possible that multiple adaptations protected the sauropod brain against anoxic injury.

Some turtles, amphibians, and fishes can survive in virtual anoxia for prolonged periods.[90,91] Certain seals and other diving mammals can withstand dramatically reduced brain-oxygen access for nearly an hour, while remaining active and engaging in complex behaviors.[92] The recently discovered oxygen-carrying molecules neuroglobin and cytoglobin, which appear to be widely distributed in vertebrates and of ancient origin, may play important roles in cerebral oxygen metabolism and hence in neuroprotection from anoxic injury.[93-95] Maybe sauropod brains were richly supplied with neuroglobin and also with metabolic protections against anoxia. Combined with microcirculatory adaptations, these protections enabled them to raise their heads high for periods long enough to scout their surroundings, fight, mate, and engage in other necessary activities despite reduced or even temporarily interrupted cerebral perfusion.

Table 3.   Proposed Mechanisms for Maintaining Perfusion to the Head in the Giant Sauropods

Mechanism	Rationale	Arguments For	Arguments Against
Circulatory function essentially the same as in mammals, with proportionally higher arterial blood pressure ($\geq$ 600 mm Hg)	By proportionality to known pressures in humans and giraffes, $\geq$ 600 mm Hg would be required to raise the blood to the required height and provide the required cerebral perfusion.	Consistent with well-studied mechanisms in living animals. Would not require any unique features not present in living vertebrates.	Are such pressures attainable, and could vascular tissues withstand them? By the law of Laplace, such pressures would require hearts much larger than those of any known vertebrates.
Multiple hearts in series in thoracic outlet and neck	Lower perfusion pressure required, and thus less ventricular-wall thickness	Pressures generated by individual pumps would be comparable to those in living mammals.	No known precedent in vertebrates. Multiple theoretical objections.
Siphon	Lower required pressures, and thus less ventricular mass	Closed system, requiring that ventricle overcome only vascular resistance, not the weight of the entire column of blood.	Pressure in closed siphon system tends to be negative at highest point, preventing brain perfusion. Collapsibility of veins.
Neck and head maintained in more horizontal position	Less vertical distance to be overcome to perfuse brain. Requires less pressure and less ventricular mass.	Supported by anatomical and computer modeling studies of living animals, and by studies of sauropod skeletons.	Sauropods would have been unable to browse highest vegetation or raise head for other activities.
Head raised to maximum height only intermittently and briefly. No perfusion to head when neck held fully erect.	Ability to function for short periods without cerebral perfusion would require less pressure and less ventricular mass.	Tolerance of periods of anoxia by diving mammals, turtles, and other vertebrates. Recent discovery of multiple mechanisms of anoxia-tolerance in vertebrates.	Falls due to loss of consciousness would probably be catastrophic. Ability to browse treetops would be constrained.

Table 3 summarizes the pros and cons of the various proposed mechanisms of circulation in the giant sauropods.

Warm-Blooded, Cold-Blooded, or Both?

Historically, dinosaurs were imagined as much larger versions of present-day reptiles: cold-blooded and sluggish. Although it had been postulated earlier, the notion that they may have been warm-blooded, and thus much more active than originally believed, became widely discussed following publication of a paper in *Nature* by Bakker in 1972.[96] Bakker provided several kinds of evidence to support this hypothesis. As demonstrated by their footprints, dinosaurs walked with fully-erect gaits and a narrow trackway, like modern mammals but unlike living reptiles. Dinosaurs had joint anatomy more like mammals than reptiles, and were probably capable of running much faster than was originally assumed. Certain aspects of dinosaur bone histology resemble those of mammals more than those of living reptiles. In addition, in several large assemblages of fossil dinosaurs of multiple species preserved together, the relative prevalence of carnivores in relation to herbivores (the predator-to-prey ratio, which is an indicator of the metabolic needs of the carnivores), is closer to that of mammals such as tigers than to their present-day reptilian counterparts such as crocodiles or Komodo dragons. Studies on the geographic distribution of dinosaurs indicate that they lived in temperate climates, and even sub-polar regions, where relying on external heat sources would seem infeasible.

The question of whether the giant sauropods were warm-blooded or cold-blooded has important implications with respect to their cardiovascular systems. Seymour and Lillywhite[85] revisited the issue of sauropod blood pressures in relation to how big their hearts must have been. They considered *Barosaurus* and assumed a blood pressure of 700 mm Hg, based on the length of its neck. They compared the known cardiac dimensions and hemodynamics of the fin whale, a warm-blooded mammal with a mass of 40 tons, to those projected for a *Barosaurus* of the same weight, assuming that its metabolism was similar to that of the whale. Table 4 summarizes that comparison,[85] which indicates that the sauropod would have to have had a heart 15 times heavier than a whale of the same body mass. Noting that the calculated dimensions of the *Barosaurus* heart were proportionally far greater than those of any living warm-blooded animals, the authors concluded that warm-bloodedness, as demonstrated by typical mammals, was most unlikely in *Barosaurus* (Fig. 7).[85] Instead they proposed that *Barosaurus* had an intermediate metabolic rate, less than that of typical warm-blooded animals, which would require substantially less cardiac muscle mass to sustain the same arterial blood pressure.

Table 4.   Cardiac Dimensions and Hemodynamics in Fin Whale Versus *Barosaurus*

Variable	Fin Whale	*Barosaurus*
Mass of animal (tons)	40	40
Systemic arterial blood pressure (mm Hg)	100	700
Mass of heart as a proportion of total body mass (%)	0.5	5
Mass of left ventricle (kg)	135	2,000
Internal diameter of ventricular chamber in diastole (cm)	52	52
Left-ventricular-wall thickness (cm)	10.4	52
Proportion of resting energy expenditure accounted for by heart (%)	10	62

(Data from Reference 85.)

Warm-bloodedness and cold-bloodedness are easy concepts to comprehend when using familiar examples: my cat generates her own body heat, is continuously active, and maintains a constant body temperature of 38.5°C, whereas my pet tortoise is dependent on the temperature of the room, may be inactive for hours or days at a time, and feels cold to my touch. However, the situation with respect to the metabolic rates and body temperatures of animals is actually far more complex than this. The tuna, a fish and thus presumably "cold-blooded," is actually "warm-blooded," with a core body temperature substantially above that of the water it inhabits.[97] The situation with respect to metabolism and thermoregulation is particularly complicated as it pertains to the largest dinosaurs.

Rather than the single oversimplified construct of "warm-blooded" versus "cold-blooded," 3 different sets of terms are used to describe animals' metabolic state and temperature regulation[98]:

1. Whether they can maintain a steady body temperature irrespective of temperature variations in their environment: they are said to be *homoiothermic* if they can, and *poikilothermic* if they cannot.

2. Whether they maintain their optimum activity temperature by means of internally generated heat: *endothermic* if they do, and *ectothermic* if they do not.

3. Whether their internal body metabolism operates at a high or low rate: *tachymetabolic* if it is high, *bradymetabolic* if low.

These 3 aspects of body-temperature regulation may appear to vary independently in certain circumstances. For example, hummingbirds, extremely active endotherms with daytime body temperatures of nearly 41°C, undergo a substantial fall in body temperature at night, to conserve energy, whereas the largest crocodiles, which are ectothermic and generally bradymetabolic, maintain essentially constant body temperatures (that is, are virtually homoio-

thermic) because of the thermal inertia of their large body mass.[99]

Given their adult size, the largest sauropods must have grown at phenomenal rates. Their eggs were relatively small,[23] and to reach an adult weight of 80 tons a 10-kg hatchling would have to increase its mass by nearly 5 orders of magnitude.[67] Indeed, it has been estimated that *Apatosaurus* attained its adult weight of about 25,000 kg in as little as 15 years, with a maximum growth rate > 5,000 kg/y.[100] Sauropods grew at least as fast as any mammal—a conclusion that is supported by histologic studies of their bones, which revealed mammalian-type growth patterns.[98,101,102] Endothermy and tachymetabolism would be highly advantageous—if not a requirement—for such rapid growth.

However, the same endothermy and tachymetabolism that facilitated rapid growth in young sauropods would have posed major problems once they reached adulthood.[56,67] The concept of thermal inertia—the propensity of larger animals to retain heat, in comparison to smaller animals—has led some authors to discount the possibility of endothermy for the giant sauropods. On the basis of allometric calculations, given their need to dissipate heat generated by physical activity, Gillooly et al[103] predicted that sauropods that weighed 50 tons would be at the upper limit of body temperature compatible with life. Because of these considerations the concept has been put forth that the giant sauropods did not maintain a single metabolic rate throughout their lives, but instead were endothermic and tachymetabolic when they were young and growing rapidly, and then slowed their metabolic rate as they approached adult size.[56] This strategy would be compatible with the intermediate metabolism proposed by Seymour and Lillywhite for the adult *Barosaurus*[85] (Fig. 7), and would imply lower food requirements as well as the ability to avoid lethal hyperthermia in the largest sauropods.[56,67]

Structure of the Dinosaur Heart

Whether the giant sauropods were endothermic or ectothermic, and whether their systemic arterial blood pressure was 700 mm Hg or 200 mm Hg, one conclusion about their cardiovascular systems seems inescapable: they had to have had 4-chambered hearts. Reptiles such as lizards and snakes have 3-chambered hearts, with 2 atria and a single ventricle (Fig. 8a).[4] With one ventricle pumping blood into both the systemic and pulmonary circuits, the pressures in these 2 circuits cannot be very different. As a result, in order for the pulmonary circulation to facilitate efficient gas exchange through thin-walled capillaries, the pressure has to be kept low. Generating systemic pressure sufficient to deliver blood to a head held very much higher than the heart would also subject the pulmonary circulation to a pressure incompatible with its function—even if,
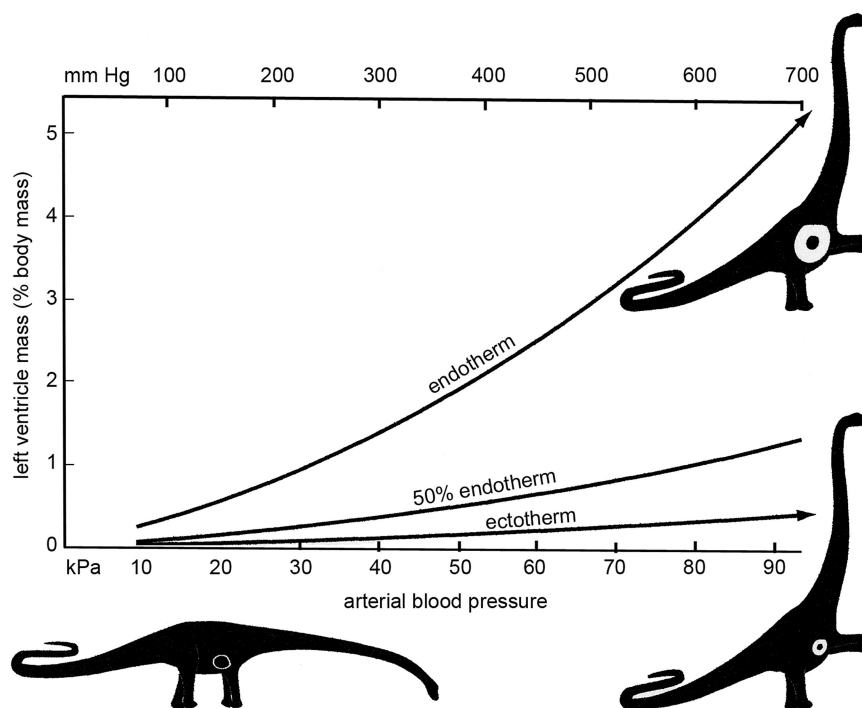
Fig. 7. Relationships between systemic arterial blood pressure (horizontal axes) and left-ventricular mass (vertical axis), determined according to the law of Laplace, for 3 possible scenarios with respect to sauropod metabolic rate and body temperature. Scaled diagrams of left-ventricular wall thickness are superimposed on *Barosaurus* silhouettes, according to models for low-pressure ectotherms (bottom left), high-pressure endotherms (top right), and an intermediate situation, as postulated by Seymour and Lillywhite. (From Reference 85, with permission.)

as in birds, the pulmonary capillaries were stronger and better supported than those of mammals.[104] However, the 4-chambered hearts of birds and mammals (Fig. 8b)[4] not only facilitate more efficient oxygenation of the blood, via elimination of the right-to-left shunt, but also permit the coexistence of a high-pressure systemic circulation with a low-pressure pulmonary circulation. Another difference between living animals with 3-chambered versus 4-chambered hearts is that the former have 2 systemic aortas, whereas the latter have only one.

That a double-pump, 4-chambered heart would have been a necessity in large dinosaurs has been pointed out by a number of authors over the years.[105-107] However, no empirical evidence was at hand, given the unlikelihood of preservation of soft internal organs in the fossil record. This situation was altered in 2000, with the publication of what was apparently anatomic documentation of a 4-chambered dinosaur heart.[108] Examination of a concretion within the uncrushed thorax of a late-Cretaceous ornithischian dinosaur, using computed tomography scanning, revealed what appeared to be a heart with 2 ventricular cavities and a single systemic aorta. The predicted design for the dinosaurian heart thus appeared to have been confirmed. However, that the reported structures actually represented a dinosaur heart was subsequently challenged, in this instance on both anatomic and geologic grounds.[40]

As with most other things in comparative physiology, the distinction between 3-chambered and 4-chambered hearts is not quite so straightforward as Figure 8 implies. Some reptiles have functional modifications that at least partially separate the systemic and pulmonary circulations, which permits a higher than expected systemic blood pressure.[42] However, regardless of the validity of the features claimed for the specific fossil in question,[108] the presence of many other avian features in dinosaurs, along with the inescapable hemodynamic challenges presented by the largest sauropods, would seem to guarantee that they had true 4-chambered hearts.

Summary: Circulation

Although no live specimens are available for direct examination, evidence from the fossil record and inference from studies on living animals leads to several conclusions about circulatory function in dinosaurs, and especially in the giant sauropods:

• Their systemic blood pressure had to have been substantially higher than in living reptiles, and potentially higher than in any known creatures: 600 mm Hg and higher if
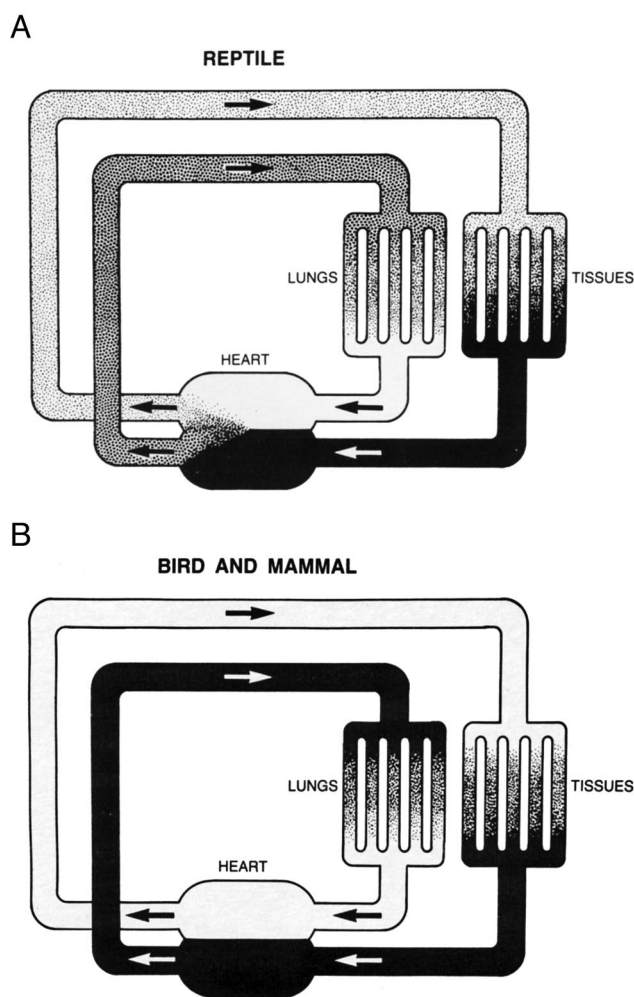
A

B

Fig. 8. Comparison of circulatory patterns with 3-chambered and 4-chambered hearts. A: In reptiles, such as lizards and snakes, the systemic and pulmonary circuits are incompletely separated. Oxygenated and deoxygenated blood are indicated by white and black, respectively, and the gray shades indicate proportions of right-to-left shunt. More importantly with respect to dinosaur blood pressures, the lack of separation of the systemic and pulmonary circuits also means that the pressures in both must be roughly the same. B: In birds and mammals the 4-chambered heart permits complete separation of the systemic and pulmonary circuits, which eliminates the right-to-left shunt and permits the pressures in those circuits to be markedly different. (From Reference 4.)

they held their necks erect and perfused their heads in that position.

- Proposed alternative pumping arrangements, such as multiple auxiliary cervical hearts, would require less extreme blood pressure but are without known precedent.

- That the circulation in their necks may have operated as a siphon, which also necessitates the generation of lower blood pressure, is conceivable but doubtful because of

the probable existence of negative intravascular pressure in the head.

- The enormous and probably unrealistic ventricular mass necessary to generate the predicted blood pressure would be much reduced if the sauropods were not "warm-blooded" in the conventional sense, but instead had lower metabolic rates when they were adults. This hypothesis is supported by bone histology and thermoregulatory evidence.

- They may not have held their necks erect, like giraffes, or only intermittently if they did so, and may have had adaptations that protected against anoxic injury during periods of reduced or absent cerebral perfusion.

- Their systemic and pulmonary circulations must have been separate, which mandates a double-pump, 4-chambered heart.

Respiration: How Could They Have Breathed Through Such Long Necks?

In addition to challenging our understanding of circulatory physiology, the huge size and especially the very long necks of the giant sauropods prompt the question, how did they breathe? Their long necks pose the most obvious challenge, with their inherent implications for airway resistance and dead space. But before discussing those factors it is necessary to take a brief detour and consider whether the sauropods could breathe underwater, snorkel-fashion, as was contended for many years.

Snorkel Breathing

When the first fossilized sauropod skeletons were discovered and attempts were made to reconstruct the animals that had left them, they were imagined as oversized versions of lizards and crocodiles: low to the ground, sluggish, and almost too heavy to move about.[68,107,109,110] They were commonly depicted partially or completely immersed in a swamp or lake, where the water would help to support their enormous bodies, and were assumed to have breathed snorkel-style, by raising their heads to the surface. This is the image of "Brontosaurus" (*Apatosaurus*) that I remember from books, magazines, and museum dioramas when I was a child in the 1950s.[111]

But they could not have breathed that way. Quite apart from the wealth of evidence that the sauropods were terrestrial animals,[17,64-66] some basic physical considerations quickly demonstrate that it would not have been physically possible (Fig. 9).[79,107,112,113] If a sauropod such as *Barosaurus* stood under water and extended its neck to the surface to breathe, the vertical distance from mouth to lungs might be 10 m. The pressure exerted by water at a
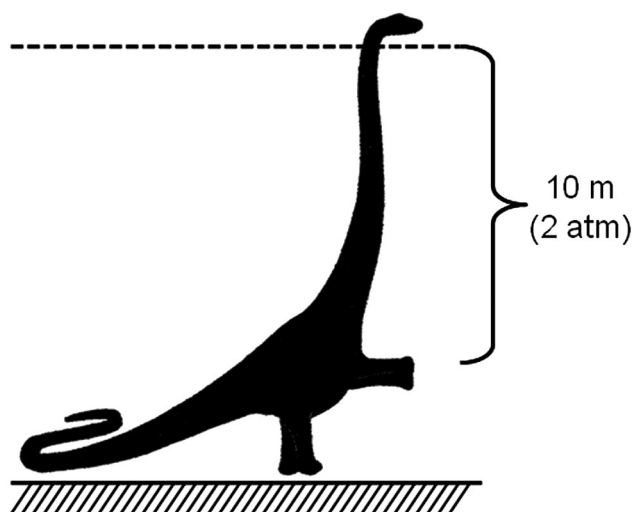
Fig. 9. Why sauropods could not have breathed snorkel-fashion while submerged. With the airway open to the atmosphere, lungs enclosed in a body 10 m below the surface of the water would be subjected to 2 atmospheres of external pressure, which would far exceed the pressure that could be generated by the respiratory muscles. More importantly, when the sauropod opened its airways to the outside air, the pressure difference between the pulmonary circulation and the air spaces in the lung would cause immediate rupture of the pulmonary vasculature and flooding of the lungs. (Adapted from Reference 85, with permission.)

depth of 10 m (2 atmospheres [1,520 mm Hg, or 2,068 cm H_2O]) is twice that at the water's surface (1 atmosphere [760 mm Hg; 1,034 cm H_2O]). Maximum inspiratory pressure in healthy adult humans is not much more than 100 cm H_2O,[114] and only a small proportion of that is normally needed, even with strenuous exertion. It is difficult to imagine a dinosaur generating inspiratory pressures 10 times that for prolonged periods.

Not only would the sauropod in Figure 9 have been unable to expand its chest to inhale, but once it attempted to do so, the pressure difference between the pulmonary capillaries and alveoli would result in immediate hemorrhage and airway flooding. Intravascular and airway pressures would increase in tandem as the external water pressure increased, so that the difference between them would remain unchanged, until the sauropod opened its mouth to breathe. At that point, though, the pressure in the airway would fall to atmospheric (zero, relative to the pressure at the water's surface) and expose the pulmonary circulation's thin gas-exchange membrane to a pressure drop far exceeding what it could withstand.

There is another reason the scenario depicted in Figure 9 could not work. As will be discussed, both the probable design of the sauropod respiratory system and accumulating evidence from sauropod bones indicate that sauropods were almost certainly lighter than water, not heavier.

Lessons From the Giraffe

One of the most intriguing questions about the giant sauropods is how they were able to breathe through such long necks. The necks—and presumably the tracheas—of some species were very long indeed. From a detailed examination of skeletons of the largest available sauropods, Wedel[115] provided the data shown in Table 5. Although some of the extreme neck lengths shown are highly speculative (and in the case of *Amphicoeleas*, based on a single neck vertebra that has since been lost), it is clear that these animals had necks (and tracheas) far longer than those of any living animal.

The problem with a very long trachea relates to the dual problems of airway resistance and dead space. Because resistance to air flow varies not only with the length of a tube but also inversely with the fourth power of its radius, small changes in airway caliber cause much larger changes in resistance and hence in the work of breathing. If its diameter were too small, airway resistance in the sauropod trachea would render breathing impossible. On the other hand, although a wider trachea would have much less airway resistance, its volume (which increases as a function of the square of the radius) and hence the anatomic dead space would increase such that the tidal volume required to maintain effective gas exchange would be prohibitive.

Insight into this problem can be gained from studies on the giraffe, the living animal with the longest neck. An adult male giraffe can reach a standing height of nearly 5.5 m (18 ft), and the trachea approaches 2.5 m (8 ft). Hugh-Jones and colleagues[116] made in vivo breathing measurements on a giraffe somewhat smaller than this from the London Zoo that required general anesthesia for an operation on its foot. The animal subsequently developed complications and had to be euthanized, so that the investigators were able to compare anatomic measurements with those they had made during life. The giraffe's in vivo respiratory rate was 8–10/min, with a tidal volume of 3.3 L and a dead-space fraction (ratio of dead space to tidal volume) of 0.30. At autopsy the trachea was 170 cm long and had an internal diameter of 3.8 cm and a dead space (calculated from the excised trachea) of 1.9 L.

Hugh-Jones et al compared the giraffe's minute ventilation to its weight, and to similar data from humans, as well as from the red deer, llama, and camel, and found that these had a constant relationship, which indicates that the giraffe's ventilatory demand and overall response were as expected.[116] However, when they compared the giraffe's tracheal dimensions to those of other large mammals (Fig. 10),[116] it was clear that the giraffe is an outlier; it has a longer, narrower trachea than the other species. These findings, along with their calculations that showed that the air flow during tidal breathing in the giraffe was such that

Table 5. Neck Lengths in the Giant Sauropods

Species	Number of Neck Vertebrae	Length of Neck (m)	Length of Neck (ft)
Diplodocus carnegii	15	6.1	20
Barosaurus lentus	16 (?)	8.5	28
Brachiosaurus brancai	13	8.5–9.6	28.0–31.5
Mamenchisaurus hochuanensis	19	9.5	31.2
*Sauroposeidon proteles**	Unknown	11.5*	37.7*
*Mamenchisaurus sinocanadorum**	Unknown	12*	39*
*Supersaurus vivianae**	Unknown	13.3–16.2*	43.6–52.2*
*Amphicoelias fragillimus**	Unknown	11.7–20.8*	38.4–68.2*

* No complete specimens have been found; these lengths are estimates/estimated ranges.
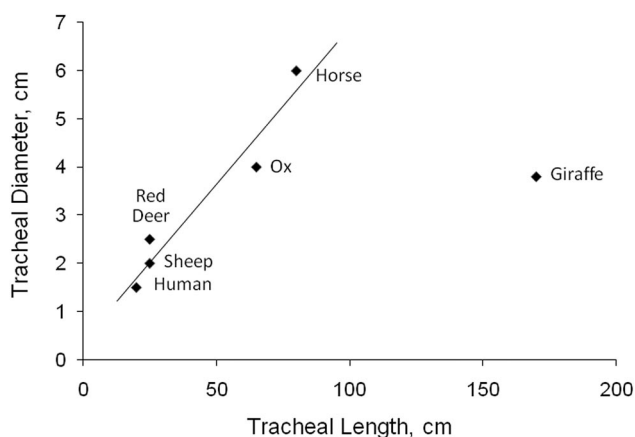(Data from Reference 115.)

Fig. 10. Length and diameter of the trachea of the giraffe in comparison with those of several other large mammals. (Data from Reference 116.)
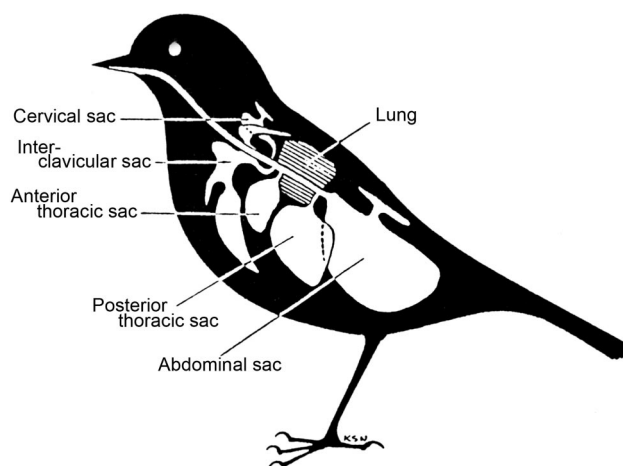

Fig. 11. General features of the avian respiratory system. The body of a bird is filled with a system of large, thin-walled air sacs that connect not only to the lungs but also to air spaces in the axial skeleton and hollow limb bones. The lung is small and dense and undergoes little volume change during respiration as the air passes through the lung unidirectionally from the air sacs. (From Reference 119, with permission.)

turbulence would be induced if it were increased even moderately, are consistent with field observations that giraffes are not capable of more than short bursts of strenuous exertion.

It is hard to imagine that an animal with tracheal proportions similar to those of the giraffe could survive with a trachea several times longer. Either the resistance or the dead space volume—or both—would seem unrealistic if the animal had mammalian-type tidal ventilation. Yet sauropods with extremely long necks not only existed but apparently flourished, which suggests that the very long trachea was not a barrier to evolutionary success. The search for a solution to this conundrum leads us to the birds, which evolved from dinosaurs and have a respiratory system very different from that of the giraffe—one in which a very large dead space is of little concern.

How Birds Breathe

Unlike mammals, birds have no diaphragm, and their respiratory organs are not confined to the thorax

(Fig. 11).[117-124] The respiratory apparatus includes a system of air sacs of various sizes, in the neck, thorax, and abdomen (Fig. 12).[125-127] These air sacs are connected to the lungs, and also to the bones of the axial skeleton and limbs, most of which are hollow and extensively invested by extensions of the air sacs. This latter phenomenon is called skeletal *pneumaticity*, and birds are the only living vertebrates in which it occurs caudal to the skull. Most birds have 9 air sacs: 1 interclavicular sac plus paired cervical, anterior thoracic, posterior thoracic, and abdominal sacs.[128] The air sacs are poorly vascularized and do not participate substantially in gas exchange.[129] The lungs themselves are relatively small, compact, and denser than their mammalian counterparts (Fig. 13).[119]

Instead of a branching bronchial tree into and out of which each breath must pass, the bird's lung consists of a richly vascularized system of parallel air tubes (parabron-
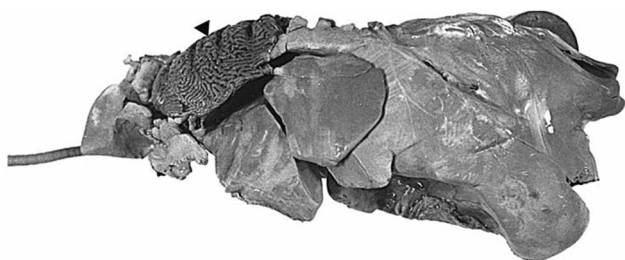
Fig. 12. Latex cast of the respiratory system of a chicken, with the air sacs fully inflated. The dense, highly vascular lung is indicated by the arrowhead. (From Reference 127, with permission.)
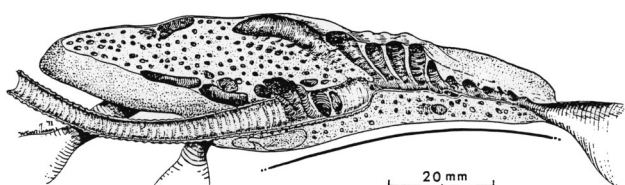

Fig. 13. Longitudinal section through one lung of a duck. The trachea is to the left, connections to an abdominal air sac are to the right, and connections to anterior thoracic and interclavicular air sacs are behind the trachea. The main bronchus (mesobronchus) to each lung connects to secondary bronchi (parabronchi) that extend into the lung tissue, but also passes through the lung to the posterior air sacs. (From Reference 119, with permission.)
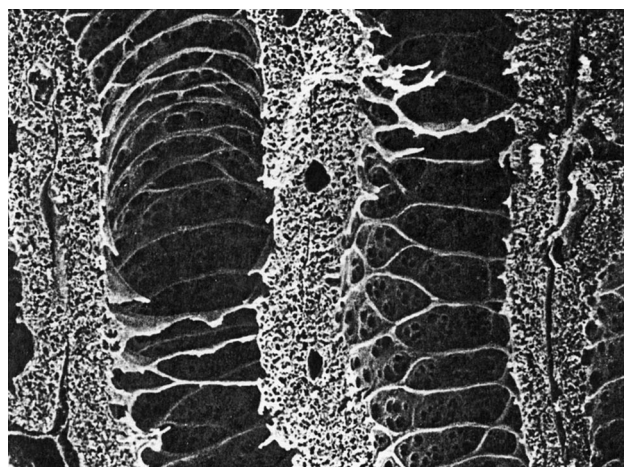

Fig. 14. Scanning electron micrograph of the lung of a duck. Instead of a tidally ventilated pool, with air entering and leaving the lung via the same conducting airways, the avian lung is more like a highly vascular sponge perforated by many parallel tubes (parabronchi), through which the air flows in one direction. (From Reference 122, with permission.)

chi), through which the air moves in one direction (Fig. 14).[122] Thus, birds breathe very differently from mammals, with a very different path for ventilation and the participation of air from more than one breath in both ventilation and gas exchange at any one moment.

Figure 15 shows conceptually how this system works.[118,119,130] Special adaptations of the skeleton and musculature permit substantial changes in the volume of the abdomen, anterior thorax, and neck, which ventilates the air sacs in those areas, while the thorax remains relatively rigid in the region near the spine overlying the lung. The lung thus changes very little in volume during the phases of respiration, and air passes through the lung between the bellows-like air sacs, in a caudal-to-cranial direction. Air movement through the various parts of the system during inspiration and expiration (see Fig. 15) is accomplished without the use of physical valves.[131,132] Instead, a fluidic mechanism (aerodynamic valving) determines the direction of air flow, in at least some instances by means of a structural adaptation in the bronchial wall known as the segmentum accelerans (or endobronchial tumescence), in association with branch points to the secondary bronchi.[55,127,133,134] As an aside, a similar fluidic valving mechanism has been applied clinically in respiratory care, in the design of the Monaghan 225 ventilator,[135] which found application in electricity-free and hyperbaric environments,[136] and was also used in the design of other less successful devices.[137,138]

The efficiency of gas exchange in the avian lung is augmented by cross-current ventilation-perfusion matching (Fig. 16),[103,121,122] which results in greater oxygen extraction than in the mammalian system. In fact, the cross-current ventilation-perfusion pattern allows the alveolar-arterial oxygen difference ($P_{(A-a)O_2}$, as calculated with the alveolar gas equation in humans) sometimes to be negative. This greater gas-exchange efficiency is illustrated in Figure 17,[119] which depicts ventilation and perfusion in a bird flying at an altitude of 6,100 m (20,000 feet). The design of the avian respiratory system (along with other adaptations)[139,140] means that birds can engage in physical activity unattainable by mammals and function normally at altitudes at which mammals could not survive.[141] One example is the semiannual migration of the bar-headed goose (*Anser indicus*), over the Himalayan mountains, to altitudes of ≥ 9,100 m (30,000 feet).[140,142] Another is the extreme feats of activity and endurance accomplished by migrating shore birds, such as the bar-tailed godwit (*Limosa lapponica baurei*). Flying is the most energetically costly form of locomotion,[143] but migrating bar-tailed godwits tracked with surgically implanted transmitters have recently been documented to fly non-stop as far as 11,680 km (7,242 mi) directly across the Pacific Ocean from Alaska to New Zealand, in flights of up to 9 days without rest, food, or water.[144]

Aspects of the structure of the gas-exchange interface, in addition to those inherent in flow-through ventilation and cross-current perfusion, probably help to explain the greater efficiency of avian lungs, compared to those of mammals. From the parallel parabronchi shown in Figure 14 there extend blind-ended terminal air spaces called
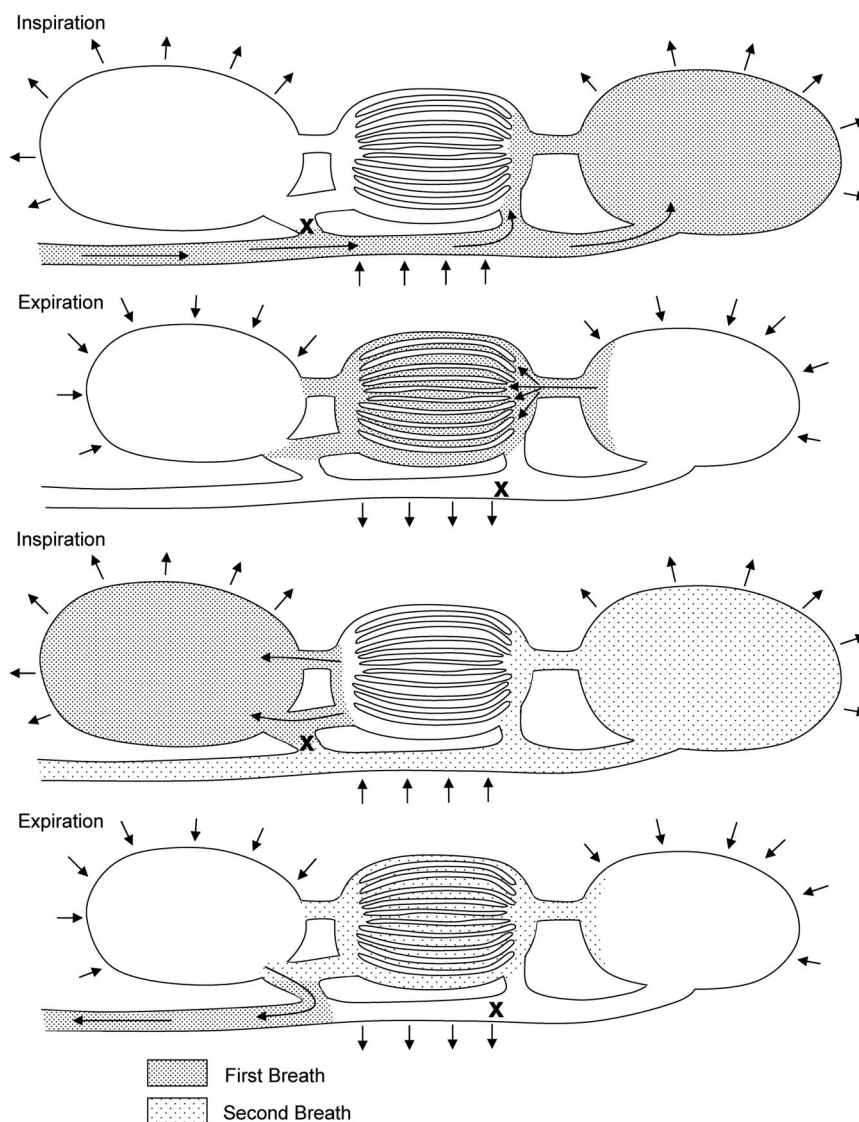
Fig. 15. Ventilation in the avian flow-through respiratory system. The far-right oval represents all the abdominal and posterior thoracic air sacs. The far-left oval represents all the anterior thoracic and cervical air sacs. From top to bottom, the diagram shows 2 complete breaths in sequence. Air passes through the trachea (lower left in each diagram), main bronchus (lower center), posterior air sacs (far right), lung (upper center), and anterior air sacs (upper left). The arrows around the air sacs indicate the pressure changes that cause air movement, and the arrows within the air spaces show the direction of air flow. The first breath initially passes through the trachea and main bronchus during inspiration, filling the posterior air sacs. Air entry into the anterior air sacs is prevented by fluidic valving (indicated by the X). During the first expiration the posterior air sacs are compressed, forcing the breath into and through the much less compressible lung, while passage back into the main bronchus is prevented by fluidic valving (X). With the next inspiration, "used" air from this first breath is drawn out of the lung and into the anterior air sacs. At the same time, the new, second breath is drawn into the posterior air sacs to repeat the sequence. With the second expiration and compression of the anterior air sacs, air from the first breath passes out through the trachea, while that from the second breath passes into and through the lung.

air capillaries, which have a thinner alveolar-capillary membrane[145] and are also smaller and more densely packed than mammalian alveoli.[146,147] Recent studies by West and colleagues on the lungs of chickens showed that changes in intravascular pressure have little effect on either pulmonary vascular resistance[148] or capillary diameter,[149] in contrast to their marked effects on these variables in mammalian lungs. These design features may help to optimize ventilation-perfusion matching in various activities and environmental conditions.

Implications of the Avian System With Respect to Tracheal Length

Many birds have long necks and thus long tracheas. However, in about 60 different bird species, representing a
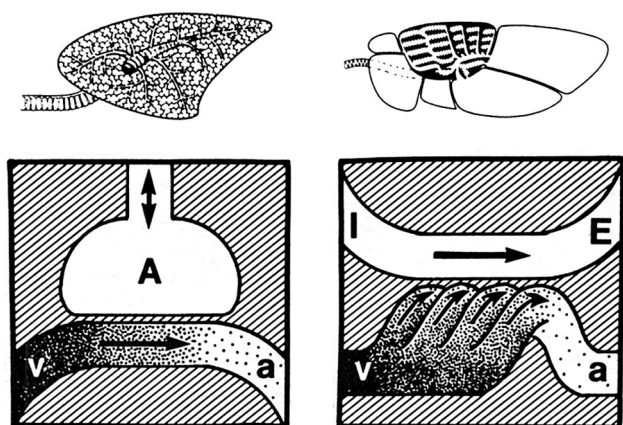
Fig. 16. Comparison of mammalian and avian lungs with respect to the matching of ventilation and perfusion. The upper diagrams depict the overall design of (left) the mammal's tidally-ventilated lung, and (right) the bird's flow-through system.[123] In the lower diagrams, deoxygenated venous blood (v) becomes oxygenated arterial blood (a) as it passes through the pulmonary capillaries.[104] In the mammal (left), ventilation partially renews a tidal pool of alveolar air (A), with which capillary blood equilibrates. About 21% of the oxygen that enters the pool is extracted. In the bird (right), inspired air (I) passes through the lung parenchyma and is exposed to a sequence of capillaries arranged in a cross-current fashion prior to leaving the lung as expired air (E). This oxygenates the blood more efficiently than in mammals, extracting 31% of the inspired oxygen in the case of the pigeon. (Upper diagrams from Reference 122; lower diagrams from Reference 4.)
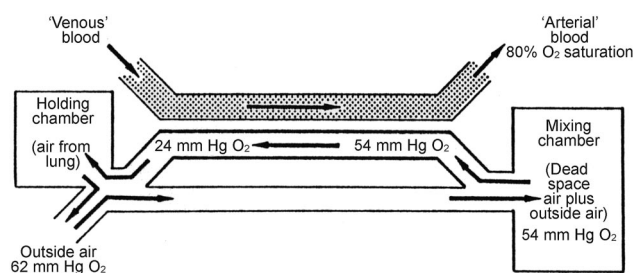

Fig. 17. Gas-exchange efficiency of the avian respiratory system, using the example of flight at 6,100 m (20,000 ft) elevation. The inspired P_{O_2} of 54 mm Hg in the posterior air sacs accounts for a partial pressure of water vapor at 39.4°C, a typical bird's body temperature. The cross-current ventilation-perfusion matching (not a strict counter-current arrangement, as shown here) results in an oxyhemoglobin saturation of 80%, which is substantially higher than could be achieved by the mammalian respiratory apparatus. (From Reference 119, with permission.)

variety of avian groups, the trachea is longer than the neck—sometimes very much longer.[150-152] In some species the trachea forms one or more loops or coils, which may be located low in the neck, cephalad to the sternum, in association with the furcula (wishbone), or especially in association with the keel of the sternum, either deep to it or subcutaneously. These tracheal elongations are gener-

ally confined to males, and in the few species in which they also occur in females they are much less pronounced than in the males.[150] Tracheal elongation is believed to develop after birth and in some species to continue with age, the trachea becoming longer and longer, extending and looping within the body.

Although it occurs in several species of swans,[150,152] exaggerated tracheal elongation is by no means confined to long-necked birds. For example, in one species of bird-of-paradise, a bird the size of a common flicker (which has a trachea 38 mm long), Clench[151] documented a total tracheal length of over 800 mm, which was almost as long as that of an ostrich.[153] Figure 18 illustrates some of the patterns and sizes of tracheal extensions and loops found in birds.[150]

The fact that tracheal elongations and loops occur in disparate groups of birds and take such varied forms suggests that these features have evolved multiple times and may have adaptive value. It has been proposed that the latter has to do with vocalization.[150,154] Birds that have elongated tracheas tend to have louder and lower-pitch voices than similar species that lack elongated tracheas, and this seems to be the case especially in species in which the loop lies next to the sternum.[150,154] From a series of acoustical experiments with cranes, Gaunt et al concluded that, "The tracheal coils that are embedded in the sternum serve a function analogous to the bridge of a stringed instrument, transmitting the vibrations of a tiny sound source to a large radiating surface, the sternum. The sternum then vibrates against the large internal air reservoir of the avian air sac system."[155]

Whatever their function may be, tracheal extensions and loops do not appear to interfere with ventilation or gas exchange in the birds that have them. More to the point, it is evidently no problem for the male of a particular species to have an anatomic dead space many times greater than the female of the same species.

The Sauropod Respiratory System: Current Concepts

The respiratory system of birds is unique, consisting of a set of large-volume, high-compliance posteriorly located air sacs used to force air through a low-volume, low-compliance, cross-current-perfused lung into other, more anteriorly located air sacs, resulting in nearly continuous lung ventilation and highly efficient gas exchange. Birds are also unique among living vertebrates in having extensive post-cranial skeletal pneumaticity, with extensive connections between the air-sac system and the air spaces within the bones. There is increasing evidence that this arrangement was present in the dinosaurs,[54,156,157] including the sauropods,[158-160] as well as other non-dinosaurian Mesozoic reptiles such as the flying pterosaurs.[161] Some
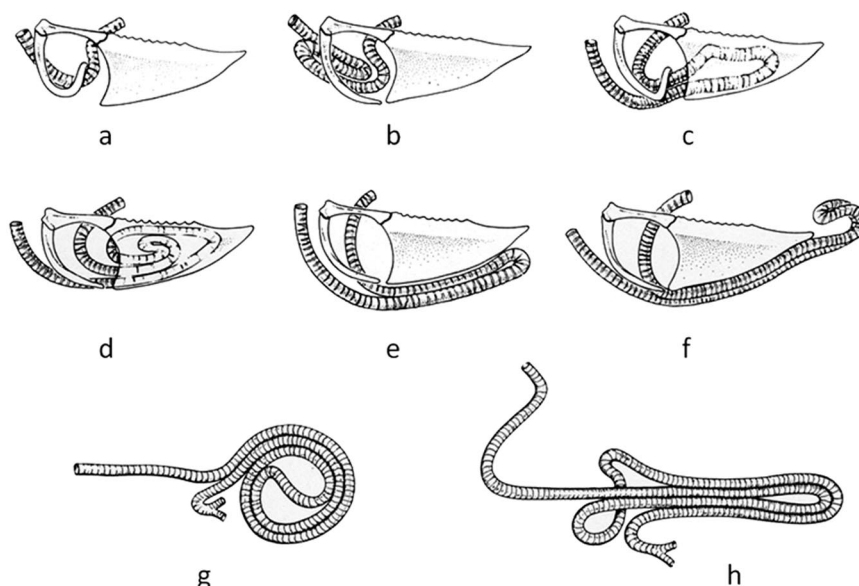
Fig. 18. Tracheal loops in various bird species. Diagrams A through F depict the furcula (wishbone), sternum, and tracheal anatomy of (a) black swan (*Cygnus atratus*), (b) white spoonbill (*Platalea leucorodia*), (c) whooper swan (*Cygnus cygnus*), (d) whooping crane (*Grus americana*), (e) a species of bird-of-paradise (*Manucodia*), and (f) helmeted curassow (*Crax pauxi*). More extreme examples of tracheal elongation include (g) the trumpet bird (*Phonygammus keraudrenii*) and (h) the magpie goose (*Anseranas semipalmata*). The additional tracheal length in the neck is not shown. (Adapted from Reference 150, with permission.)

authors have presented evidence to support the contention that dinosaurs had metabolisms and respiratory systems similar to those of crocodiles, with a tidally ventilated lung rather than the flow-through avian system,[162-166] but currently most investigators of dinosaur physiology reject that view,[167,168] particularly with respect to theropods and sauropods.

In the axial skeletons of both theropod and sauropod dinosaurs there was extensive replacement of vertebral bone with what appears to have been empty space. Evidence from isotopic and imaging studies indicates that this "empty space" represents pneumatization, just as in birds.[157,159,169-171] Figure 19 shows a cross-section through a cervical vertebra of *Camarasaurus*, a typical sauropod, and illustrates the relatively scant amount of solid bone it contains.[172] Figure 20 shows a similar vertebra from the neck of *Diplodocus*, seen in lateral view, as it appears grossly[46] and with the air-filled diverticulae added.[173] Although the pattern of bone elements differs considerably in the vertebrae of different sauropod species, much of the cervical skeleton consisted of air spaces. Wedel examined computed-tomography sections, photographs, and published images of transverse sections of the vertebrae of more than a dozen genera of sauropods and found a mean air-space proportion (the fraction of each vertebra that would have been filled with air) of 0.61 (61%), and that fraction exceeded 80% in several species.[115]

Reconstruction of the neck and thorax of *Diplodocus*, taking into consideration the air spaces indicated by the
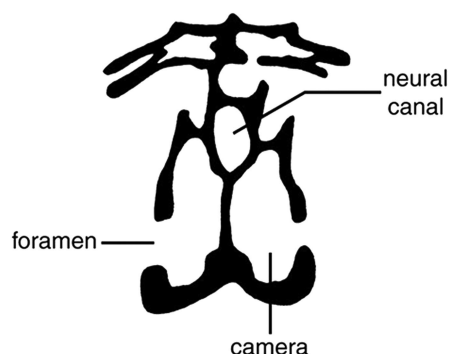

Fig. 19. Axial view (cross-section) of a cervical vertebra of the sauropod *Camarasaurus*. Within the bony structure are numerous internal cavities (camerae), which open to the adjacent tissues and/or to each other via foramina. (From Reference 172, with permission.)

osteological evidence, results in a striking image, with extensive pneumatization of the axial skeleton.[45,173] Figure 21 shows the presumed avian-type lung and an anteriorly-placed air sac. However, what role—if any—the extensive skeletal pneumatization may have played in respiration is not known. Even if they did not participate in gas exchange, the skeletal air spaces would have substantially decreased body weight, especially in the neck,[115,171,174] which calls into question the traditional dinosaur-weight estimates, which were based on the assumption of approximately the same overall density as water.[175] Recently an additional hypothesis was put forth: pneuma-
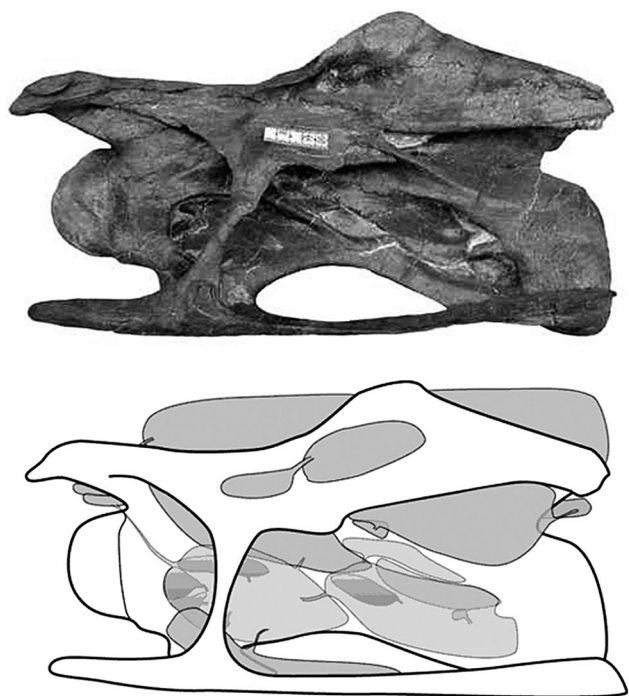
Fig. 20. Lateral view of 8th cervical vertebra of *Diplodocus*, as a photograph (above) and rendered with pneumaticity (air-filled diverticulae) (below). (Upper image from Reference 46, lower image adapted from Reference 173, with permission.)

tization may also have helped directly in the support and stabilization of the neck, quite apart from any effect on respiration.[46]

The extensive air-containing spaces within the sauropod body may provide an answer to a problem previously mentioned: how to get rid of heat in such a large body.[103] It has been postulated that both the large air sacs and the many smaller air spaces involved in skeletal pneumatization played an important role in conditioning the air and cooling the venous blood.[56] The higher compliance and more efficient gas exchange, and, thus, lower minute-ventilation requirement, of the avian respiratory system, compared to that of existing reptiles and mammals, would also have reduced heat production by decreasing the work of breathing.[56] One study found that panting increases the efficiency of the avian air sac system in cooling inspired air,[176] and perhaps this also played a role in tropical environments.

Additional evidence in support of an avian-type respiratory apparatus comes from studies of skeletal movement during ventilation and the role of the uncinate processes, which are small extensions from the caudal edges of birds' vertebral ribs. Uncinate processes were once believed to be involved in locomotion, through stabilization of the shoulders, but they have now been shown to play a crucial role in respiration during both inspiration and expiration.[177,178] The identification of uncinate processes in sev-

eral types of dinosaurs further strengthens the avian-dinosaur connection and the likelihood that dinosaurs had avian-type respiratory systems. Similarly, recent studies of theropod dinosaur bones and muscle attachments involved in "pelvic aspiration" (the mechanism by which birds fill their abdominal air sacs) further support the contention that they had this ventilation mechanism and an avian-type respiratory system.[179]

Figure 22, from Wedel, presents a more complete depiction of the respiratory system of a sauropod such as *Diplodocus*, with the pneumatic diverticulae less dramatically shown than in Figure 21.[171] Although much of this discussion has focused on sauropods because of the greater challenges posed by their bulk and long necks, there is increasing evidence that essentially all the described sauropod features were present in the theropods as well.[54,156,157]

Influence of the Ancient Atmosphere

The fluctuations in the atmospheric O_2 concentration during the last 550 million years (Fig. 23)[57] are now believed to have profoundly affected the evolution of animals.[59,62,180] A 100-million-year spike in atmospheric O_2 concentration spanning the mid-Devonian, Carboniferous, and Permian periods, during which O_2 was as high as 35%, coincided with the biggest surge in animal gigantism prior to the emergence of the dinosaurs.[181] Insects rely on direct diffusion of atmospheric oxygen into their tissues for respiration, and during the Devonian-through-Permian O_2 spike they attained sizes never seen before or since—including dragonflies with 70-cm wingspans.[181,182] Amphibians, in which a substantial proportion of total oxygen consumption is via skin-diffusion, reached lengths well in excess of 2 m—much larger than any amphibians since that time.[182,183]

Although it took perhaps 50 million years, the atmospheric O_2 concentration then fell from its zenith about 300 million years ago to its lowest level since the beginning of the Phanerozoic (10% or 11%, according to the most widely accepted model)[58,60] at the end of the Permian period and the beginning of the Triassic (Fig. 23). The giant insects and amphibians had disappeared. In the hypoxic early Triassic the ancestors of both the dinosaurs and the mammals were present. However, during perhaps 50 million years with the atmospheric O_2 roughly equivalent to a present-day altitude of 4,300 m (14,000 feet), it was the dinosaurs, not the mammals, that emerged, diversified, radiated widely, and in some instances became huge. There is evidence that atmospheric O_2 gradually increased during the Jurassic, reached a percentage in the low 20s at the time of the largest sauropods, and then diminished somewhat until another, smaller O_2 spike during the mid-Tertiary, about 50 million years ago.[62] It was only during that time (after the
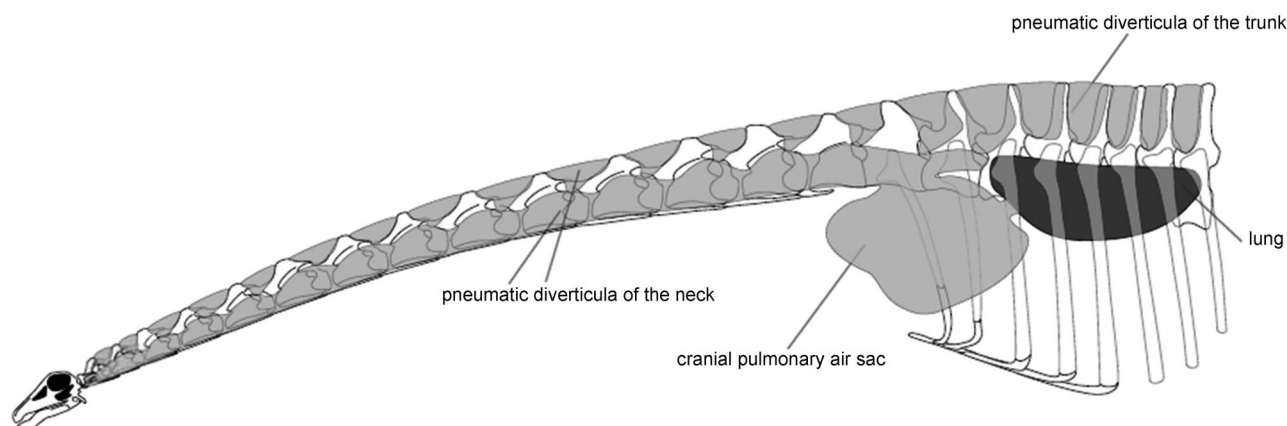
Fig. 21. Reconstructed distribution of pneumatic diverticula along the neck of the sauropod *Diplodocus*. This reconstruction is not intended to represent a model for respiratory mechanisms in sauropods, but rather a depiction of the extent of potential pneumatization, based on the osteological findings. (From Reference 46, with permission.)
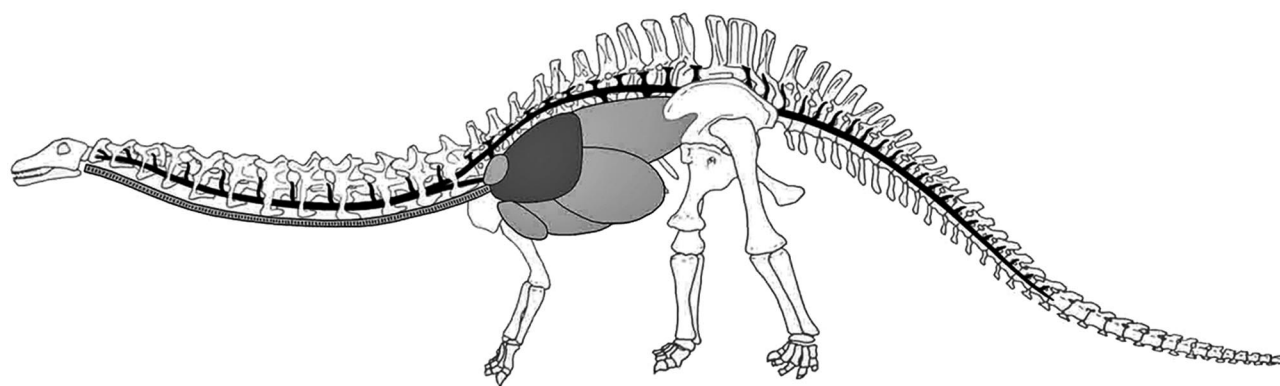

Fig. 22. Hypothetical conformation of the respiratory system in a sauropod such as *Diplodocus*, as reconstructed by Wedel. The left forelimb, pectoral girdle, and ribs have been removed for clarity. The lung is dark gray, the air sacs are light gray, and the pneumatic diverticulae are black. (From Reference 171, with permission.)

dinosaurs had become extinct) that mammals grew larger and became the dominant land vertebrates.

It is tempting—almost inescapable—to conclude that a crucial breakthrough with respect to respiration occurred during the period of prolonged hypoxia in the Triassic, which enabled the dinosaurs to emerge and leave the early mammals behind. That breakthrough appears to have been the flow-through avian respiratory system. The inspired O_2 tension depicted in Figure 17 is about the same as that which was present 220–180 million years ago, at the time of the great dinosaur radiation. As Figure 17 shows, and as migrating birds demonstrate, the avian respiratory system works just fine in that relatively hypoxic environment. The avian system, with its greater oxygen-extraction efficiency and its freedom from the constraints of tracheal dead space, appears to have played a key role in the emergence of the dinosaurs—at least the emergence of the theropods and the

giant sauropods—and to have enabled them to dominate terrestrial life on earth for more than 150 million years.

Summary: Respiration

Application of physical principles that affect respiration, evidence from living long-necked animals, comparison with other vertebrate respiratory systems, exciting breakthroughs in the study of dinosaur fossils, and inference from knowledge about the ancient atmosphere permit more confident conclusions about how the dinosaurs breathed than would have been possible 2 or 3 decades ago:

• The giant sauropods could not have been amphibious, extending their long necks from under water to breathe from the surface snorkel-fashion, because the weight of the water would have made it impossible to inflate their
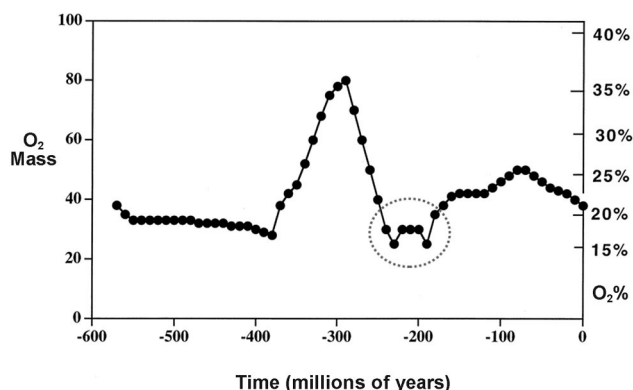
Fig. 23. Oxygen concentration of the earth's atmosphere over the last 550 million years (the Phanerozoic eon), according to Berner's modeling studies. The dotted oval marks the emergence and diversification of the dinosaurs, especially the giant sauropods. (Adapted from Reference 57, with permission.)

lungs, and the pressure differential from pulmonary capillaries to alveolar air would have produced catastrophic leakage.

- It is exceedingly unlikely that a respiratory system similar to the giraffe's could have worked in the sauropods, because of excessive airway resistance, excessive dead space, or both.

- Extensive pneumatization of the post-cranial skeletons of both sauropods and theropods has been convincingly demonstrated, which strongly supports the assertion that they had avian-type respiratory systems, with air sacs and flow-through lungs.

- An avian-type respiratory system, in which dead space in even a greatly elongated trachea does not present an insurmountable impediment to ventilation or gas exchange, would explain how the giant sauropods were able to breathe with such long necks.

- The development of such a respiratory system at a time when the atmospheric O_2 concentration was much lower than today could explain why the dinosaurs were able to increase in size and dominate the terrestrial world, and why the mammals, which had the less efficient tidal ventilation system of ancestral reptiles, were not.

Conclusions

Writing this article in the 1970s, when I first began wondering how comparative respiratory physiology might apply to the largest dinosaurs, would have been a very different undertaking—one in which speculation would have been much less hindered by the presence of actual data. In the last few years there has been a veritable explosion of new knowledge—from new dinosaur discover-

ies to new types of evidence and application of new technology to increased insight into existing evidence.

The available evidence clarifies some of the issues, and though it does not definitively answer the questions posed at the beginning of this article, it permits a number of conclusions to be drawn. How to perfuse a head 12 m (40 ft) above the ground poses hydrodynamic problems without ready solutions, which encourages speculation about alternative strategies for both blood flow and hypoxia tolerance in the largest sauropods. New hypotheses about the metabolic status of these giant creatures are gaining both theoretical and empirical support. Increasing confidence in the dinosaurian ancestry of birds, and mounting evidence of an avian-type respiratory system in theropods and sauropods suggest answers to the problems of why the large tracheal dead space of their very long necks did not prevent their evolutionary success, and why dinosaurs rather than mammals came to dominate the terrestrial world during the early Mesozoic, when there was much less O_2 in the atmosphere than there is today.

Although in addressing the physiology of dinosaurs I have ventured far from the bedside and included topics that Dr Egan might not have anticipated, I have tried to be true to the intent of the lectureship bearing his name: to summarize new information in a rapidly evolving field; to increase understanding and insight in subject areas important to the foundation of respiratory care; and to stimulate and broaden the interests of those involved in this field.

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