**A letter contests the view that a CT scan of *Australopithicus africanus*** "is about to wreak havoc on our view of hominid evolution." **Other letter writers discuss theropod dinosaur and ancient bird** "breathing mechanisms," **looking at how** "lung ventilation and gas exchange" **relate to the dinosaur-origin-of-birds hypothesis.**

**No Surprises?** Dean Falk's Research commentary "Hominid brain evolution: Looks can be deceiving" (*Science*'s Compass, 12 June, p. 1714) contends that "another new specimen…is about to wreak havoc on our view of hominid evolution" and that it changes the big picture. A cranium (Stw 505) found at Sterkfontein, South Africa, in 1989 was no surprise—the site has been producing specimens for more than 50 years. A coffee-table book (*1*) and "the grapevine" speculated that it had a 600+ cubic-centimeter (cm$^3$) brain. To test this, brain volume was estimated by using a computed tomography (CT) scanner. The digital measure matched the volume obtained by traditional water displacement, but not the coffee-table book or the grapevine. Conclusion: CT scanners are more accurate than rumors. To have these sources match, or to have found a brain, *would* have been surprising. A mere volume of 515 cm$^3$ for *Australopithicus africanus* is not. Readers still searching for the surprise, anticipating havoc in the field and changes in their "big picture," may be disappointed by these facts, but not all summer "blockbusters" live up to reviews by friendly critics.

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***Response:***

Stw 505 is important because of its unexpected cranial capacity of 515 cm$^3$, which suggests that the cranial capacities of other hominid fossil specimens may have been incorrectly estimated. Since writing my commentary, my colleagues and I have extensively researched the endocasts in our collection and have begun to compare them with 3D-CT reconstructions from the actual specimens from which they were taken. We are mighty surprised, and intend to publish our results as quickly as you can say "*Ardipithecus*." When reading a film review, I always hope that the critic (friendly or otherwise) has actually seen the picture. Worthwhile science, like a credible film review, depends on knowledge of the subject matter. In other words, the proof, as it relates to the significance of Stw 505, is in the pudding. I believe that White and I are both attending a small workshop in August. I'm bringing the pudding. White should bring a spoon.

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**Lung Ventilation and Gas Exchange in Theropod Dinosaurs** John A. Ruben and his colleagues suggest (Reports, 14 Nov. 1997, p. 1267) that the lung of theropod dinosaurs was most likely similar in form to that of several extant reptiles and was therefore incapable of sustaining high oxygen (O$_2$) exchange rates characteristic of endothermy. We disagree for two reasons. First, we examined the comparative physiology literature and determined that maximum oxygen exchange rates (VO$_2$max) of some extant reptiles overlap the oxygen consumption rates measured in some mammals during activity. Specifically, exceptionally active reptiles with multicameral lungs (*1*) (for example, monitor lizards and sea turtles) have values of VO$_2$max that overlap or approach the oxygen exchange rates measured in similar size mammals during activity (*2*). Therefore, the septate lung in those reptiles must be capable of sustaining rates of gas flux characteristic of endotherms. However, mammals and birds "typically" have a greater VO$_2$max. Therefore, we addressed the question of what modifications in the oxygen transport system of an extant reptile would be necessary to support higher rates of oxygen consumption.

We used morphological and physiological measurements of extant reptiles and well-established respiratory equations to model the gas exchange potential of the reptilian oxygen delivery system and to examine the role of lung structure in constraining gas exchange. Each step in the oxygen cascade is described by a set of respiratory equations and, consequently, it is possible to describe mathematically the flux of oxygen through the entire cascade and to evaluate the impact of modifications in any of its components (*3*). We used this approach to predict the effects of modifying several parameters in the oxygen cascade on VO$_2$max in a 1-kilogram lizard, *Varanus exanthematicus* (*4*). Our analysis included four modifications: (i) a small increase in the maximum cardiac output; (ii) an increased oxygen carrying capacity of the blood from reptilian to mammalian values; (iii) an increase in maximum cardiac output combined with the changes in blood oxygen–carrying capacity; and (iv) an increased respiratory gas exchange area in the dorsal region of the lung through elaboration of the intercameral septa with a membranous region in the ventral portion of the lung. Without modification of the lung structure, our analysis predicts that changes in blood oxygen capacity and cardiac output support a VO$_2$max that is 50% of the value for a "typical" 1-kilogram (kg) mammal (*5*). However, if we combine these changes with conservative modifications in lung morphology, we predict a VO$_2$max that is nearly 70% of the typical mammalian value. Our analysis indicates that modifications in several of the steps of the oxygen cascade have a cumulative effect on VO$_2$max (*6*). The resulting high oxygen flux rate mandates an increase in lung ventilation that is 233% above the maximum level measured in extant lizards.

Lizards have a mechanical constraint on simultaneous vigorous locomotion and costal ventilation that arises from the design of the axial musculoskeletal system, and this mechanical constraint was probably the primitive condition for all tetrapods (*7*). Consequently, the fundamental change required to support sustainable high oxygen exchange rates was the development of new mechanisms to increase ventilation (*7*). This constraint has been circumvented to varying degrees in some extant lizards, for example, the use of the gular pump to assist costal ventilation during activity (*8*) and in the lineages that gave rise to endotherms by the evolution of ventilatory mechanics that are not limited by locomotor requirements (*7*).

Inadequate preservation of the soft-tissue components of the oxygen transport system precludes accurate assessment of the aerobic potential of theropod dinosaurs. However, on the basis of metabolic patterns in extant reptiles and our theoretical analysis, we find that the notion that nonavian septate lungs constrain high oxygen flux rates is not supported. Our analysis suggests that modifications in lung structure were not a prerequisite for supporting higher oxygen consumption rates. In the mammalian and archosaur lineages that evolved endothermy, higher oxygen consumption rates could have been supported through changes in ventilatory mechanics and increases in blood oxygen content and cardiac output.

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Ruben *et al.* are to be commended for bringing forth yet another intriguing argument concerning dinosaur physiology. While there may be evidence that theropod dinosaurs maintained a separate thoracic and abdominal cavity by means of a septum, stronger evidence is needed to support the idea that this membrane served as a diaphragmatic hepatic piston. The authors compare by analogy the partitioning of the body cavity of an alligator with *Sinosauropteryx* (their figure 5). It would be beneficial to show in a similar illustration how this condition differs in other reptiles, as well as in birds. Teiid lizards (such as *Tupinambis*), for example, independently developed a non-muscular posthepatic septum dividing the lungs and liver from the abdominal viscera (*1*), yet unlike in crocodilians, this structure does not participate in ventilation. Varanid lizards (such as *Varanus*) similarly separate their lungs (which occupy most of the thorax) from the peritoneal cavity by means of a non-ventilatory, postpulmonary septum (*1*). Birds also developed a complex, nonmuscular, septal partitioning of their body cavity by means of two membranes: the horizontal and the oblique septa (the latter separates all but the abdominal air sacs from the viscera, spanning the vertebrae to the stemal margin) (*2*). These septa, also, are nonventilatory in function. How can we rule out that we are not seeing something similar in *Sinosauropteryx*?

Ruben *et al.* also note the lack of an "expansive sternum," "hinged ribs," and evidence for "inhalatory filling of the abdominal air sacs" as indicators that theropods lacked modem avian lungs. The primary reason for the elongation of the sternum, however (along with the development of the sternal carina), appears to have been to increase the surface area for the origin of the flight muscles. The hinged ribcage can also be considered an adaptation to counter the forces incurred by the thorax during flight. What is the empirical evidence to argue that these features must have been in place before a modern avian lung could have developed? Additionally, the lack of air sac diverticula into bone may not have precluded the possibility of that air sac's presence. Modern birds use caudal thoracic air sacs in addition to abdominal air sacs during inspiration, and the former do not typically ramify into the skeleton (*3*). Diverticula foramina are variable and are not well surveyed systematically in modern birds; they may have been an inconstant feature in pre-ornithiurine birds as well.

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Ruben *et al.*'s report about theropods' breathing mechanisms and ancient birds dovetails well with data on dinosaur ventilation mechanics. In presenting arguments using the Extant Phylogenetic Bracketing method propounded by Witmer (*1*), fossil evidence, and morphological correlation, the paper advances intriguing ideas of how theropods breathed and raises interesting questions about the timing of avian origins. For several years, we have studied the costal breathing mechanics of dinosaurs. Dinosaur ribs have two prominent sites (capitulum and tuberculum) that articulate with equally well-defined vertebral structures (the parapophysis and diapophysis), and these establish the direction of costal breathing motion. Because respiratory muscles are subject to well-established contractile limitations, it is possible to predict maximal rib movement to make predictions of alligator breathing.

Costal realignment potentially improves ventilation with only small increases in muscle effort. Such a progression is observed in the fossil record. Theropods from the Triassic and earliest Jurassic show uniform costal-vertebral angles throughout the thoracic sequence. Rib movement tends to be directed more anteriorly, and somewhat laterally, similar to the pattern seen in modern lizards. This is undoubtedly inherited from an earlier state in which intercostal muscles participated in both locomotion and respiration (*2*). A stiff back and parasagittal stride removed Carrier's constraint from dinosaurs, allowing selection for optimal ventilation mechanics. Most Jurassic theropods exhibit improved vertebral-costal angles, with a potential of moving up to 40% more air per breath than their Triassic counterparts. There appears to be no further evolution occurring in North American theropods after the late Jurassic (*3*). This has been puzzling for two reasons: first, additional biomechanical reserves existed, yet were not tapped; second, different clades of theropods converged on similar costal-vertebral angles. This may have been a consequence of the hepatic piston suggested by Ruben *et al.* for theropods.

A hepatic piston creates medially and posteriorly directed forces during inspiration. As a result, posterior thoracic ribs which create the greatest lateral motion are being moved by muscles placed at less advantageous angles for this movement. This less effective movement requires more muscle effort than more anterior ribs and muscles. Thus, the limiting angles seen across distinctly different theropod clades may be a compromise between ventilation volumes, intercostal effort, and hepatic piston forces.

What is clear is that all theropods measured to date converge on rather similar rib-vertebral morphology by the Middle Cretaceous, and this suggests physical, rather than evolutionary, restrictions.

The morphology of theropod breathing is consistent with an anteriorly ventilated bellows lung. Among Triassic theropods, *Staurikosaurus* (*4*) alone shows slight modification, indicating that breathing selection for optimal angles began early.

Because Jurassic birds already show unique costal-vertebral angles, divergence may well have occurred at an early stage before joint optimization occurred, possibly as early as the Triassic.

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***Response:***
Hicks and Farmer present a scenario for a three-fold expansion of respiratory exchange capacity in the varanid septate ("reptilian") lung. Nevertheless, we stand by our original conclusion that the nonavian septate lung is probably unalterably constrained from supporting respiratory exchange consistent with maximal aerobic metabolic rates typical of active endotherms.

As Hicks and Farmer point out, no extant reptile is capable of aerobic respiratory exchange rates greater than about 20 milliliters (ml) of $O_2$ per kg per minute (min), or about 15 to 20% of those of typical endotherms (that is, "Initial condition" $VO_2max$ in their table 1). With a hypothetical mammal-like "upgrade" of the circulatory system and optimized pulmonary diffiision capacity ($D_{LO2}$), they calculate that with an idealized reptilian lung, a 1-kg animal might be capable of sustaining $VO_2max$ of 67 ml $O_2$ $kg^{-1}$ $min^{-1}$. However, this is still only about 57% of $VO_2max$ for a typical 1-kg mammal [116 ml $O_2$ $kg^{-1}$ $min^{-1}$, based on Taylor *et al.*'s preferred regression (*1*)], where $VO_2max$ (ml per second) = $1.94M^{0.79}$, mass (M) in kilograms. To our eyes, this difference remains substantial and serves to emphasize that even with major modification, the reptilian septate lung seems constrained from supporting gas exchange rates typical of most extant endotherms.

Nassar questions the basis for our assumption that the fore-aft partitioning of the visceral cavity in theropods was necessarily associated with a dynamic, functional hepatic-piston diaphragms rather than with a passive, teid lizard–like, post-hepatic septum. We assert that theropod visceral anatomy was associated with a dynamic, crocodile-like diaphragm primarily because of the shared presence of striking skeletal specializations in theropods and crocodiles. All species of both taxa possess robust posterior gastralia and, in particular, a distinctive, tri-radiate pelvis that bears an elongated, spoke-like pubis. As discussed in our original paper, these skeletal modifications in crocodilians are tightly associated with their service as major points of origin for the diaphragm-aticus muscles, which provide power for generating the piston-like movement of the liver during lung ventilation. In light of the crocodile-like morphology of the theropod visceral cavity, pelvis, and gastralia, principles of uniformity suggest that this anatomical complex in theropods is best interpreted as having also functioned in a crocodile-like manner (that is, in association with a dynamic diaphragm). In this regard, it is particularly significant that Hengst interprets theropod posterior costalrib morphology as having been consistent with presence of a functional, muscularized diaphragm. Nassar also asserts that the absence of bird-like thoracic skeletal specializations in theropods is not necessarily an indicator that dinosaurs lacked an avian-style lung. Rather, Nassar suggests that the mobile, expansive sternum and uniquely hinged ribs of modern birds are specializations that might have more to do with the biomechanics of flight than with lung ventilatory requirements per se. However, birds have high lung ventilatory requirements (*2*), and these skeletal modifications are associated with a doubling of avian lung ventilatory capacity beyond that provided by nonspecialized, lateral ribcage expansion alone (*3*). Significantly, even flightless birds (for example, ratites) retain virtually identical axial skeletal specializations for lung ventilation as occur in flighted birds (*4*). In contrast, the relatively simple theropod ribcage was unlikely to have been capable of sustaining lung ventilation rates consistent with an avian-style respiratory system.

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