# Lung Structure and Ventilation in Theropod Dinosaurs and Early Birds

John A. Ruben, Terry D. Jones,* Nicholas R. Geist, W. Jaap Hillenius

Reptiles and birds possess septate lungs rather than the alveolar-style lungs of mammals. The morphology of the unmodified, bellowslike septate lung restricts the maximum rates of respiratory gas exchange. Among taxa possessing septate lungs, only the modified avian flow-through lung is capable of the oxygen–carbon dioxide exchange rates that are typical of active endotherms. Paleontological and neontological evidence indicates that theropod dinosaurs possessed unmodified, bellowslike septate lungs that were ventilated with a crocodilelike hepatic-piston diaphragm. The earliest birds (*Archaeopteryx* and enantiornithines) also possessed unmodified septate lungs but lacked a hepatic-piston diaphragm mechanism. These data are consistent with an ectothermic status for theropod dinosaurs and early birds.

Some fossil evidence indicates that a variety of dinosaurs maintained ectothermal or near-ectothermal lung ventilation and metabolic rates during periods of low-level or routine activity (*1*). Additionally, correlational evidence suggests that the earliest birds (*Archaeopteryx* and enantiornithine "opposite birds") were also likely to have been ectotherms or near-ectotherms and that avian endothermy probably developed after the evolution of powered flight (*2*). However, these data do not provide information about the metabolic capacities of dinosaurs and early birds during periods of exercise; further information on internal structure is needed. We report here paleontological and neontological evidence on the lung morphology and ventilatory mechanisms of dinosaurs and the earliest birds.

Mammalian lungs consist largely of millions of tiny (radius ≈14 μm), highly vascularized, blind air sacs, the alveoli (Fig. 1A). Ventilatory air flow is bidirectional. During inhalation, each alveolus functions in a bellowslike manner, expanding passively in response to costally and diaphragmatically generated negative intrapleural pressure. Exhalation is accomplished largely by elastic rebound of the alveoli. Consequently, during the respiratory cycle, each alveolus actively participates in its own ventilation, thereby facilitating homogenous maintenance of a constantly refreshed supply of alveolar oxygen as well as continuous elimination of carbon dioxide. These attributes, combined with a particularly thin alveolar blood-gas barrier, provide the mammalian lung with a high anatomical diffusion factor (ADF) (*3*), an attribute that is essential for maintenance of high rates of oxygen consumption during extended periods of intensive activity.

Lung morphology in nonavian sauropsid amniotes (reptiles) is distinct from the alveolar lungs of mammals (Fig. 1, C and D). The nonavian sauropsid septate lung is analogous to a single, oversized mammalian alveolus. Vascularized ingrowths, or septae, penetrate centrally from the lung's perimeter and subdivide the pulmonary lumen into a series of spatial units termed ediculae or faveoli (Fig. 1C). Respiratory exchange takes place principally on the septae. As in the mammalian lung, air flow during lung ventilation in reptiles is bidirectional and bellowslike. However, unlike mammalian alveoli, ediculae or faveoli are relatively passive participants and contribute little to the movement of air during inhalation and exhalation. In partial compensation, a large part of the lung volume in nonavian sauropsids is maintained as an essentially nonvascularized region whose primary function is to assist in ventilation of vascularized portions of the lung (Fig. 1D) (*4*). Additionally, in comparison to mammalian alveoli, reptilian septae are invariably less well vascularized. The result is that the nonavian septate lung exhibits a reduced pulmonary ADF and is probably unalterably constrained from supporting respiratory exchange that is consistent with the aerobic metabolic rates typical of active endotherms (*3*, *5*).

Birds, like all of the sauropsids, possess septate lungs (Fig. 1B), but have circumvented the inherent limitations on respiratory gas exchange rates posed by the structure of the nonavian, sauropsid, bellowslike septate lung. Especially high parabronchial ADF in the avian lung (*3*) is associated, in part, with modification of the nonvascularized pulmonary chambers of reptiles into a series of extensive, highly compliant air sacs that extend into both thoracic and abdominal cavities. During lung ventilation, the air sacs function to generate a unidirectional flow of air through the relatively noncompliant vascularized part of the lung, during both inhalation and exhalation. As a consequence, birds are able to maintain a particularly efficient cross-current pattern of gas exchange at the pulmonary blood-air interface (*6*).

Skeletomuscular mechanisms for powering lung ventilation vary widely among extant amniotes. Lizards and snakes rely solely on costal ventilation, in which alteration of

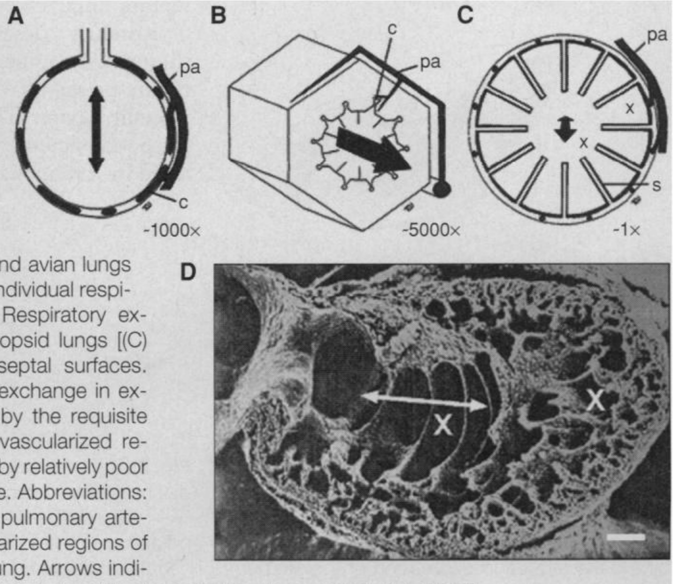

**Fig. 1.** Histological sites of $O_2$-$CO_2$ exchange surfaces in (**A**) alveolar (mammalian) and (**B**) modified septate (avian) lungs. Whole-lung cross (**C**) and longitudinal (**D**) sections of unmodified sauropsid septate lungs (from *Varanus*; scale bar = 1 cm). Mammalian and avian lungs consist of millions of these individual respiratory units [(A) and (B)]. Respiratory exchange in unmodified sauropsid lungs [(C) and (D)] takes place on septal surfaces. Rates of maximal $O_2$-$CO_2$ exchange in extant reptiles are restricted by the requisite presence of extensive nonvascularized regions of the lungs as well as by relatively poor vascularization of the septae. Abbreviations: c, pulmonary capillary; pa, pulmonary arteriole; s, septa; x, nonvascularized regions of the unmodified sauropsid lung. Arrows indicate direction of air flow. [The photo of the *Varanus* lung is courtesy of J. Hicks]

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*To whom correspondence should be addressed. E-mail: jonest@bcc.orst.edu intrapleural pressure results from simple ribcage expansion and contraction. To some extent, mammals and crocodilians also utilize costally assisted lung ventilation. However, both mammals and crocodilians rely extensively on diaphragm-assisted lung ventilation. In mammals, the diaphragm consists of an airtight, muscularized, vertically oriented septum that completely subdivides the visceral cavity into pleuro-pericardial and abdominal regions (Fig. 2A). Muscular contraction of the dome-shaped diaphragm results in expansion of the pleural cavity and filling of the lungs.

In crocodilians, the vertically oriented diaphragm (hepatic septa) also completely divides the visceral cavity into anterior pleuro-pericardial and posterior abdominal regions (Fig. 2B). Unlike in mammals, the crocodilian diaphragm consists of a sheet of nonmuscular connective tissue that adheres tightly to the dome-shaped anterior surface of the liver. Lateral, dorsal, and ventral aspects of the posterior portion of the liver serve as sites of insertion for the paired diaphragmatic muscles that take origin primarily from the pubic bones and their distal cartilages, as well as from the last pair of gastralia (Figs. 3 and 4). Bilateral contraction of the diaphragmatic muscles fills the lungs when the liver-diaphragm complex is pulled posteriorly in a pistonlike manner (*7*). To accommodate the diaphragmatic muscle origin, the distinctive crocodilian pubis is robust and elongate (at least as long as the liver is deep), much like the pubis in theropod dinosaurs (Fig. 4).

Birds, like lizards, rely primarily on costally powered lung ventilation and lack a crocodilelike or mammallike thoracic-abdominal subdivision of the visceral cavity (Fig. 2C). Birds utilize highly modified costal movement in association with a well-developed sternum to ventilate their nonvascularized air sacs. The ribs of ornithiurine birds possess unique synovial intracostal joints, the shape of which enables fore-aft movement of the ribcage during lung ventilation. Consequently, during ventilation, avian ribs rotate so that the posterior end of the sternum is depressed upon inhalation, thus generating negative intra-abdominal pressure and filling of the large abdominal air sacs (*8*).

Given their affinity to other sauropsids, dinosaurs probably possessed septate lungs. However, theropod dinosaurs were unlikely to have possessed avian-style, flow-through septate lungs. The theropod ribcage-pectoral girdle complex is devoid of indications of skeletomuscular capacity for inhalatory filling of abdominal air sacs [for example, theropods lacked avianlike jointed or hinged ribs and an expansive sternum (*9*), structures without which proper ventilatory airflow cannot be maintained in the modern bird lung]. These modifications first appear in Cretaceous ornithiurine birds, such as *Chaoyangia* (*10*). Moreover, theropods exhibit evidence that, like modern crocodilians, they probably possessed a vertical thoracic-abdominal subdivision of the visceral cavity and relied on a hepatic piston diaphragm to ventilate a bellowslike septate lung.

Recently described Early Cretaceous theropod specimens [*Sinosauropteryx* (*11*)] retain preserved outlines of much of the visceral cavity. The cavity exhibits complete thoracic-abdominal separation, defined by a remarkably crocodilianlike vertically oriented partition coincident with the apparent dome-shaped anterior surface of the liver (Fig. 5). These observations, combined with the occurrence among theropods of a distinct, relatively vertical, crocodilelike, highly elongate pubis (Figs. 4 and 5), as well as well-developed gastralia, provide evidence that theropod dinosaurs, like modern crocodiles, probably possessed a bellowslike septate lung and that the lung was probably ventilated, at least in part, by a hepatic-piston diaphragm that was powered by diaphragmatic muscles that extended between the pubic bones and liver (*12*).

Like theropod dinosaurs, most early birds, including *Archaeopteryx* and the enantiornithines, were likely to have retained bellowslike septate lungs. These taxa possessed a relatively unremarkable ribcage-sternum apparatus and clearly lacked the skeletomuscular capacity to have ventilated abdominal air sacs (*10*, *13*). There is, however, evidence that, like many modern flighted birds, both *Archaeopteryx* and the enantiornithines utilized pelvic and tail movements to assist in pulmonary ventilation (*14*).

The pelvis of these primitive birds is conventionally assumed to be closely comparable to that of theropod dinosaurs, especially *Unenlagia* (Fig. 4) (*15*). However, in these birds the pubis is rotated so far posterodorsally (severe opisthopuby) that its distal extremity is situated markedly posterior to both the ilium and ischium and considerably dorsal to its equivalent position in any theropod dinosaur (Fig. 6B) (*16*, *17*). Additionally, unlike theropod dinosaurs, primitive birds possessed a well-developed, reversed hypopubic cup (Fig. 6B) that probably served as a major site of origin for extensive suprapubic musculature. Both of these conditions are broadly inconsistent with the notion that the primitive avian pelvis served as a site of origin for muscles powering diaphragmatic ventilation. Rather, the pubis in these ancient birds closely foreshadows the condition of the pelvis in modern flighted, and especially perching, birds

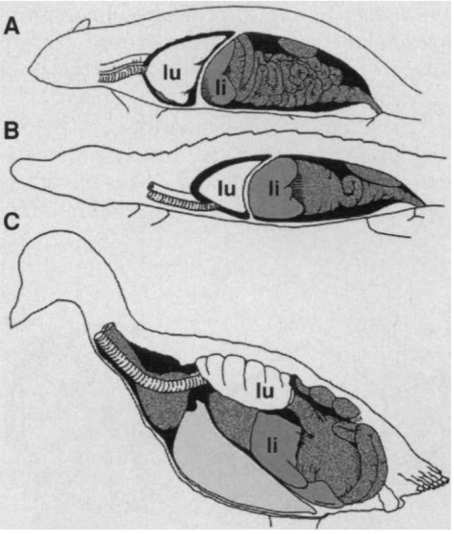


**Fig. 2.** Correlation of body cavity partitioning and lung ventilation mechanism in amniotes. Among modern amniotes, only mammals (**A**) and crocodilians (**B**) utilize active diaphragmatic lung ventilation. Active diaphragmatic breathing necessitates a complete vertical separation of the pleuropericardial cavity from the peritoneal (abdominal) cavity. In modern birds (**C**) and lepidosaurs (such as lizards and snakes), there is no similar separation of the body cavity. Lepidosaurs are exclusively costal (rib) breathers; extant birds possess a unique flow-through lung ventilated in large part by the elevation and depression of the sternum. Abbreviations: lu, lung; li, liver.

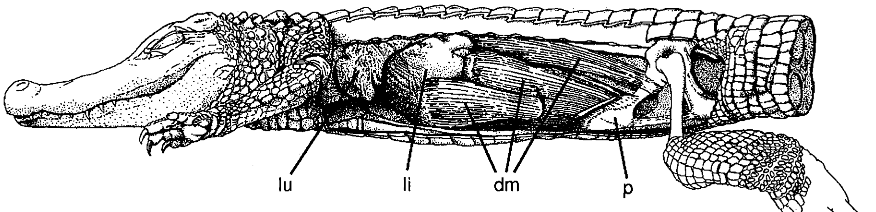


**Fig. 3.** The hepatic-piston lung ventilatory mechanism of crocodilians. Extensive diaphragmatic muscles take origin primarily from the pubic foot and insert on the liver (see also Fig. 4A). Some portions of these muscles also take origin from the posteriormost pair of gastralia. Upon contraction, these muscles pull the liver posteriorly, thus producing negative intraplural pressure and filling of the lungs. Abbreviations: lu, lung; li, liver; dm, diaphragmatic muscle; p, pubis.

where, as a result of marked opisthopuby, the pubic extremity also projects posterior to the ilium and ischium (Fig. 6A). This morphology in living birds facilitates suprapubic muscular rotation of the pelvic girdle and ventral movement of the tail, motions thought to assist in lung ventilation, especially when arboreally roosting birds rest the mass of their anterior trunk on tree limbs. Consequently, it is reasonable to conclude that although early birds lacked the modern avian flow-through lung, *Archaeopteryx* and the enantiornithines, when roosting in trees, probably also utilized pelvic and tail movements to assist in ventilation of nonvascularized air sacs (*14*).

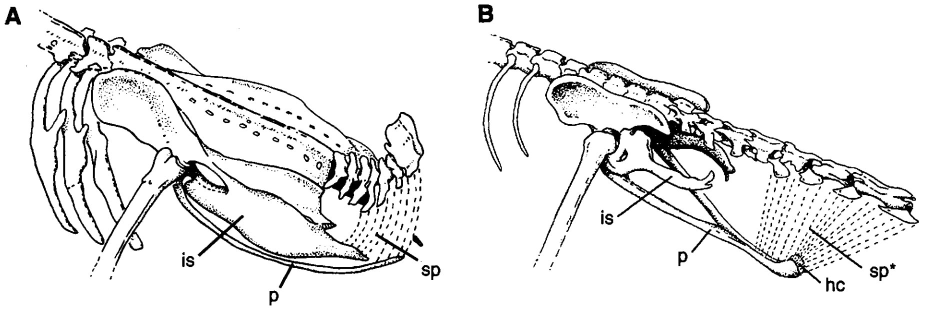
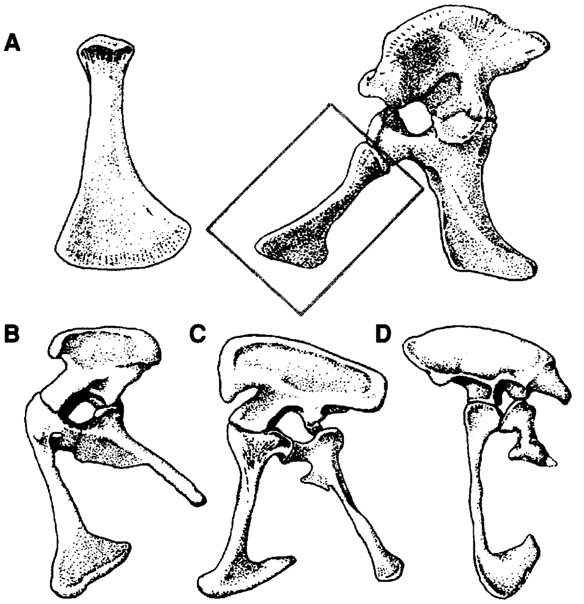


**Fig. 6.** Pelvic and tail skeleton and suprapubic musculature of (**A**) modern perching birds (such as the pigeon) and (**B**) *Archaeopteryx* and the enantiornithine birds (*17, 22*). In both (A) and (B), marked dorsal position and the projection of the distal pubis posterior to the ilium and ischium are associated with suprapubic muscular rotation of the pelvis and tail. Such movements facilitate ventilation of nonvascularized air sacs during arboreal roosting. This condition of the pubis is broadly inconsistent with the morphology of the theropod pelvis as well as with hepatic-piston diaphragmatic breathing. Anterior is to the left of the figures. Abbreviations: is, ischium; p, pubis; hc, hypopubic cup (of the pubis); sp, suprapubic muscles; sp*, probable suprapubic muscles.

In view of the constraints on pulmonary gas exchange rates in modern sauropsids with bellowslike septate lungs, it seems unlikely that either theropod dinosaurs or the earliest birds were capable of the exercise-related rates of $O_2$-$CO_2$ exchange that are typical of modern endotherms. Thus, evidence for the ectothermic, or near-ectothermic, metabolic status of these Mesozoic Era taxa (*1*) is provided by these data.

Recently, conventional wisdom has held that birds are direct descendants of theropod dinosaurs. However, the apparently steadfast maintenance of hepatic-piston diaphragmatic lung ventilation in theropods throughout the Mesozoic poses fundamental problems for such a relationship. The earliest stages in the derivation of the avian abdominal air sac system from a diaphragm-ventilating ancestor would have necessitated selection for a diaphragmatic hernia in taxa transitional between theropods and birds. Such a debilitating condition would have immediately compromised the entire pulmonary ventilatory apparatus and seems unlikely to have been of any selective advantage.

Finally, the enantiornithines have been cited as perhaps the most ancient adaptive radiation of perching, or arboreal, birds



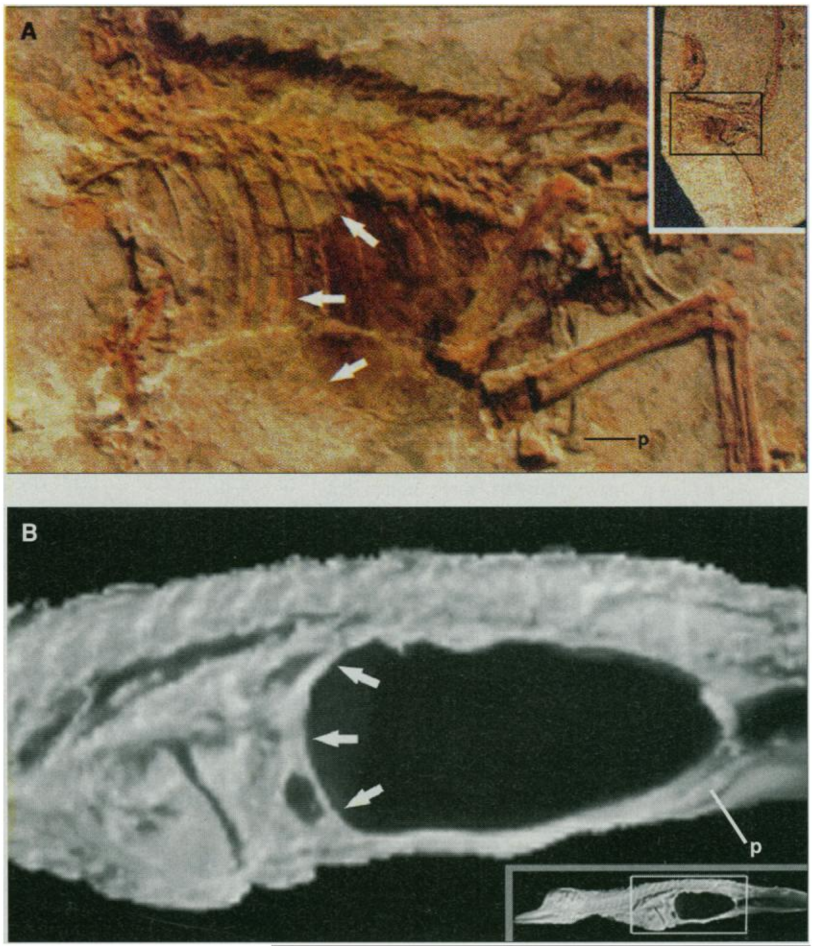


**Fig. 4 (left).** Left lateral view of the pelves of (**A**) crocodilians (inset: pubis in slight posteroventral view) and theropod dinosaurs, (**B**) *Herrerasaurus* [modified from (*20*)], (**C**) *Allosaurus*, and (**D**) *Unenlagia* [modified from (*15*)]. The marked similarity of pubic morphology in crocodilians and theropods has long been recognized (*21*). The distal curved extremity of the crocodilian pubis serves as a major site of origin for ventral diaphragmatic muscles. The distal cartilaginous portion of the crocodilian pubis is not shown. **Fig. 5 (right).** Similar body cavity partitioning and position of the pubis (p) in (**A**) the compsognathid theropod dinosaur *Sinosauropteryx* (×0.5) and (**B**) the American alligator (*Alligator*) (×0.5). Arrows delineate the complete vertical subdivision of the pleuro-pericardial and abdominal cavities. Insets show the entire animal for perspective.

(*10*). As described above, the severely opisthopubic condition of their pelvis is consistent with the notion that these birds roosted in trees. In contrast, based primarily on disputed measurements of claw curvature, *Archaeopteryx* has been interpreted as adapted primarily for a terrestrial rather than an arboreal existence (*18*). However, as in the enantiornithines, the morphology of *Archaeopteryx*'s pelvis is best interpreted as adapted for a largely, if not exclusively, arboreal existence.

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5. Maximal rates of lung $O_2$-$CO_2$ exchange are limited primarily by hydrostatic pressure constraints on pulmonary blood flow (*19*). Thus, in order for a modern reptile (the active lizard *Varanus*, for example) with a bellowslike septate lung to attain endothermlike rates of maximal oxygen consumption {about 10 times those of active ectotherms [A. F. Bennett and J. A. Ruben, *Science* **206**, 649 (1979)]}, maximal pulmonary blood flow would have to be accelerated by about 10 times, or about 5 times if blood oxygen carrying capacity were to approximate that in many mammals {20 volume % rather than the actual 10 volume % in modern lizards [A. F. Bennett, *J. Comp. Biochem. Physiol.* **46**, 673 (1973)]}. In either case, because pulmonary hydrostatic pressure is largely a product of blood flow rate, pulmonary capillary pressures would be far in excess of dangerous levels [≈ 45 millimeters of mercury (mmHg)], approaching at least 100 mmHg if not far higher {based on the observed similarity of resting mean pulmonary arterial pressure in mammals and normal *Varanus* (about 20 mm Hg at a body temperature of 35°C) [A. Ischimatsu, J. W. Hicks, N. Heisler, *Respir. Physiol.* **71**, 83 (1988)] and the assumption that (i) pulmonary capillary recruitment is maximal in exercising tetrapods and (ii) that mean arterial pressure during intense exercise in normal *Varanus* is actually broadly equivalent to that in mammals (about 35 mm Hg) (*19*)}. Hypothetically, these pressure constraints on the bellowslike septate lung might be overcome either by increasing the magnitude of lung vascularization (thus decreasing pulmonary capillary resistance to blood flow) or by increasing total lung volume by a factor of at least 5. However, a substantial increase in lung vascularization would necessarily restrict the volume of nonvascularized portions of the lung, thereby reducing capacity for lung ventilation. Alternately, an increase by a factor of 5 in total lung volume would leave little, if any, space in the visceral cavity for organs other than the lung.
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12. Rather than representing primitive archosaurian structures, it is probable that the hepatic-piston diaphragm systems in crocodilians and theropods are convergently derived. Pelvic anatomy in early "protodinosaurs" such as *Lagosuchus*, as well as in all ornithischian dinosaurs, shows no evidence of the pubis having served as a site of origin for similar diaphragmatic musculature (pubic bones are comparatively less well developed, and in ornithischian dinosaurs a pubic symphysis is absent). See R. Carroll, *Vertebrate Paleontology and Evolution* (Freeman, New York, 1988).
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16. A few theropod dinosaurs [for example, *Segnosaurus* and *Adasaurus* (*9*)] possess a moderately opisthopubic pelvis, but the distal pubis remains ventrally situated and the degree of dorsal rotation of the pubis does not approximate that in *Archaeopteryx* and the enantiornithine birds.
17. The position of the pubis in *Archaeopteryx* has occasionally been interpreted as having been vertical rather than severely opisthopubic [for example, J. H. Ostrom, *Biol. J. Linn. Soc. London* **8**, 91 (1976)]. However, the overall similarity of the pelvis of *Archaeopteryx* to those of the enantiornithine birds, especially the presence of the hypopubic cup, as well as the morphology of the London and Berlin *Archaeopteryx* specimens, offer support for our interpretation of the pelvic structure of these early birds [L. D. Martin, in *Origin of the Higher Groups of Tetrapods*, H. P. Schultze and L. Trueb, Eds. (Cornell Univ. Press, Ithaca, NY, 1991), pp. 485–540.
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23. We thank J. Baumel, A. Bennett, P. Dodson, J. Farlow, A. Feduccia, J. Hicks, L. Martin, S. Perry, L. Witmer, and G. Zug for invaluable discussions and constructive criticisms. We offer special thanks to D. Bubier and D. Wolberg (Philadelphia Academy of Sciences) for *Sinosauropteryx* photos. R. Elsie provided alligator specimens. Figures 3, 4, and 6 were drawn by R. Jones. This work was supported by NSF grant IBN-9420290 to W.J.H. and J.A.R.

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# Belated Decision in the Hilbert-Einstein Priority Dispute

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**According to the commonly accepted view, David Hilbert completed the general theory of relativity at least 5 days before Albert Einstein submitted his conclusive paper on this theory on 25 November 1915. Hilbert's article, bearing the date of submission 20 November 1915 but published only on 31 March 1916, presents a generally covariant theory of gravitation, including field equations essentially equivalent to those in Einstein's paper. A close analysis of archival material reveals that Hilbert did not anticipate Einstein. The first set of proofs of Hilbert's paper shows that the theory he originally submitted is not generally covariant and does not include the explicit form of the field equations of general relativity.**

It took Einstein 8 years, from 1907 to 1915, to complete the general theory of relativity, based on the field equations

$$R_{\mu\nu} = -\kappa\left(T_{\mu\nu} - \frac{1}{2} g_{\mu\nu} T\right) \qquad (1)$$

where $g_{\mu\nu}$ is the metric tensor representing the gravitational potentials, $R_{\mu\nu}$ is the Ricci tensor, $\kappa$ is a constant, $T_{\mu\nu}$ is the stress-energy tensor of matter, and $T$ is its trace. The principal difficulty he had to overcome was finding the right balance between the mathematical implications of a generalized principle of relativity and physical requirements such as the existence of a Newtonian limit (*1*, *2*). Hilbert, on the other hand, only began to work seriously on gravitation in mid-1915. Concerning physics, his interests had focused since the end of 1912 on the structure of matter, and in particular, since mid-1913, on Gustav Mie's special-relativistic electromagnetic theory of matter. Then, after Einstein's visit to Göttingen in the summer of 1915, Hilbert attempted to forge a synthesis between Mie's theory and Einstein's approach to gravitation based on $g_{\mu\nu}$ (*3*, *4*).

A recent comprehensive Einstein biography, which shows promise of becoming the standard reference, offers a succinct

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