Were the respiratory complexes of predatory dinosaurs like crocodilians or birds?

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**Abstract**

The majority opinion that theropod dinosaurs evolved a lung complex dominated by air sac ventilation has been challenged by arguments that soft tissues preserve the presence of a crocodilian system dominated by a pelvovisceral pump operated by pelvis-based diaphragmatic muscles. A reanalysis of the soft tissue evidence shows that it is at best ambiguous, and is in some cases based on postmortem damage rather than real anatomy. The osteological data strongly support the presence of a preavian respiratory tract in the archosaurs ancestral to birds. The most bird-like theropod dinosaurs may have had a better developed lung–air sac system than the urvogel.

**Keywords**

Air sacs, birds, crocodilians, dinosaurs, evolution, lungs, respiration, theropods.

**Introduction**

Recent years have seen broad agreement that theropod dinosaurs probably evolved a preavian lung complex that was ventilated at least in part by air sacs (Perry 1983, 1989, 1992; Paul 1988, in press; Reid 1996, 1997; Britt 1997; Currie 1997; Britt et al. 1998; Claessens and Perry 1998; Burnham et al. 2000). This largely osteology-based conclusion supports the majority view that birds descended from derived predatory dinosaurs. Ruben and co-workers (Ruben, Jones et al. 1997; Ruben, Leitch et al. 1997; Ruben et al. 1999) have proposed that theropod dinosaurs instead possessed a crocodilian-like pelvovisceral pump (piston) lung ventilation system, based largely on their interpretations of the preserved soft tissues of *Sinosauropteryx* and *Scipiónyx*. In their view this favors at most a sister group, rather than a direct ancestor–descendent, relationship between dinosaurs and birds.

To verify the presence of either a pelvovisceral pump or pulmonary air sacs some requirements must be met. When soft tissues are preserved, it must be shown that it is possible to discriminate between a crocodilian-like and a bird-like set of fossilized central organs. It must also be shown that the fossil soft tissues of concern have actually been preserved and identified correctly, and that the tissues retained their correct anatomical configurations and positions; multiple specimens must confirm that the characteristics of the tissues do not vary significantly within the taxon under consideration. It must be also shown that the skeletal anatomy is more compatible with the operation of a pelvovisceral pump than with air sacs, or vice versa, especially if soft tissue analysis proves inconclusive.

Institutional abbreviations used in this paper are: BMNH, Natural History Museum, London, U. K.; MIG, Mongolian Institute of Geology, Ulan Bator, Mongolia.
Soft Tissue Analysis

**Organ identification and configuration in the specimens**

Distinct internal organs are preserved in the well-prepared type of *Scipionyx* (Figure 1B; Dal Sasso and Signore 1998; Ruben et al. 1999). The heart appears to be absent. Part of the tracheal cartilage is positioned well ventral to the caudal cervicals. The intestines are exquisitely preserved, perhaps because digestive chemicals altered preservation in their favor. The digestive tract is set in the caudal half of the body cavity, with the cranial edge of the intestines below dorsal vertebra 9. The colon runs immediately ventral to the caudal dorsals and sacrum. The material identified as the liver is in the correct position for this organ; it is less well preserved than the intestines. The liver appears to have been so deep that it filled the entire body cavity from top to bottom. The liver also sits immediately behind and below the caudalmost end of the scapula blade, and between the distal ends of the tucked up humeri. The organ also sits above the cranial end of the gastralia, which probably marked the caudal end of the cartilaginous sternum; so the liver sat above the caudal end of the sternum in birds as well (Figure 2A). None of the thin septa that separate internal organs is preserved. Ruben and his colleagues (1999) noted the presence of possible muscle traces immediately cranial to the distal pubes. They proposed that these are oriented in the manner expected of diaphragmatic muscles.

The type of *Sinosauropteryx* (Figure 1A; Morell 1997:36–37, cover; Ruben, Jones et al. 1997; Chen et al. 1998) is much less well preserved, and was damaged more during collection and preparation by an amateur. The slab was shattered into about two dozen pieces, probably as it was removed from the ground. After splitting revealed the skeleton, the fragments were reattached with cement. Cement was often used to fill in broad cracks, and in some cases was colored to match the sediment, thereby obscuring the damage.

The conclusions of Ruben, Jones and others (1997) concerning *Sinosauropteryx* were based on examination of photographs rather than direct examination of the specimen, which was not described in some detail until Chen et al. (1998). Figure 1A shows that even high resolution photographs of the thorax are hard-pressed to record the actual condition of this specimen because it is so damaged and severely crushed, and the repair work so well matched to the matrix. Nor did Ruben et al. (1999) mention the breakage and repairs. The two studies included rather low quality photographs of the main slab, with the first photograph marked by three arrows that point to the edge of an alleged septal boundary that forms the cranial border of the dark material present on both slabs (Ruben, Jones et al. 1997, fig 5A; Figure 1A). Because the material lies medial to the ribs it appears to be carbonized internal tissue. Direct examination of the main slab confirms that the breakage is especially extensive at the dorsocranial edge of the carbonized material (Figure 1A). The ribs are also broken at this location. This break occurred when a thin layer of sediment dislodged from the main slab and remained attached to its counterpart. The dorsal arrow in Ruben, Jones et al. (1997) points directly to the edge of this break. A large, complex set of breakage astride and running perpendicular to the anterocentral edge of the dark tissue is present on both slabs. The damage is partly filled in with cement, which seems to have been colored to better match the dark material. A narrow, irregular zone of dark material lies immediately forward of the crack. The material’s cranial extent is further obscured by the presence of a rib, but it extends too far craniodorsally to conform to the smooth convex arch described by Ruben and his colleagues. On both slabs the ventrocranial border of the dark material is another illusion created by an irregular, flaky zone of the superficial layer of sediment; the ventral arrow (Ruben, Jones et al. 1997; Ruben et al. 1999) points towards this pseudo border. Caudal to the central and ventral damage there is a very irregular zone of darker material. Because over 60% of the cranial boundary of the dark material consists of breakage, and the preserved edges of the tissues are irregularly formed, there is no well-formed, semicircular structure present on either slab. Instead, the smoothly arched septum is a mirage created by cracks, breaks and cement filler shared by the symmetrically damaged slabs, and accentuated by poor quality photography. Neither of the other two *Sinosauropteryx* specimens shows evidence.
FIGURE 2. Comparative anatomy of the thorax in archosaurs, with emphasis on the respiratory complex. A, contents of thorax in diapsids: top, varanid lizard with conventional liver (after Duncker 1979); second from top, modern crocodilian with enlarged, fore-and-aft sliding pelvovisceral piston and strong fore-and-aft partitioning of body cavity (after Duncker 1979; Ruben, Jones et al. 1997); second from bottom, flightless ostrich with small, cranially placed liver (after, in part, Fowler 1991); bottom, flying pigeon with normal-sized liver (Dorst 1974). B, cross section at midthorax of flying carrion crow with enlarged liver that extends dorsally between lungs, also note the air sacs lateral to the guts (after Duncker 1979). C, articulation between ribheads (solid black) and dorsal series: top, modern crocodilian; second from top, Coelophysis; third from top, Yangchuanosaurus; bottom, duck. D, variation of ossification (black bone, white cartilage) of sternum and sternal ribs and absence of uncinate processes: left, ostrich hatchling; center, very large emu; right, precocial king rail chick at about two and a half weeks. Livers with heavy borders and light stippling, heart with heavy border, kidneys with heavy stippling, muscles solid black. E, Articulated gastralia of archosaurs: from left to right, Euparkeria (Ewer 1965), crocodile (Mook 1921), basal neotheropod Syntarsus (Raath 1977), dromaeosaur (Norell and Makovicky 1997), basal bird Changchengornis (Ji et al. 1999). Abbreviations: l, lung; d, digestive tract; a, air sac. Not to same scale.
Respiratory complexes of predatory dinosaurs

of a septal boundary (Ackerman 1998:78–79; Chen et al. 1998, fig. 4a, in which eggs contribute to the cranial portion of an irregular abdominal dark area).

The cranial region of the dark material is so poorly preserved that separate organs are not distinguishable. Ruben and his co-workers (Ruben, Jones et al. 1997; Ruben et al. 1999) identified this material as the liver. However, the space above the cranial end of the gastralia just behind the caudalmost extent of the scapula and between the tucked up humeri is empty (Figure 1A), so the liver was probably not preserved. The caudalmost dark material is below dorsal 8, and the caudal region has a pattern suggestive of the digestive tract, possibly containing some fecal material. This arrangement is similar to the pattern of the digestive tract seen in Scipionyx (compare Figure 1A and 1B). I therefore conclude that the dark material is probably all that remains of the digestive tract, barely preserved because of its chemistry. In this case both the liver and heart rotted away.

Interpretation of the specimens

Some of the soft tissue anatomy discussed in this section is discussed in further detail later. Ruben and his co-workers (Ruben, Jones et al. 1997; Ruben et al. 1999) proposed that the cranial border of deep livers in Scipionyx and Sinosauropteryx indicates the presence of a smooth, cranially convex arch that spanned the middle of the body cavity from top to bottom. They further suggested that the configuration of the arch is compatible with a postpulmonary septum that partitions the body into distinct fore-and-aft compartments in the manner seen in crocodilians but not in birds (Figures 2A and 3B). Because the actual septum is not preserved in either theropod specimen, the presence and nature of fore-and-aft compartmentation must be inferred only after inferring the configuration of the septum, which in turn is based on configuration of the preserved liver. Such a series of inferences is potentially weak. The absence of any preserved septa, and the apparent absence of the liver in Sinosauropteryx, leaves only the great depth and configuration of the liver of Scipionyx subject to further analysis.

Livers are multipurpose organs with both physiological and anatomical functions, and whose size, shape and location are very variable. Livers tend to be larger in carnivores than in herbivores (Siwe 1937), and liver size can vary within a given species (Secor and Diamond 1995; Perry, personal communication based on wet preserved crocodilian specimens). In modern crocodilians the liver is so tall that it spans the body cavity from nearly the top to nearly the bottom of the ribcage (Figures 2A and 3B; Duncker 1979; Ruben, Jones et al. 1997). In many birds the liver is much less enlarged and is set low in the body cavity, often well forward in the chest region (Figure 2A). However, in some birds the liver is so large and tall that it spans most of the distance from the sternum to the vertebrae, to the point that it even extends up between the high-set lungs (Figure 2B; Duncker 1979; Brackenbury 1987:41, fig. 1). There is not, therefore, a consistent correlation between the presence of a very tall liver and the presence of a pelvovisceral pump. The cranially convex arch that characterizes the cranial border of the liver and the postpulmonary septum in crocodilians is also seen in birds (Figure 2A; Brackenbury 1987:41, fig. 1). The presence of a fossil liver that spans the entire depth of the body cavity and is cranially convexly arched is compatible with either the crocodilian-like or bird-like conditions, so it does not tell us whether a missing septum divided the body cavity into distinct fore-and-aft compartments, or whether or not the liver was mobile. Consider that if the skeleton of a fossil bird with a large liver was preserved on its side, the deep liver would give the illusion that a vertical septum divided the body into fore-and-aft compartments in the crocodilian manner. Lacking preserved septa, it can only be said that the soft tissues observed in the small theropods are compatible with either the crocodilian or avian conditions, especially since flesh eaters are prone to having large livers.

To determine pelvovisceral mobility using fossil soft tissues would require the discovery of unambiguous pelvis-based diaphragmatic muscles. The little patch of possible tissues identified as such muscles by Ruben and his co-workers (1999) does not reach cranially to the liver, is poorly preserved, and lacks the fine fibers that characterize the less ambiguous muscle tissues.
Figure 1. Compressed dinoavepod specimens with preserved soft tissues. A, Sinosauropteryx type in which the ill-defined, badly damaged dark material probably represents the digestive tract; dots mark points of arrow tips in fig. 5A in Ruben, Jones et al. (1997) B, Scipionyx type with preserved intestines and probable liver and trachea, ventrally displaced cervical vertebra indicated by arrow. In both the probable caudal cartilaginous sternum is indicated by the dashed line; note that there is no organ preserved in A in the same position (indicated by question mark) as the liver in B. Abbreviations: g, gastralia; h, humerus; p, pubis; v, vertebrae. Not to same scale.
FIGURE 3. Phylogenetic chart of thoraxes, pelves and respiratory tracts restored and known in archosaurs: A, basal archosaur *Euparkeria*, which probably had a little-modified, basal tetrapod system. B, modern crocodilian with divergent pelvovisceral pump. Neotheropods with increasingly well-developed air sac complexes: C, *Coelophysis* with long chest ribs. Tetanurans with shorter chest ribs: D, *Yangchuanosaurus* with moderately shortened chest rib (see Dong et al. 1983:76, fig. 51). Avetheropods with short cranial chest rib: E, *Allosaurus*. Bird-like theropods with bellows action ossified sterna, sternal ribs and uncinate processes: F, velociraptorine dromaeosaur; G, flightless kiwi with short sternum and free caudal ribs; H, flying duck with extremely large sternum attached to all ribs. Articulated pubes with deep pelvic canals in cranial view of: I, *Archaeopteryx*; J, *Avimimus* (Kurzanov 1987); K, alvarezsaur *Patagonykus* (Novas 1997). B, E and F include articulated pubes in cranial view; lungs are irregularly lined, pulmonary diverticula are stippled, diaphragmatic muscles are fine-lined, ossified gastralia, uncinate processes, ribs, sternal ribs and sterna are solid black, restored cartilaginous sternal elements and sternal ribs have heavy lines; hinge articulation of sternum with coracoid (only ventral half included) indicated by arrows in F, G and H; sternocostal articulations in D and E after Lambe (1917) and Currie and Zhao (1993); all based on articulated ribcages. The relationship between the midribcage ceiling and respiratory anatomy and function shown by transverse cross section, and sagittal sections along transverse processes in lateral view: L, modern crocodilian with liver in solid black (in part after data from Klein and Perry, personal communication), liver supporting ligaments lined, liver sac stippled, arrows indicate anterocaudal motion of liver; M, generalized avetheropod–bird with lung and bone diverticula sections on right side. Abbreviations: r, rib; t, transverse process. Not to same scale.
described by Dal Sasso and Signore (1998). Therefore, the actual length and orientation of the muscle fibers are not certain. The longitudinally oriented undulations observed by Ruben and colleagues may be superficial in nature. The configuration of these tissues resembles the superficial, pubis-based abdominal wall muscles of birds, especially the caudalmost M. obliquus and M. rectus components of the abdomini (compare Ruben et al. 1999, fig. 3 to Fedde 1987:6, fig 1). At this time the material can only be said to represent a small patch of probable tissues whose identity, extent and orientation are uncertain. Definitive evidence for diaphragmatic muscles is lacking in Scipionyx and in other theropods because of the lack of additional specimens.

The dorsal position of the colon in Scipionyx is more like that of crocodilians and mammals than the avian configuration, in which the terminal sections of the alimentary canal are more ventrally placed (Duncker 1979:50, fig. 2.11 and 2.17e, f; Fowler 1980:212, fig. 8). Ruben and co-workers (1999) suggested that the avian arrangement is tightly linked to function of the caudal air sacs. However, their explanation for this link was not clear. It has not been shown that dorsally placed colons are consistently absent in tetrapods without diaphragmatic respiration; the hypothesis of preavian respiration in theropod dinosaurs does not necessarily require fully avian caudal air sacs, and ventrally placed colons are probably present in some theropod dinosaurs (see below).

In deep-lunged crocodilians the trachea sits low in the neck base; in shallow-lunged birds it often runs more dorsally. Ruben and co-workers (1999) cited a ventral position of the preserved trachea in Scipionyx (Figure 1B) as evidence in favor of the first condition. The level of the trachea below the neck base is variable in birds—even in a given individual, tracheal position may change on the position of the neck at any given moment—and can be as low as seen in Scipionyx (Nickel et al. 1977:67, fig. 69; McLelland 1989a:79, fig. 2.8a). Nor is it certain that the position of the trachea in the dinosaur can be relied on. Ruben and colleagues (1999) failed to observe that cervical 10 is displaced ventrally relative to its neighboring vertebrae, and the errant cervical may have pushed the trachea in the same direction. The position of the trachea in theropods remains open to question until other examples become available, and a low-set trachea is compatible with either deep or shallow lungs.

The actual preservation of shallow, dorsally placed lungs or air sacs that would favor the presence of a bird-like respiratory complex is improbable, because the air-filled organs are poorly suited for preservation. This is especially true because they inconsistently lie partly lateral to more preservable central organs such as the heart and liver, which will obscure the original extent of the lungs if the specimen is flattened on its side. Consider that in crocodilians the lobes of the lungs are lateral to the heart but not the liver; in some birds the opposite is true (Figure 2A, B). Because the walls of air sacs are very thin (McLelland 1989b), fossilizing these bags of air is as improbable as fossilizing a balloon, even more so if the specimen is flattened. Most of the thoracic sacs lie lateral to the internal organs (Figure 2B), so organ-free spaces are not expected to mark the sites of air sacs if the specimen is flattened and lying on its side.

The type of Sinosauropteryx can at most be said to include very poorly preserved and badly damaged amorphous dark material that lies between the ribs in the caudal half of the thoracic cavity and that is most compatible with representing traces of the intestines. Despite its exceptional preservation, the type of Scipionyx is a single, somewhat damaged, very small juvenile whose internal structure—especially the depth of the liver—may have changed with ontogeny or physical condition, and whose preserved internal anatomy is compatible with either a crocodilian-like or a preavian—but not fully avian—system. At this time a diaphragm, fore-and-aft partitioning of the thoracic cavity, and deep lungs have been directly observed in theropod dinosaurs. The soft tissue evidence that any dinosaur possessed a crocodilian-like respiratory complex is at best weak.

Functional Osteological Analysis
Because the soft tissue evidence is not definitive, it is necessary to turn to osteological data to attempt to restore the respiratory complex of dinosaurs. To do so, the skeletal and pulmonary adaptations of modern archosaurs must first be cross-correlated.
Crocodilians

In crocodilians (Figures 2A, C and 3B, L), the trunk is long, shallow and flexible, chest ribs are long, vertebrae–rib articulations are simple along most of the dorsal series, and the pubes are procumbent. The dead-end lungs are highly flexible and deep, but are smaller than in other diapsid reptiles, perhaps because they are internally more complex and correspondingly efficient. A subvertical septum separates the tall liver from the rest of the abdominal cavity, forming a fore-and-aft separation of the body cavity. The pelvic canal is immediately below the sacrum.

The lungs are highly compliant, and are deeply indented only by the first two thoracic ribs (Perry 1988, personal communication). Only the first three ribs are double-headed, and they articulate with the vertebrae in the normal archosaur manner. The midthoracic ribs articulate only with the lateral ends of hyperelongated, dorsally flattened transverse processes (Mook 1921). This unique feature forms an exceptionally smooth bony ceiling to the ribcage (Figures 2C and 3L). The gastralia, which do not articulate along the midline (Figure 2E), are set in a continuous cartilage sheet (Mook 1921). The combination of the smooth ribcage ceiling and cartilage-embedded gastralia basket help form a well-braced, subcylindrical body tube through which the viscera can easily slide strongly back and forth as the lungs are ventilated (Gans and Clark 1976; Perry 1988, 1990). The diaphragmatic muscles that help operate this pump attach to the capsula fibrosa of the liver rather than directly to the liver (Duncker 1978; Perry, personal communication). A large, rib-free lumbar region cranial to the pelvis allows the volume of the abdomen to change dramatically as the pelvovisceral pump operates. This feature is also seen in mammals with diaphragm–lung ventilation. The pulmonary septum is airtight and maintains a pressure differential between the fore and aft thoracic compartments. The viscera is pulled backwards by large diaphragmatic muscles anchored to the cranial edges of the ventral pelvis, and to caudal gastralia. Because of the involvement of the pelvis, and because organs other than the liver participate in the piston-like action, the term “pelvovisceral,” rather than “hepatic,” more appropriately describes this piston–pump. Crocodilian pubes are only about one-tenth trunk length, are much shallower than the liver, and are about as broad as they are long, so by no means are the pubes “elongate” as Ruben and colleagues (Ruben, Jones et al. 1997) claimed. Nor is there a true pubic boot; the pubes are distally transversely expanded to form broad, shovel-like plates. The abdominal surface of this expansion faces strongly forward and a little medially, thereby helping support the broad abdomen. Crocodilian pubes are able to swing rostrocaudally, and work by Farmer and Carrier (2000) indicates that this unique mobility enhances mobility of the viscera. Lacking hinged joints with either the coracoids or sternal ribs, the narrow and largely cartilaginous sternal elements are not highly mobile. At most poorly ossified, the sternal ribs are doubled, an unusual feature whose respiratory functions are obscure. Nor is the function of the cartilaginous or poorly ossified uncinate processes present on crocodilian ribs well documented.

Modern birds

The small lungs of modern birds are internally very complex (Figures 1 and 2G, H, N) (Huxley 1882; King 1966; Duncker 1971, 1979; Lawiewski 1972; Schmidt-Nielsen 1972; Nickel et al. 1977; Fedde 1987; McLelland 1989a, 1989b). Lungs are semirigid, so the dorsal column is correspondingly inflexible. The series is also very short because the number of dorsal vertebrae is very reduced. Also short are the cranial chest ribs, which need to only hold rather than ventilate the shallow, stiff lungs. The midthoracic ribheads’ ventral processes are long and set well below moderately long, "T" cross-sectioned transverse processes. These features create a series of deep ridges along the entire ceiling of the ribcage. Dorsal lobes of the lung tightly fill the intervening recesses. The lungs are further immobilized in most birds by invasion of pulmonary diverticula into consistently pneumatic vertebrae and ribs. However, the vertebrae and ribs of many small fliers, most divers, and kiwis are reported to be weakly or not pneumatic despite the presence of well-developed air sacs (Bellairs and Jenkin 1960; King 1966; McLelland 1989b). The pubes are elongated, slender, and extremely retroverted. The pelvic canal is very deep. A
pubic boot and gastralia are absent. The pubes and central organs are not highly mobile.

Large ventrocaudal air sacs (clavicular, thoracic and abdominal) fill much of the body cavity. These act as bellows to ventilate the lungs through a complex set of pulmonary plumbing (Zimmer 1935; King 1966; Duncker 1971; Lawiewski 1972; Schmidt-Nielsen 1972; Dorst 1974; Nickel et al. 1977; Brackenbury 1987; Fedde 1987; McLelland 1989b; Scheid and Püper 1989; Brackenbury and Amaku 1990). Air flow is predominantly unidirectional, moving from the back to the front. The bronchi connecting the lungs and caudal air sacs breach the arched horizontal septum, which does not maintain a strong pressure differential; another septum separates the liver from the abdomen (Schmidt-Nielsen 1972; Duncker 1979). The caudal thoracic ribs of all birds are elongated, so there is no lumbar region. The caudal thoracic ribs also have well-developed double heads, which are also angled relative to the main axis of the body. These unusual ribhead articulations serve to tightly control the rotation of these ribs (Zimmer 1935; King 1966; Duncker 1971, 1978; McLelland 1989b). They are prevented from rotating so far medially that they collapse the laterocaudal air sacs. Instead, the resulting hinge joint allows the ribs to move freely in a single plane. Because the double heads are angled, the rotation of the ribs is rostrolateral and caudomedial, which significantly changes the volume of the caudal body cavity in transverse as well as front and back directions. The rotation of the caudal thoracic ribs is accomplished at least in part with intercostal and other axial muscles. The resulting rotation changes the volume of the thoracic and abdominal air sacs that they enclose. Cranially, the sternum is connected to the ribcage through hinged sternocostal joints with ossified sternal ribs, which are not doubled. The hinged joint formed by the transversely broad articulation between the coracoids and sternum allows the raisable and depreessable sternal plate to help ventilate the cranial and ventral air sacs. The mobile ribs, sternal ribs and sternum work in concert to form an integrated unit that ventilates the air sacs (Zimmer 1935; King 1966; Duncker 1971; Lawiewski 1972; Schmidt-Nielsen 1972; Fedde 1987; McLelland 1989b; Scheid and Püper 1989; Ruben, Jones et al. 1997).

Most avian ribcages include well-developed ossified uncinate processes, which are thought to assist respiration by improving the action of the intercostal muscles (Zimmer 1935; Duncker 1971; Fedde 1987; Ruben in Feduccia 1996), and help strengthen the ribcage (Bellairs and Jenkin 1960). However, some flying and flightless birds, both juvenile and adult, living and extinct, lack prominent uncinate processes (Figure 2D; Heilmann 1927; Zimmer 1935:14, figs. 21–23; Murray and Megirian 1998), showing that their development is not critical to air sac driven respiration.

The above analysis applies to birds in general. Almost all studies of modern avian respiration have focused on flying birds, many of which have extraordinarily high sustained exercise oxygen demands. The caudal air sacs of flying birds (Figure 3H) are very large, in most cases extending along the sides of the abdominal cavity all the way to the extreme rear end of the body cavity. The caudal thoracic ribs are very elongated to help ventilate these sacs. All but the cranialmost ribs are connected to the sternum by ossified sternal ribs. The sternum is so long that it is often as long as the entire ribcage, and its caudal end is beneath the cranial end of the pelvis. The geometric result of such a greatly elongated sternum is such extensive dorsoventral movement at the caudal end that the sternum helps ventilate the enormous posteroventral air sacs.

Birds whose flight abilities are reduced or absent have largely been neglected, although they are likely to be better models for early birds and their ancestors. Schmidt-Nielsen's (1972) observation that ratite and flying bird respiration are similar is not entirely true; there are major differences between the two types. In all ratites the abdominal air sacs are not as large as in most birds (Huxley 1882; King 1966; McLelland 1989b). Kiwis (Figure 3G) and cassowaries have the smallest abdominal air sacs among modern birds (the sole lateral illustration of ratite diverticula is of the kiwi, by Huxley [1882]; Beale [1985] stated that an unpublished radiograph confirmed the prior study). The sacs do not extend caudally into the abdominal cavity, but they remain large and extend to the pelvis. The reduced air sacs of female kiwis may or may not be related to the extreme size of their eggs, but this does not apply to males or to cassowaries. The
FIGURE 4. A, the thorax as preserved of the “fighting” *Velociraptor* (MIG 100/25) in oblique cranioventrolateral view (based on Tomida and Sato 1995:13). Large ossified sternal plates articulated with ossified sternal ribs, as well as a series of ossified uncinate processes, are visible. The scapulocoracoids are no longer in articulation with the coracoidal grooves on the cranial edges of the sterna, and the furcula is missing. Ossified thoracic items of dromaeosaurs: B, sternum of MIG 100/25 (after Barsbold 1983). C, left uncinate processes: top, *Deinonychus* tentative identification; middle, MIG 100/25; bottom, turkey (note that the cranial ends are deep and flattened to help form sternocostal joints). D, sternal ribs: top, *Deinonychus*; bottom, pigeon. E, transverse sections of articulated dromaeosaur chests: left, outdated restoration (after Ostrom 1969) with double sternal ribs and narrow sternum, at sixth dorsal and rib; right, updated version with ossified uncinate, single sternal rib and broad sternal plate, at fifth segment (in part after Paul 1988). *Abbreviations*: c, coracoid; f, femur; g, gastralia; h, humerus; is, ischium; p, pubis; s, scapula; sr, sternal rib; st, sternum; u, uncinate process. Not to same scale.
caudal thoracic ribs of ratites are shorter than in other birds (compare Figure 3G to 3H), but have the well-developed, offset, mobile double heads. Because the caudal thoracic ribs are not attached to the sternum, they must work independently of, albeit in concert with, the sternal complex, which is relatively weakly attached to the ribcage. The hinged sternocoracoid joint is retained, but ratite sternae are also shorter than in flying birds. The shortness of these sternae geometrically limits their dorsoventral rotation at the caudal end, comparatively limiting their ability to alter thoracic volume. The short sterna do not extend caudally to under the pelvis, even with the aid of a short cartilaginous extension. The ossified sternal plates of kiwis and elephant birds are set well cranial on the chest and are very short, only a third or less the length of the ribcage (Figure 3G). These sterna are unable to influence directly the caudal air sacs, which should therefore be ventilated primarily by the free caudal ribs through the muscles that operate them. The failure of ratites to retain large sternae consistently shows that these are primarily flight-related features not necessary to operate an effective air sac complex in flightless archosaurs. The number of ossified sternal ribs may be as few as two or three.

Precocial rail and ratite chicks quickly become fully energetic and active outside the nest (del Hoyo et al. 1992–99). At hatching and for weeks afterwards their sternae remain short and cartilaginous, and the sternal ribs are only partly ossified (Figure 2D; Olson 1973). Fully grown yet not fully mature domestic fowl also have poorly ossified sternae. Precocial chicks indicate that even a cartilaginous, weakly connected sternum does not prevent the operation of a fully functional air sac complex.

Among adult birds with reduced flight performance, roadrunners have short sternae that seem unable to ventilate caudal air sacs. Only three ribs are directly connected to the sternum by ossified sternal ribs, and a fourth indirectly by a partial sternal rib. This reduced respiratory apparatus is able to oxygenate sustained high speed ground movement as well as short flights. Short sternae are also observed in other poor fliers, such as the ash-colored tapaculo (Feduccia 1996:264). It is also important that when as much as 70% of air sac capacity is disabled in chickens the birds remain functional and able to sustain normal walking speeds, although flight aerobic capacity is limited (Brackenbury and Amaku 1990).

Because flightless birds probably descended from, or are the juveniles of, flying birds, their respiratory tracts probably reflect a heritage of flight. Even so, the respiratory anatomy and function of flightless birds is the best comparative model we have for restoring the respiration of the bird ancestors.

Neotheropod dinosaurs and basal birds
The thoraxes of these dinosaurs and early noncarinate birds (Figures 1, 2C and 3C–K, M) were similar enough that they can be discussed together. Their trunks were shortened, by at least three vertebrae relative to crocodilians, and were stiffened by extra intervertebral articulations, partly ossified interspinal ligaments, or both (Ostrom 1969; Paul 1988). The trunk was transversely narrow. The ceiling of the body cavity was deeply corrugated by unusually deep vertebra-rib articulations of the avian type along most or all of the dorsal series, and there were no hyperelongated transverse processes. Therefore, there was no smooth bony ceiling of the ribcage of the type seen in crocodilians. In most neotheropods at least some vertebrae and ribs were consistently pneumatic, in some cases as far caudally as the sacrum and tail (Russell and Dong 1993; Britt 1997). The caudal ribs had mobile double heads and were elongated, so a lumbar region was absent. Pubes were always very long, at one-third to one-fourth trunk length. They were always gracile and transversely narrow, especially distally; overall length to width ratio was 3 or 4 to 1. Development of the distal boot was highly variable, ranging from absent in early theropod dinosaurs, bird-like troodonts and derived alvarezsaurids, to moderately or very large in most predatory dinosaurs and basal birds (Figure 3C–F). The main surface of the boot faced laterally; the abdominal surface was very narrow. Pubic orientation was very variable, ranging from strongly propubic to strongly retropubic in theropods, and minimally to strongly retropubic in basal birds. The boot projected caudally to the distal tip of the ischia only in dro-
<table>
<thead>
<tr>
<th><strong>TABLE 1. Skeletal adaptations associated with crocodilian and avian respiratory systems.</strong></th>
<th><strong>Associated with the operation of a pelvovisceral pump</strong></th>
<th><strong>Associated with the operation of air sac ventilation</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Exclusive to system</strong></td>
<td>Bony ribcage ceiling smooth (formed by elongated, flattened transverse processes articulating with ribs only at their tips)</td>
<td>Various postcranial bones consistently pneumatic (due to invasion by pulmonary, diverticula), sometimes posterior to pulmonary septum</td>
</tr>
<tr>
<td></td>
<td>Gastralia do not meet on midline and are set in cartilage sheet</td>
<td>Bony ribcage ceiling strongly corrugated (because medial ribheads are set well below transverse processes)</td>
</tr>
<tr>
<td></td>
<td>Pubes mobile</td>
<td>Posterior ribs elongated and highly mobile in stereotypical manner (because of well-developed, angled double heads)</td>
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<tr>
<td></td>
<td></td>
<td>Large sternum articulates with coracoids through a hinge joint</td>
</tr>
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<td></td>
<td></td>
<td>Sternocostal articulations are hinge joints</td>
</tr>
<tr>
<td><strong>Probably critical to system, but may be found in other tetrapods</strong></td>
<td>No consistent excavation of bones, especially posterior to pulmonary septum</td>
<td>Dorsal series short and stiff</td>
</tr>
<tr>
<td></td>
<td>Sternal ribs doubled</td>
<td>Sternal ribs single</td>
</tr>
<tr>
<td></td>
<td>Well-developed lumbar region</td>
<td></td>
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<tr>
<td></td>
<td>Pubes at least fairly broad</td>
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</tr>
<tr>
<td><strong>Associated with, but not exclusive to, system</strong></td>
<td>Uncinate processes are at most poorly ossified</td>
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<tr>
<td></td>
<td>Ribcage broad</td>
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<tr>
<td><strong>Often associated with, but not exclusive to, system</strong></td>
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<td>Ossified uncinate processes</td>
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<td></td>
<td></td>
<td>Short anterior ribs</td>
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<td></td>
<td></td>
<td>Sternal ribs ossified</td>
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<td></td>
<td></td>
<td>Pubes very narrow</td>
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<td></td>
<td></td>
<td>Pubes retroverted</td>
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<td></td>
<td></td>
<td>Pelvic canal deep</td>
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<tr>
<td><strong>Present in basal birds</strong></td>
<td></td>
<td>Gastralia articulate on midline with an overlapping zig-zag pattern</td>
</tr>
<tr>
<td></td>
<td>None of these adaptations observed in theropods</td>
<td>These adaptations observed in all, most or some theropod dinosaurs</td>
</tr>
</tbody>
</table>
maeosaurs and many basal birds (Figure 3F; Norell and Makovicky 1997; Xu et al. 1999), but probably not *Archaeopteryx* (Wellnhofer 1993). In most neotheropods the pelvic canal was immediately below the sacrum, and was set above exceptionally deep distal pubes (Figure 3E and F). In dromaeosaurs, oviraptorosaurs, rahnovids, avimimids, alvarezsaws, archaeopterygiforms and all other birds the pelvic canal was deepened (Figure 3F, I–K); in avimimids and alvarezsaws the canal was deeper than in *Archaeopteryx*.

The trunks of theropod dinosaurs and crocodilians could hardly have been more different. The double-heading of the entire theropod thoracic rib series is opposite the winglike transverse processes of crocodilians (contra Hengst 1998). A triradiate pelvis is not only a common diapsid feature, it is absent in some theropods. Table 1 shows that the two groups share not a single osteological adaptation that supports the presence of a pelvovisceral pump in any predatory dinosaur. Indeed, the operation of a pelvovisceral piston seems to have not been possible in the latter. The absence of a smooth bony ribcage ceiling means that it was not specialized to accommodate, and may have hindered, the easy back and forth movement of an expandable lung and a pelvovisceral piston. The exceptionally deep corrugation, pneumatic-style excava-

tion of the dorsals and proximal ribs, and lack of a need for well-developed intracostovertebral muscles in stiff-backed theropods did not favor the presence of the smooth muscular thoracic ceiling seen in some other tetrapods (Carrier 1989); instead they suggest the presence of dorsal air sacs that would have precluded the presence of such muscles. The lack of a well-developed lumbar region contradicted the major abdominal volume changes inherent to the operation of a pelvovisceral pump. The abdominal surface of the most gracile pubes appear to have been too transversely narrow to anchor large diaphragmatic muscles. Pubic immobility would not have enhanced the operation of a pelvovisceral pump; indeed, it is difficult to see how the pubis could have been an important part of the respiratory complex when its orientation and boot development were so variable in neotheropods. Because the position of the colon is a function of the depth of the pelvic canal, the variation of the latter in the dinosaurs indicates that the configuration of the colon was similarly variable, and those neotheropods with deep pelvic canals probably had low-set colons in the manner of birds.

Claessens and Perry (1998) have argued that the unusual interlocking midline articula-
tions of theropod gastralia (Figures 2E and 4A) allowed ventilation of abdominal air sacs. Whether theropod abdominal air sacs extended so far posteroventrally that they could be di-
rectly operated by the gastralia is uncertain. But it is significant that basal bird gastralia had the same distinctive midline, zig-zag articulation and presumably function, as seen in theropods, and was markedly different from that of crocodilians and other archosaurs (Figure 2E). This situation suggests that theropod gastralia were not set in a cartilage sheet in the crocodilian manner.

**Evolution of the Theropod–Bird Respiratory Complex**

Theropod dinosaurs exhibit a progressive development of increasingly bird-like respiratory adaptations. The following is a tentative outline of the evolution of the theropod–bird respiratory complex.

**Tetradactyl theropods**

Absence of pneumatic postcranial bones or elongated caudal ribs with double heads indicates that diverticula were at most poorly developed. Long cranial chest ribs suggest that the lungs remained deeper and more flexible than in birds. The dorsal series was shortened and corre-

dondingly more rigid than in basal archosaurs. The ceiling of the ribcage cavity was more strongly corrugated because the number of double-headed ribs increased, from 9 to 11, while the number of caudal dorsals that lacked mobile ribs declined, from 2 to 5 (Galton 1977:237, fig. 3; Novas 1993:402, fig. 1). The rigidity and dorsal corrugation of the ribcage suggest that the lungs were less flexible than in reptiles. The dominance of double head ribs indicates that the ventilation capacity of the ribcage had expanded. The combination of these adaptations sug-
gests that the dorsal portion of the lung was rigid, and that flexible nonvascular ventrocaudal diverticula were being ventilated by the highly mobile ribs that encompassed them.

**Basal neotheropods**
Complete ribcages (Figures 2C and 3C) show that the chest ribs were still long, and corrugation of the body cavity ceiling remained modest in that the depth of the vertebrae—rib articulations was not great. Therefore, central lung anatomy may not have changed much from the basosaureropod condition. However, the dorsal series was shorter, and pneumatic cervicals indicate that well-developed lung diverticula were present. Most importantly, all but one of the caudal thoracic ribs had well-developed, strongly angled double heads—for a total of 12—and the caudal thoracic ribs were more elongated than in more basal archosaurs (compare Figure 3C to A). It is difficult to explain bird-like caudal ribs that were able to dramatically alter the volume of the upper abdominal cavity as anything other than a mechanism to ventilate the initial caudal extension of the respiratory tract, probably in the form of a saclike organ.

**Basal Tetanurae and Avetheropoda**
In basal Tetanurae and Avetheropoda the trunk was deeper relative to its length. Complete ribcages (Figures 2C and 3D, E) show that the cranial chest ribs of basal tetanurans such as
yangchuanosaurs were beginning to shorten (compare Figure 3D to C). In compsgnathians, allosaurs and the rest of avetheropods the cranial ribs were as reduced as those of birds (compare Figure 3E, F to 3G,H). This is not due to bipedalism or forelimb reduction, because basal theropods were small-handed bipeds with long cranial thoracic ribs, and these ribs were persistently short in avetheropods regardless of whether the arms were small or large. The ceiling of the body cavity was strongly corrugated because the middle vertebral-rib articulations were deep. The cranial dorsals and ribs were pneumatic. All these vertebral and rib adaptations suggest that the lungs were becoming locked firmly into the ribcage ceiling, and were becoming semirigid and as shallow or nearly as shallow as in birds, while diverticula were further enlarged (Claessens and Perry 1998). At the same time, more elongated caudal thoracic ribs—equaling in length those of ratchets (compare Figure 3D–F to 3C and 3G)—imply a further caudal shift in the volume expansion capacity of the ribcage. The further reduction of the lumbar region opposed the operation of an abdominal pump. Therefore, primary ventilation of the rigid lungs should have been through large thoracic and abdominal air sacs.

The unusually long-booted pubes common in tetanurans, avetheropods especially, do not appear to have been primarily an adaptation for limb function, since such pubes are absent in other erect-limbed, bipedal dinosaurs. They may have allowed the air sac system to operate unhindered while the dinosaur rested on the boot, with the chest clear of the ground. This negated the need for the caudopelvic system for air sac ventilation used by resting birds.

Unidirectional pulmonary airflow may have been developing in basal tetanurans. Perry (1992) has proposed how avian pulmonary air flow evolved from the archosaur pattern. The shortening of the chest ribs and further increase in caudal rib length and mobility is opposite the crocodilian condition, and entirely inconsistent with the presence of a dynamic diaphragm.

**Caudipterygians, oviraptorosaurs, dromaeosaurs, troodonts, alvarezsaurus and basal birds**

See Figures 3F, I–K, 4 and 5. Ruben and co-workers (Ruben, Leitch et al. 1997) reproduced a crocodilian-like restoration of a dromaeosaur ribcage that included doubled sternal ribs and a narrow sternum (Figure 4E). The restoration was based on incomplete, disarticulated remains complete and articulated thoraces of dromaeosaurs and other derived theropods show that they were bird-like to the point of being avian (Figures 3F and 4A, F). Troodonts (Figure 4F), caudipterygians (Ji et al. 1998), oviraptorosaurs (Barsbold 1983; Morell 1997:40), dromaeosaurs (Figures 3F and 4A, B; Norell and Makovicky 1997, 1999; Xu et al. 1999; Burnham et al. 2000) and basal birds (Wellnhofer 1993; Feduccia 1996; Martin et al. 1998; Ji et al. 1999) had broad sternal plates that articulated with the broad, transversely oriented ventral edges of coracoids whose superficial surfaces faced strongly cranially (Paul 1988). This arrangement formed a hinged sternocoracid articulation, which allowed the dorsoventrally mobile sternum to help ventilate the cranioventral air sacs in a manner approximating that of kiwis and juvenile precocial birds. Hinged sternocostal joints are also present (Figure 4C; Xu et al. 1999). Dromaeosaur sternal plates were 40% to 50% as long as the ribcage (ossified sterna were about half as long as the ilia and femora in Velociraptor [MIG 100/25 and 100/985]; in Sinornithosaurus and Bambiraptor the sternum was as long as the ilium [Xu et al. 1999; Burnham et al. 2000]), relatively larger than those of some birds (Figures 3F, G and 5). At the other extreme the ossified sternum of Archaeopteryx was only about 12% ribcage length (Wellnhofer 1993). The fairly long, albeit narrow, ossified sternum of alvarezsaurus may also have been useful in inspiration.

Vertebral aeration was almost as variable in the bird-like theropods as in birds themselves (McLelland 1989b; Russell and Dong 1993; Britt 1997; Britt et al. 1998). In some it was absent; in others caudal dorsals, sacrals and even caudals were pneumatic. The tendency towards caudal pneumatization of the vertebrae suggests that the caudal air sacs were fairly well developed (see above). The deepening of the pelvic canal, and a corresponding drop in the position of the colon, may have been associated with this expansion of the caudal thoracic air sacs.

In addition to their enlarged sterna, caudipterygians (personal observation; Ji et al. 1998), oviraptorosaurs (Norell et al. 1995, fig. 1a; Morell 1997:40) and dromaeosaurs (Figures 3F and
4A, C; Paul 1988; Claessens and Perry 1998; Norell and Makovicky 1999; Xu et al. 1999; Burnham et al. 2000) were exceptionally bird-like in having ossified uncinate processes and up to five undoubled ossified sternal ribs. Not only were these systems better developed and more avian than those of archaeopterygiforms, they rivaled the ratite condition. The last point suggests that the complexity and capacity of these dinosaurs’ air sacs approached or equaled those of ratites. Only in possessing a somewhat deeper pelvic canal was the archaeopterygiform respiratory apparatus more bird-like. Very slender, rod-like, retroverted, closely applied to the ischia, and with a very deep pelvic canal, the pubes of derived alvarezsaurids were remarkably like those of derived birds, much more so than those of archaeopterygiforms (Perle et al. 1994; Karhu and Rautian 1996).

The air sac complex of derived theropods appears to have been so well developed that, if unidirectional air flow had not previously appeared, it was probably present by this stage (Claessens and Perry 1998); indeed, it may have been fully developed.

Ruben, Jones and others (1997) suggested that *Archaeopteryx* was capable of the caudopelvic air sac ventilation practiced by modern birds. According to Ruben and his co-workers, modern birds can breathe in this manner because their slender, flexible pubic shafts project far enough caudally to be operated by tail-based muscles. Because the pubes of archaeopterygiforms probably did not extend strongly caudally, and their pubic shafts were fairly robust, it is improbable that they could use caudal muscles to breathe this way. Strong pubic shafts probably inhibited dromaeosaurs from practicing such caudopelvic breathing despite the projection of their pubes caudal to the ischia. Because the pubes of derived alvarezsaurids were slender, and may have projected caudal to the ischia, these animals may have been able to practice caudopelvic respiration.

Ruben and colleagues (Ruben, Jones et al. 1997) cited the presence of a hypopubic cup (Martin 1991) in *Archaeopteryx* as further evidence for caudopelvic respiration. In specimen BMNH 37001 the pubic boot is craniocaudally crushed, and the caudal projections are broken off, so the resulting damage appears to have been mistaken for a depression set in a laterally broad boot. In the rest of the specimens the pubic boot is transversely narrow in the typical theropod manner (Figure 3I), and contrary to the distal lateral expansion of the *Confuciusornis* pubis restored by Martin et al. (1998), the distal pubis of other basal birds are similarly too narrow to accommodate a hypopubic cup (Hou and Zhang 1993, pl. 1; Ackerman 1998:93; Ji et al. 1999, figs. 2, 3). Nor has the presence of a hypopubic cup in *Rahonavis* (Forster et al. 1998), dromaeosaurs (*Sinornithosaurus*, *Bambiraptor* and *Deinonychus* pubes definitely lack such a structure; its presence in *Velociraptor* is very doubtful [Norell and Makovicky 1999]) or any theropod been verified.

Ruben and colleagues (Ruben, Jones et al. 1997) concluded that the air sac complex was only weakly developed even in basal ornithothoracines, because these animals lacked ossified uncinate processes or sternal ribs, and their ossified sternal plates were short. However, the latter were as large as in ratites and precocial chicks, and the lack of ossified sternal ribs and uncinate processes does not preclude the presence of well-developed air sac ventilation in certain modern birds. What is true is that respiratory capacity was almost certainly not as extremely high as in flying birds with hyperelongated sterna and numerous ossified sternal ribs. The latter condition was present in derived enantiornithines (Chiappe and Calvo 1994).

**Conclusion**

Considering the radical transformations in form and function that evolution has generated, the possibility that the modern avian air sac operated pulmonary system evolved from a dramatically different and crocodile-like pelvovisceral pump cannot be ruled out. But it can be considered implausible, especially in view of the absence of any apparent reason for such a major change to occur—after all, bats power their flight with a diaphragm-based lung system whose function is more similar to that of crocodilians than birds. Such speculations seem moot in that the above analysis indicates that the respiratory anatomy and function of neotheropod dinosaurs
was most similar to that of flightless birds, and the thorax of Archaeopteryx was still basically dinosaurian in organization (see Table 1). In addition, there is a progressive acquisition of increasingly bird-like respiratory features in theropods, to the point that the thoraxes of the most bird-like dinosaurs were essentially avian in organization. One could hardly ask for a better pattern of incremental evolution regarding the skeletal features needed to operate respiratory air sacs progressing to the avian condition. It is not logical to conclude that theropod dinosaur respiration was more similar to that of crocodilians than birds, when the dinosaur’s respiratory apparatus became increasingly bird-like rather than crocodilian-like. This fact reinforces the case for preavian pulmonary air sac ventilation in predatory dinosaurs. No evidence for progressive evolution of a pelvovisceral pump in predatory dinosaurs has been presented. Nor did Ruben, Jones et al. (1997) properly correlate the anatomical features associated with crocodilian in contrast to avian respiratory complexes. They did not show that crocodilians and theropods share any unique respiratory adaptations, and they mistook damage and repairs made by an untrained collector for soft tissue anatomy. There is no unambiguous soft tissue or skeletal evidence that theropods had a pelvovisceral pump; there is abundant osteological evidence that they did not, so it is probable that pelvovisceral piston lung ventilation is limited to crocodilians.

The last probability is not surprising. The unusual crocodilian pelvovisceral piston is elaborate compared with other reptiles whose aerobic capacity is equally low, nor does it increase gas exchange capacity, so it may have evolved for purposes other than respiration. The ability to extend the air-filled lungs strongly backwards with the pelvovisceral pump seems to allow crocodilians to precisely regulate their center of buoyancy in a way that allows them to assume various underwater postures and depths at will (Gans 1976). This selective advantage may help explain the great success of aquatic crocodilians since the Triassic. It is interesting that critical features associated with the pelvovisceral pump—elongated transverse processes and short, broad, mobile pubes—were absent among the most basal gracile, highly terrestrial sphenosuchian protocrocodilians (Crush 1984). Although the presence of a lumbar region indicates that some form of abdominal pump was probably operational in protocrocodilians (Carrier 1987), the thorax is so different from that of their modern relatives that it is improbable that the former had yet evolved the well-developed respiratory system found in the latter (because the pulmonary complex of sphenosuchians is unknown, they cannot be used to test the compatibility of any particular respiratory system with their skeletal anatomy). The requisite thoracic features for a well-developed pelvovisceral pump began to appear in more derived sphenosuchians that may have been partly aquatic, and were further developed among crocodilians that show adaptations for being semiamphibious (flattened skull, secondary palate; e.g., Notochampsidae and Protosuchus). In this view, aquatic habits may have facilitated the development of the strong action pelvovisceral pump that helped control the center of buoyancy. Because it dominates the respiratory apparatus it must also be used during normal breathing.

The presence of respiratory adaptations (ossified uncinate processes and sternal ribs, up to five sternocostal articulations, and long sternal plates) more derived than those of the urvogel in dromaeosaurs, caudipterygians and oviraptorosaurs is interesting, because these adaptations are similar to those of secondarily flightless birds. This adds to the evidence that these exceptionally bird-like dinosaurs may also have been secondarily flightless, and closer to modern birds than archaeopterygiforms (Paul 1988, in press).

Note added in proof: Martill et al. (2000) presented tentative soft tissue evidence for the presence of an inflated air sac in a three-dimensionally preserved theropod dinosaur. They also showed that the fossilized colon was set well below the dorsal column immediately before the pelvic canal in a position more typical of birds than reptiles.

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Respiratory complexes of predatory dinosaurs


