# The Integration of Ventilation and Locomotion in Archosaurs[1]

DAVID R. CARRIER AND COLLEEN G. FARMER

*Department of Biology, University of Utah, Salt Lake City, Utah 84112, and Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92697*

SYNOPSIS.    **Movements of the pelvis have recently been found to contribute to ventilation in both crocodilians and birds. Alligators have a kinetic pelvis in which the ischiopubic and ischiotruncus muscles rotate the pubic bones ventrally to increase abdominal volume and thereby facilitate inspiration. In birds, the entire pelvis rocks on the axial skeleton to produce ventilation. Although the mechanisms of pelvic aspiration are very different in crocodilians and birds, it is unusual among vertebrates for the pelvic musculoskeletal system to play an active role in inspiration. This observation raises the possibility that the pelvic musculoskeletal system may have played an important role in the ventilation of basal archosaurs. Based on the mechanism of pelvic aspiration in crocodilians and the structure of gastralia in basal archosaurs, we suggest that an ischiotruncus muscle pulled the medial aspect of the gastralia caudally, and thereby helped to produce inspiration by increasing the volume of the cuirassal basket. The proposed mechanism of cuirassal breathing in non-avian theropods leads us to suggest that the phase relationship of the ventilatory and locomotor cycles in running theropods was the opposite of that observed in running birds. Furthermore, we suggest that the ventilatory cycle of flying pterosaurs was entrained to the locomotor cycle with a phase relationship that was the opposite of that observed during flight in modern birds.**

## INTRODUCTION

Vertebrate morphologists and physiologists have often studied the axial musculoskeletal system as if it were an entity that is independent from the appendicular system. Given the complexity of a naturally behaving fish or tetrapod, it is understandable, and maybe even desirable, that researchers try to find ways to simplify the musculoskeletal system. But, increasingly, evidence is emerging that should provide a clear warning that an atomistic approach to the axial musculoskeletal system is misleading. Obviously, the axial and appendicular systems are integrated in regards to locomotor function. Less obvious is the influence locomotor forces have on functions that have traditionally been considered to be within the realm of the axial system, such as lung ventilation (Bramble and Jenkins, 1994; Boggs, 1997; Lee and Banzett, 1997) and circulation (Simmons *et al.,*

1999). Dramatic examples of these locomotor influences are the constraint on running and costal breathing in lizards (Carrier, 1987*a*; Wang *et al.,* 1997; Owerkowicz *et al.,* 1999) and the evolutionary tuning of the locomotor and ventilatory cycles to have the same natural frequency both in mammals (Young *et al.,* 1992) and in birds (Nassar *et al.,* 1995). These examples illustrate that if our goal is to understand the function and evolution of the vertebrate axis, we should not view the axial musculoskeletal system in isolation.

Archosaurs appear to be an example in which traditional distinctions between axial and appendicular function may be particularly inappropriate. New evidence suggests that the pelvic musculoskeletal system actively contributes to lung ventilation in both crocodilians and birds. These observations raise the possibility that archosaur axial and appendicular characters, that have been thought to be related to body support and locomotion, may actually be associated with lung ventilation (Carrier and Farmer, 2000). In this paper, we review what is know of pelvic aspiration in modern birds

---

[1] From the Symposium on *The Function and Evolution of the Vertebrate Axis* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 6–10 January 1999, at Denver, Colorado.
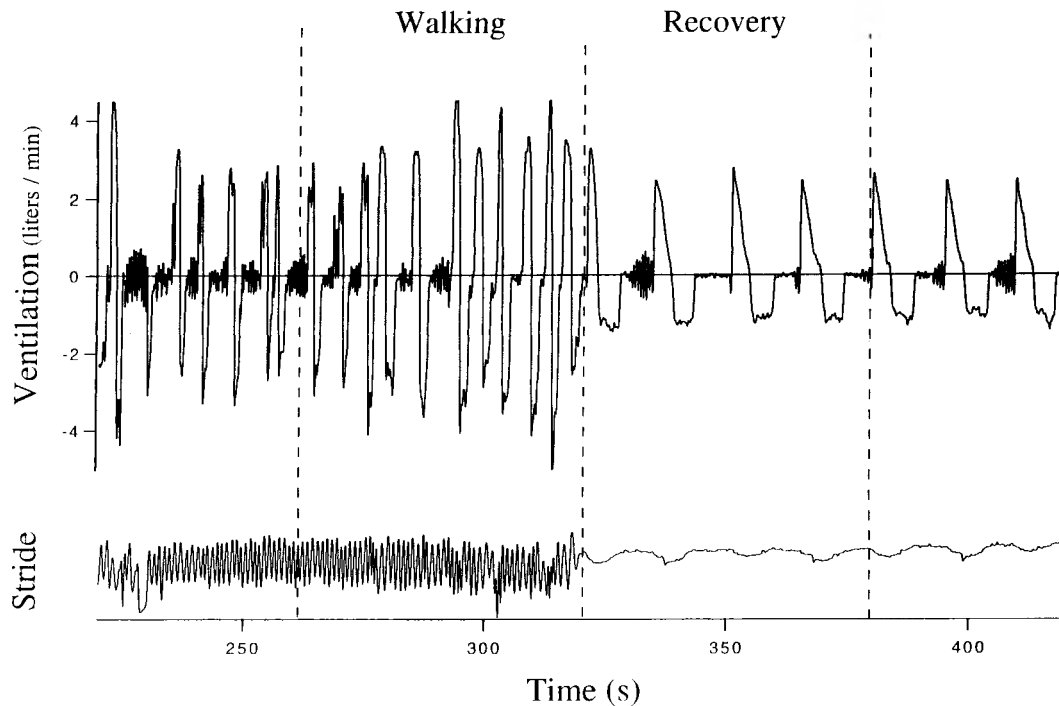
[2] E-mail: carrier@biology.utah.edu

FIG. 1. Ventilation and stride from an American alligator (*Alligator mississippiensis*) illustrating the exercise-recovery transition. The top trace shows the signal from the pneumotachometer; exhalation is the positive portion of the trace. The high frequency signals that occur at times during apnea are due to movement of air into and out of the buccal area. This air-flow did not contribute to lung ventilation and was not included in the ventilation analysis. A dramatic decrease in ventilatory frequency is apparent upon cessation of exercise. The bottom trace is the signal from a strain gauge that monitored the locomotor cycle. The constant frequency and amplitude of the oscillations in this trace are indicative of steady locomotion. Notice that the larger breaths are not associated with pauses in the locomotion. The small amplitude oscillations of the strain gage during recovery are due to motion of the thorax and abdomen during ventilation, not from locomotion. From Farmer and Carrier (2000a).

and crocodilians, suggest a novel mechanism of ventilation in basal archosaurs, and speculate on how ventilation may have been integrated with locomotion in non-avian theropods and pterosaurs.

### LUNG VENTILATION IN THE AMERICAN ALLIGATOR

*Ventilation and gas exchange during walking*

Given their low capacity for aerobic activity metabolism and their use of lateral bending of the trunk during walking, alligators might be expected to have a limited ability to breath during terrestrial locomotion, as is the case in lizards. Nevertheless, alligators have no trouble breathing when they walk (Farmer and Carrier, 2000a).

They inspire with large breaths in which air-flow is not interrupted by their locomotor efforts (Fig. 1). Lung ventilation, oxygen consumption, and carbon dioxide production all increase with locomotor speed (Fig. 2). Alligators also hyperventilate relative to their metabolic demand during walking, as is indicated by greatly elevated air convection requirements for oxygen and carbon dioxide (Fig. 2). Most striking is the dramatic drop in both ventilation and air convection requirement that occurs immediately upon cessation of locomotion (Fig. 2). The elevated air convection requirements during walking and the drop in ventilation during the first minute of recovery from exercise suggest that ventilation in alligators is not limited by their locomotor
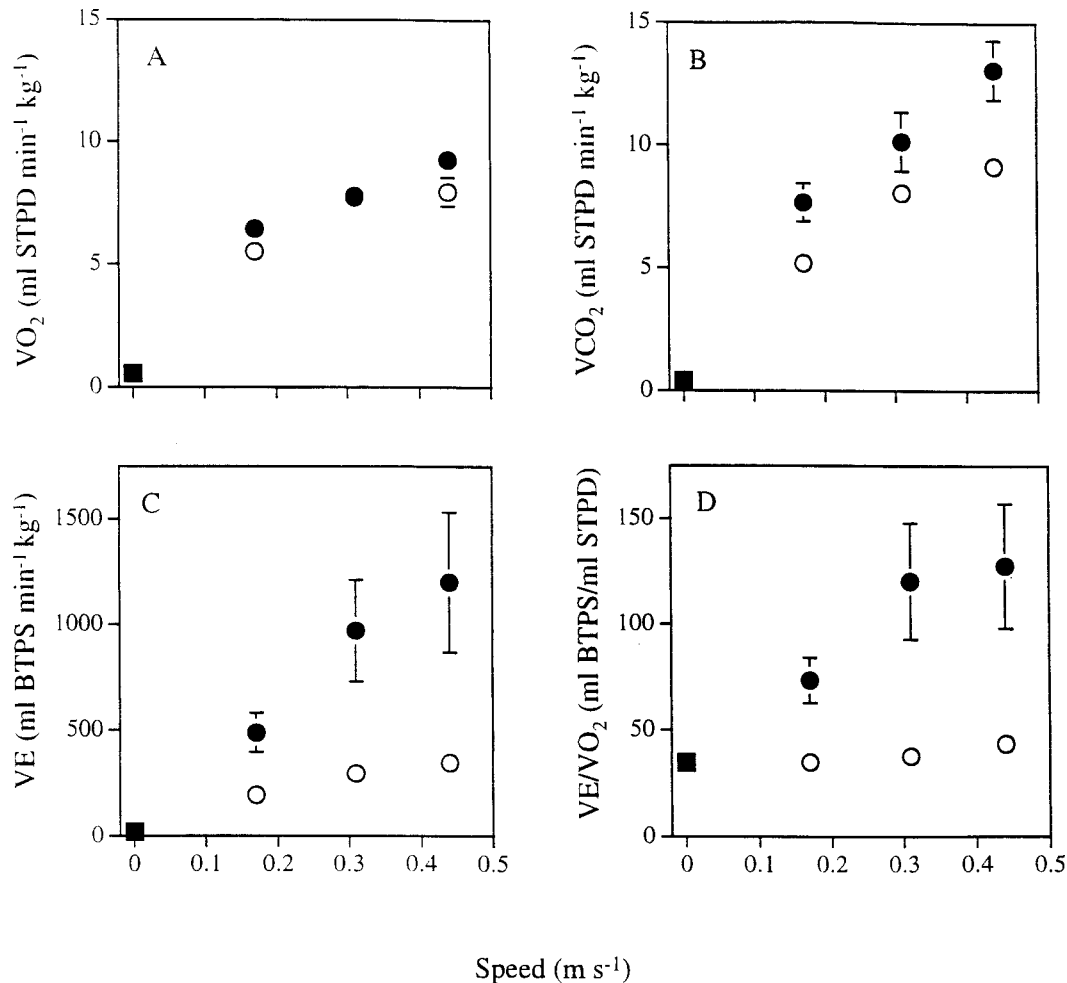
FIG. 2. Ventilation and gas exchange during walking and the first minute of recovery in the American alligator: A. oxygen consumption *vs*.walking speed; B. carbon dioxide production; C. ventilation; D. air convection requirement for oxygen. In each graph, the square denotes the pre-exercise value, solid circles represent the exercise values, and open circles represent the values recorded during the first minute of recovery. Values are means ± S.E.M (n = 5). Modified from Farmer and Carrier (2000a).

movements. Indeed, relative to their metabolic demand, walking alligators appear to breath much more than is necessary.

*Evidence for a new mechanism of lung ventilation*

In addition to costal and diaphragmatic mechanisms of ventilation, crocodilians employ a pelvic mechanism in which the pubic bones rotate dorso-ventrally to change the volume of the abdominal cavity (Farmer and Carrier, 2000b). Crocodilians are unique among extant tetrapods in having pubic bones that are excluded from the acetabulum and are attached at their proximal end to the ischia via movable joints (Fig. 3). From these joints the pubic bones extend cranially and ventrally. At their distal ends, the pubic bones expand laterally and medially into broad plates that form the ventral margin of the posterior belly. Two muscles, the ischiopubic and the ischiotruncus, extend from the ischia to the cranial edge of the pubic plates and the last two
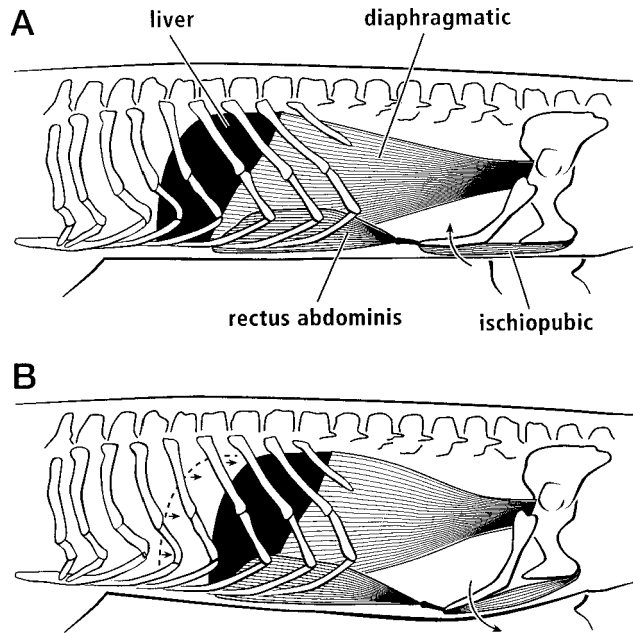
FIG. 3. Illustration of the ventilatory mechanism of the American alligator. A. During expiration the rectus abdominis and transversus abdominis muscles elevate the pubes and constrict the abdominal cavity. This forces the viscera to move anteriorly, decreasing the volume of the thorax. B. During inspiration, contraction of the ischiopubic and ischiotruncus muscles rotate the pubes ventrally, increasing abdominal volume. At the same time, the diaphragmaticus muscle pulls the viscera posteriorly and the intercostal muscles rotate the ribs anteriorly. This increases thoracic volume. From Farmer and Carrier, (2000b).

(most caudal) gastralia. Activity of these muscles produces a ventral rotation of the pubic bones, a drop in intra-abdominal pressure, and inspiration (Fig. 4). Ventral rotation of the pubic bones expands the posterior abdominal cavity, presumably to provide space for the caudal displacement of the viscera by the diaphragmaticus muscle during inspiration (Fig. 3). During expiration, contraction of the rectus abdominis and transversus abdominis muscles draw the pubic plates dorsally, decreasing abdominal volume. This apparently helps to shift the viscera cranially, decreasing thoracic volume. Thus, the highly derived pelvic musculoskeletal system of crocodilians appears to play a role in lung ventilation.

PELVIC ASPIRATION IN BIRDS

Baumel (1988) observed that the tail moves during vocalization in crows, warbling vireos, and lovebirds. Based on those observations, he initiated a study of the role of the pelvic and tail musculature in the ventilation of pigeons (Baumel et al., 1990). That study demonstrated that in anesthetized birds, resting on their sternum, one of the epaxial muscles (the longissimus dorsi) was consistently active during inspiration. Activation of the longissimus dorsi elevated the pelvis at the notarial-synsacral joint and increased the volume of the thoracoabdominal cavity. Subsequent depression of the pelvis during expiration was attributed to the action of the infrapubic abdominal muscles, which had previously been shown to be active during expiration (Fedde et al., 1969; Kandano et al., 1963). Additionally, Baumel and his coworkers found three extrinsic tail muscles (the caudofemoralis, pubocaudalis externus, and pubocaudalis internus) and one suprapubic abdominal muscle (the transversus cloacae) to be active during expiration. These muscles depressed the tail and constricted the caudal abdominal wall, acting to decrease the thoracoabdominal cavity. Baumel and his collaborators speculated that the venti-
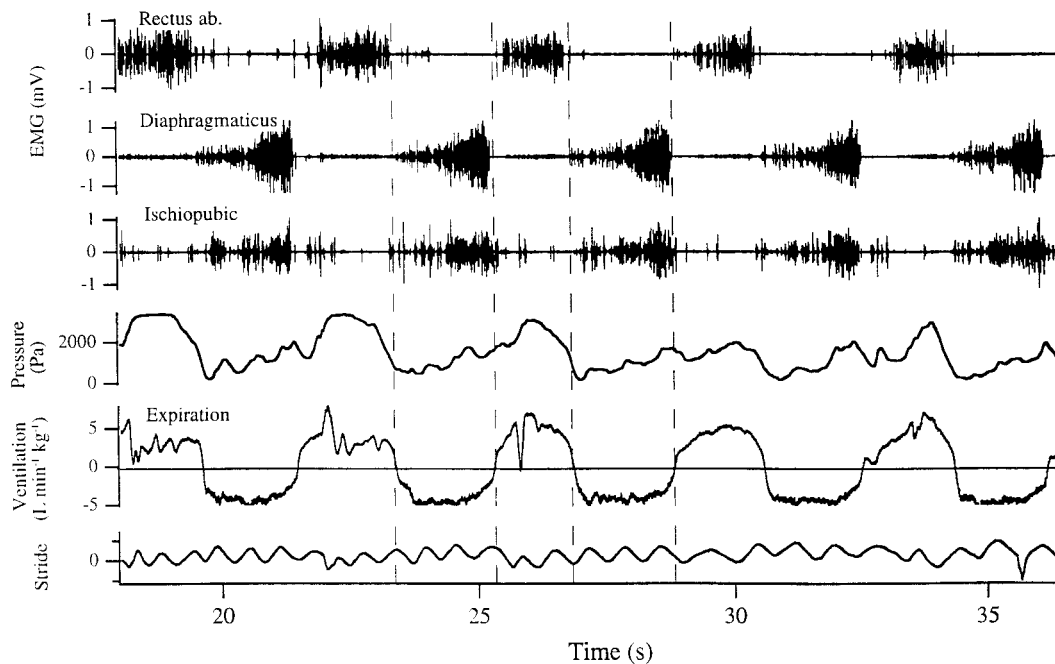
FIG. 4. Sample recording of the activity of the rectus abdominis, diaphragmaticus, and ischiopubic muscles, plotted relative to changes in abdominal pressure, ventilatory air flow, and the timing of the locomotor cycle from an American alligator. The sixth trace is a recording of the lateral bending of the trunk; each cycle of the trace represents a complete locomotor cycle. Dashed vertical lines mark the beginning and ending of the expiratory and inspiratory phases of ventilation. From Farmer and Carrier (2000b).

latory movements of the pelvis and tail of pigeons may be important for ventilation when birds are resting on their chest and possibly during flight.

Some evidence indicates that pelvic aspiration is used by birds during flight. Cineradiographic studies of black-billed magpies (*Pica pica*) showed that in some individuals the synsacrum rotates ventrally during the downstroke of the wing in a manner that would contribute to abdominal compression, and it rotates dorsally during the upstroke of the wing, contributing to abdominal expansion (Boggs et al., 1997). Whether these pelvic movements are passive effects of the lift and recovery phases of the wing-beat cycle or the result of active recruitment of the axial muscles remains to be determined. However, the timing of activity of the longissimus dorsi, levator caudae, and depressor caudae muscles (Gatesy and Dial, 1993) and the pattern of ventilation (Boggs, 1997) is consistent with the possibility that the pelvis is actively elevat-

ed and depressed to facilitate ventilation during flight in pigeons.

THE EVOLUTION OF CUIRASSAL BREATHING
IN ARCHOSAURS

The mechanisms of pelvic aspiration are very different in crocodilians and birds. Nevertheless, it is unusual among vertebrates for the pelvis to play an active role in inspiration. The inspiratory role of the pelvis in both birds and crocodilians raises the possibility that the pelvic musculoskeletal system may have contributed to ventilation in the common ancestor of these two groups. The lineages that gave rise to modern crocodilians and birds split very early in archosaur phylogeny and have been separated since the Early Triassic (Gauthier and Padian, 1985; Gauthier, 1986). Hence, if a homologous link does exist between the pelvic aspiration systems of birds and crocodilians it would have been present in basal archosaurs. However, given the highly derived pelvic girdles of crocodilians and
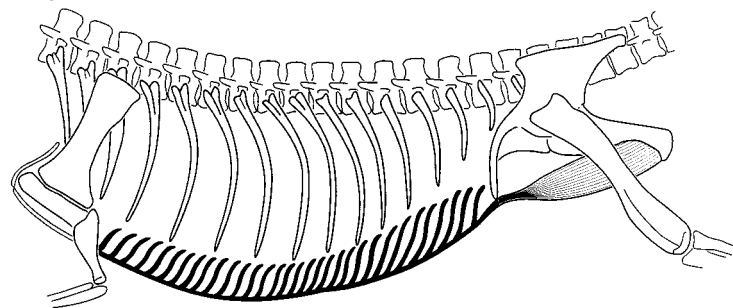
**Expiration**
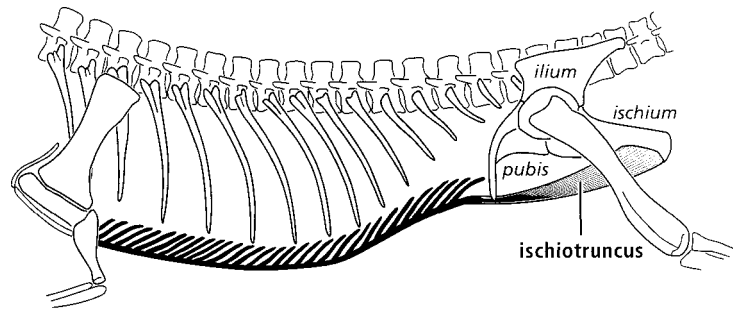


**Inspiration**



FIG. 5.    Illustration of proposed cuirassal breathing mechanism in the archosauromorph *Euarkeria capensis*. A. During expiration, contraction of the rectus abdominis muscle pulled the medial portion of the gastralia anteriorly, causing an elevation of the ventral body wall. B. During inspiration, contraction of the ischiotruncus muscle pulled the medial portion of the gastralia posteriorly, causing a depression of the ventral body wall and an increase in the volume of the body cavity. From Carrier and Farmer (2000).

birds, we cannot expect basal archosaurs to have used the pelvic mechanisms of either crocodilians or birds.

The structure of gastralia and pelvic girdle in basal archosaurs lead us to propose a novel mechanism that may have assisted costal aspiration (Carrier and Farmer, 2000). Gastralia are primitive for amniotes and appear to be derived from the ventral body armor of Paleozoic amphibians (Romer, 1956). In amniotes, they are present in the ventral body wall as a series of narrow chevrons. The number varies from taxon to taxon, but the apex of the chevron always points cranially. Each chevron consists of a variable number of slender bones that angle laterally and caudally across the belly from the midline. In some taxa the distal ends of the chevrons curve dorsally into the lateral hypaxial muscles. The function of gastralia has generally been associated with mechan-

ical protection of the ventral body wall (Romer, 1956). Several authors have suggested that gastralia may participate in lung ventilation (Lambe, 1917; Perry, 1983; Claessens, 1996, 1997). Claessens (1996) has proposed a ventilatory mechanism in theropods involving the hypaxial muscles of the belly wall. We suspect that Claessens is correct, but we also believe that gastralia could have contributed to ventilation through the action of parasagittally located ischiotruncus muscles which had the motor pattern observed in modern alligators.

An ischiotruncus muscle which pulled on the gastralia at their medial aspect could have functioned to swing the apex of the chevrons ventrally and thereby increase the volume of the abdominal cavity (Fig. 5). Such a mechanism would have been analogous to expansion of the buccal and gular cavities of fishes and many tetrapods by the

hyobranchial (*i.e.,* sternohyoideus) muscles acting on the hyoid arches. If the lateral ends of the gastralia were anchored against caudal translation by hypaxial muscles, such as the external oblique muscle, a caudally directed force on the apex of the chevrons would have caused a caudoventral rotation. For this mechanism to have worked, the fulcrum, or point of rotation, of the gastralia would have been located dorsal to the ventral end of the pubes. This would have allowed the pubes to function as a guide that directed the muscular force so that a moment was applied to the fulcrum of the gastralia.

This mechanism, which we call cuirassal breathing, provides a plausible functional explanation for the architecture which characterizes gastralia in many taxa: rhynchosaurs (Romer, 1956); early archosauriformes such as *Euparkeria* (Romer, 1956; Ewer, 1965), and pseudosuchians (Colbert and Mook, 1951; Crush, 1984); pterosaurs (Wellnhofer, 1978); prosauropods and theropods (Lambe, 1917; Claessens, 1997). Thus, based on the presence of pelvic aspiration in both birds and crocodilians, the function of the ischiotruncus muscle in crocodilians, and the presence of well developed gastralia in early archosauriforms such as *Euparkeria,* we suggest that cuirassal breathing was present in basal archosaurs. From this early involvement in inspiration, the pelvic musculoskeletal system of basal archosaurs appears to have undergone independent specialization for pelvic aspiration in crocodilians, pterosaurs, birds, and some ornithischians (Carrier and Farmer, 2000).

### INTEGRATION OF LOCOMOTION AND VENTILATION

#### Cuirassal breathing in non-avian theropods

The anatomy of non-avian theropods is consistent with the mechanism of cuirassal breathing we have proposed for primitive archosaurs (Carrier and Farmer, 2000). Non-avian theropods are characterized by well developed gastralia in the belly wall between the pubis and sternum (Claessens, 1997). In theropods, the pubis was elongate and had a cranial and caudal expansion at the distal end, called a foot (Fig. 6). The ventral margin of the foot was often convex in shape, covered by cartilage, and aligned with the distal end of the long ischium. This alignment was such that an ischiotruncus muscle, originating on the distal end of the ischium, would have crossed the ventral surface of the pubic foot to reach the gastralia. If an ischiotruncus muscle did extend from the ischium to the gastralia, then the long pubis would have served to orient the force of the ischiotruncus muscle on the gastralia. Such an arrangement would have given the muscle a sufficient moment arm to cause ventral rotation of the gastralia.

The gastralia of non-avian theropods were highly derived (Claessens, 1997). Instead of a simple union of lateral elements at the ventral midline, the gastralia of theropods crossed the midline and articulated with two gastralia from the opposite side of the body (Fig. 7). The crossing arrangement of the gastralia constituted a lever system, which, through the action of hypaxial muscles, could have widened or narrowed the cuirassal basket (Claessens, 1997). There were small fossa on the ventral side of the proximal ends of the gastralia, which we believe were the site of attachment of the ischiotruncus muscle. If the proximal ends of the gastralia were drawn caudally by the ischiotruncus muscle, the special lever system of theropods would result in a lateral expansion of the belly.

In summary, we suggest that the highly derived pubis and ischium of non-avian theropods are modifications of the basal archosaur condition that facilitated cuirassal breathing in animals with parasagittal limb posture. The exceptionally long pubis and ischium provided proper alignment for an ischiotruncus muscle to increase abdominal volume by drawing the medial aspect of the gastralia caudally and ventrally. The ischium functioned as the site of origin of the muscle and the expanded foot of the pubis oriented the force of the muscle.

#### Running and breathing in non-avian theropods

The bipedal posture, large tail, and hypothesized cuirassal breathing mechanism
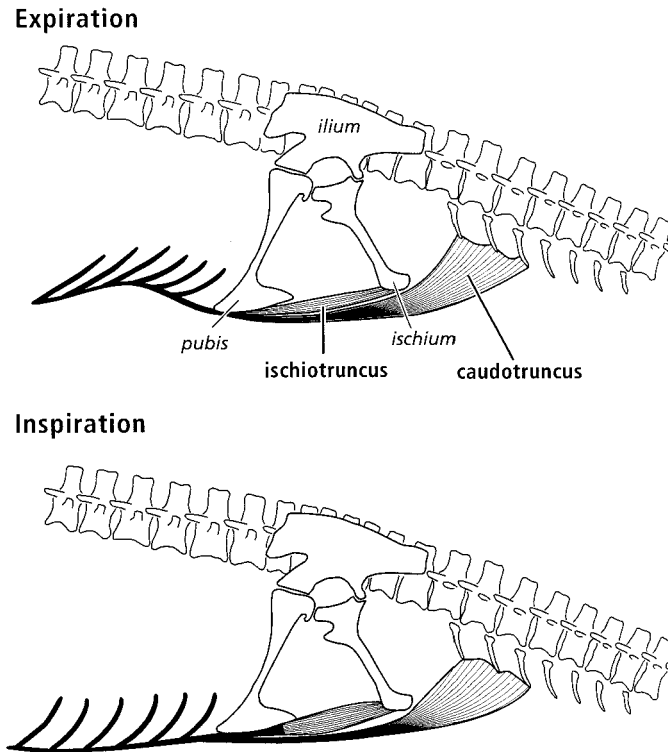
**Expiration**

**Inspiration**

FIG. 6. Illustration of the proposed mechanism of cuirassal breathing in the theropod *Allosaurus sp.* A. During expiration, contraction of the rectus abdominis muscle pulled the medial portion of the gastralia anteriorly, causing an elevation and lateral compression of the ventral body wall. B. During inspiration, contraction of the ischiotruncus and caudotruncus muscles pulled the medial portion of the gastralia posteriorly, forcing the body wall to expand ventrally and laterally. From Carrier and Farmer, 2000.

of non-avian theropods lead us to suspect that theropods may have integrated venti- lation and locomotion in a unique manner (Fig. 8). During a running step in a bipedal theropod, the vertical force applied to the acetabulum by the limb would act to cause a downward collapse of the trunk and tail around the pelvic girdle. The trunk and tail would be stabilized against the vertical force by the epaxial musculature of the back. The trunk and tail would have tended to collapse downward during the first half of limb support and then to rebound upward during the second half of limb support. If the trunk did, in fact, sag a bit about the hip at the beginning of limb support, the volume of the body cavity would decrease, due to a decrease in the angle between the axial skeleton and the elongate pubis which defined the posterior boundary of the ab- domen. At the same time, the vertical sag

of the tail about the pelvic girdle would have decreased abdominal volume through the cuirassal apparatus (Fig. 8). The drop- ping of the tail at the beginning of foot sup- port would have placed slack in a caudo- truncus muscle similar to that of crocodil- ians (Romer, 1923; Farmer and Carrier, 2000*b*). This would have resulted in the an- terior rotation of the gastralia and a de- crease in abdominal volume. During the second half of limb support, as the trunk and tail rebounded upward, the volume of the body cavity would have increased, due to the rotation of the axial skeleton away from the pubis and the application of ten- sion to the caudotruncus muscle by the ver- tical rise of the tail. Thus, we are suggesting that the sagittal bounce of the trunk and tail during running in non-avian theropods would have produced a tendency for expi- ration to occur during the first half of limb

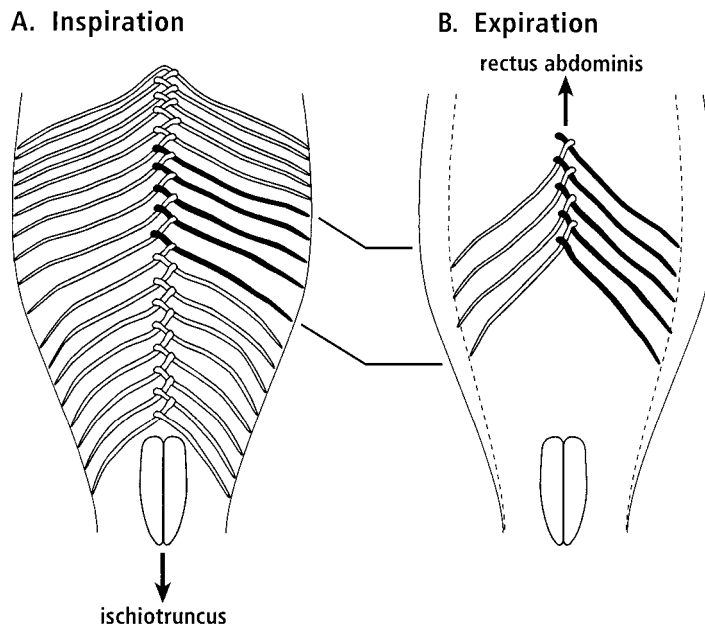## A. Inspiration  B. Expiration

rectus abdominis

ischiotruncus

FIG. 7.   Ventral view of the gastralia of *Allosaurus sp.* showing the lever mechanism that is proposed to have caused lateral expansion of the abdominal cavity. The ischiopubic muscle is suggested to have inserted on the expanded facets of the medial ends of the gastralia. A. Contraction of this muscle would have pulled the medial ends posteriorly, thereby forcing cranial rotation of the lateral ends of the gastralia and expanding the body wall laterally. B. Contraction of the rectus abdominis muscle would have pulled the medial ends of the gastralia anteriorly, thereby forcing the lateral ends of the gastralia to swing posteriorly and reducing the volume of the body cavity. From Carrier and Farmer, 2000.

support and inspiration to occur during the second half of limb support (Fig 8).

Sagittal bounce of the trunk and tail would likely have had less effect on the ventilation of running ornithischian dinosaurs. Because ornithischians lacked gastralia, locomotor induced excursions of the tail would have been less coupled to ventilatory air flow. Ornithischians were also characterized by a strong lattice of ossified tendons associated with the neural spines of the dorsal and caudal vertebrae. This lattice was centered over the pelvis such that little or no sagittal flexion of the trunk and tail would likely have occurred during running. In contrast, the tail of theropods often had ossified tendons associated with the neural spines, but these ossifications were restricted to the tail and did not extend to the pelvis. In ornithischians, the posterior orientation of the pubis, loss of gastralia, and increased stabilization of the axial skeleton with ossified tendons may all have been a function of a large gut associated with their

herbivorous diet. These modifications may have entailed compromises in the mechanics of lung ventilation. The possibility of kinetic pubes and ischia in some highly derived ornithischians may have helped to overcome limitations imposed by their large gut (Carrier and Farmer, 2000).

The pattern of ventilation and locomotion we are suggesting for non-avian theropods, in which expiration occurs during the first half of limb support and inspiration occurs during the second half, is the opposite of that found in modern running birds. Running birds synchronize their breathing with the locomotor events and exhibit less flexibility in breathing pattern than do mammals, suggesting that their breathing is tightly constrained by the mechanics of locomotion. When Guinea fowl are just starting a running bout they take one breath every three steps (*i.e.,* one and a half locomotor cycles) (Nassar personal communication). After they have warmed up and have begun panting they take one
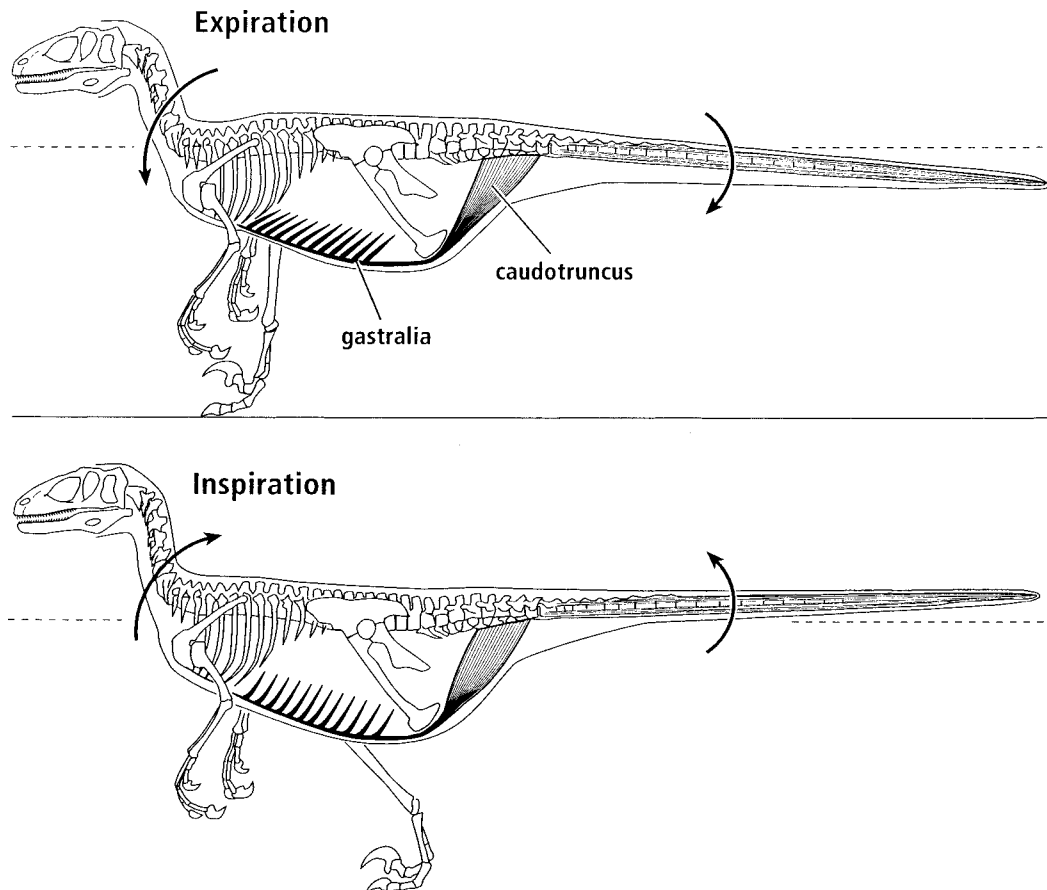
Fig. 8. Illustration of the proposed coupling of locomotion and ventilation in the theropod *Deinonychus antir-rhopus*. During the beginning of limb support (top panel), the inertia of the tail and trunk caused them to sag around the pelvis. This decreased thoracic volume by decreasing the angle between the pubis and dorsal vertebrae and by putting slack in the truncus muscle. During the second half of the step (lower panel), the tail and trunk rebounded, increasing thoracic volume.

breath per step (*i.e.,* two breaths per loco-motor cycle). Inspiration occurs during the first half of limb support as the foot touches down and the bird decelerates. Expiration occurs as the bird accelerates upward and forward. This pattern has also been observed in running chickens (Brackenbury and Avery, 1980).

Inspiration occurs during the first half of limb support in running birds and is associated with the downward displacement of the sternum that occurs early in the step (Nassar, personal communication). As the bird lands and decelerates the weight of the pectoralis and sternocoricoideus muscles causes the sternum to swing ventrally, in-creasing the volume of the thorax. In the second half of limb support the sternum rebounds upward, decreasing the volume of the thorax. Hence, we are suggesting that the pattern of lung ventilation during running in non-avian theropods was the opposite of that observed in recent birds.

During the evolution of birds, four changes from the theropod configuration may have necessitated the change in breathing pattern we are proposing: i) the great reduction in the mass and length of the tail, ii) the caudal rotation of the pubis, and iii) the loss of gastralia would have eliminated any benefit to ventilation from a sagittal bounce of the axial musculoskeletal system.

Coincident with these three modifications was iv) the trend toward an enlarged flight musculature and sternum, which causes an increase in thoracic volume during the first half of limb support. Thus, the evolution of birds entailed a change in the way the forces of terrestrial locomotion influenced the volume of the body cavity. Rocking of a large sternum appears to have come to dominate the ventilatory mechanics of running birds.

*Flying birds, bats, and pterosaurs*

One of the intriguing puzzles of locomotor-respiratory integration is the striking difference in the breathing patterns of flying birds and bats. In birds that take one breath per locomotor cycle, such as pigeons, downstroke of the wing-beat is associated with the beginning of expiration and upstroke is associated with the beginning of inspiration (Berger *et al.,* 1970; Boggs, 1997). In birds that breathe more slowly, such that a breath lasts for several wing beats, downstroke is associated with an increase in expiratory flow rate and a decrease in inspiratory flow rate (Boggs, 1997). This pattern is explained by the fact that contraction of the pectoralis muscle during downstroke elevates the sternum toward the vertebral column (Jenkins *et al.,* 1988; Boggs *et al.,* 1997), compressing thoracic volume, and increasing pressure in both the interclavicular and posterior thoracic air sacs (Boggs, *et al.,* 1997; Boggs, 1997). In contrast, flying bats exhibit the opposite pattern; downstroke of the wing is associated with the beginning of inspiration and expiration begins during upstroke of the wing (Suthers *et al.,* 1972; Thomas, 1981; Carpenter, 1986). All species of bats that have been studied, both megachiroptera and microchiroptera, breathe in this stereotypic pattern during flight. Even vocalization during the echolocation of microchiroptera does not alter the pattern of expiration during upstroke and inspiration during down stroke (Suthers *et al.,* 1972).

The contrasting breathing patterns of flying birds and bats may reflect the different roles that the pelvis plays in the generation of lift forces in these groups. In birds, the tail and hindlimbs are mechanically separated from the wing, whereas, in bats, the wing membrane is partially supported by the hindlimbs. Each downstroke of the wing of birds produces a small upward acceleration of the body to support the weight of the body and overcome drag (Pennycuick, 1972). The mass and drag of the tail can be expected to resist this acceleration and produce a small downward directed force on the tail. In contrast, because the wing membrane of bats attaches to the hindlimb, the downstroke of bats must result in the application of a large upward directed force on the pelvis. This force can be expected to dorsally extend the lumbar and pelvic regions of the trunk, which would enlarge the abdominal cavity and may facilitate diaphragmatic inspiration. Thus, lift forces exerted on the hindlimbs may explain why bats inspire during the downstroke of their wings and expire during the upstroke. This hypothesis remains to be tested, but we believe it provides a compelling explanation for the striking difference in the breathing patterns of flying birds and bats.

If the architecture of the wing in birds and bats does explain the difference in their breathing pattern, then pterosaurs would almost certainly have breathed the way bats do. Although a debate continues over the structure of the wing membrane of pterosaurs, there is growing evidence that the wing membrane attached to the hindlimb (Unwin, 1999). Impressions of the wing patagium of the Late Jurassic pterosaur *Sordes pilosus* clearly show the membrane connected to the hindlimb all the way to ankle and a well developed cruropatagium stretched between the hindlimbs (Unwin and Bakhurina, 1994). The best preserved impressions of patagium in Pterodactylus show the membrane connected to the thigh about two-thirds of the distance along the femur (Wellnhofer, 1987; Padian and Rayner, 1993). Thus, during downstroke of the wing an upward directed force would have been applied to the hind limbs and this would have tended to dorsally extend the vertebrae and pelvis. The breathing pattern of flying pterosaurs may have consisted of one breath cycle per wing beat cycle, with inspiration occurring during downstroke of
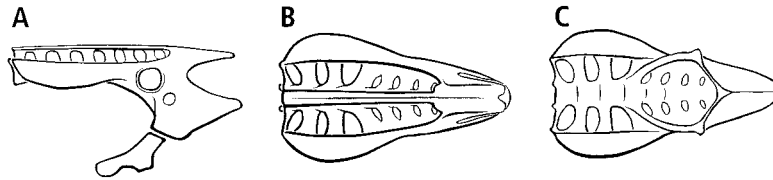
FIG. 9.   Pelvic girdle of *Pteranodon*. A. Lateral view, B. dorsal view. C. ventral view. From Eaton, 1910.

the wing and expiration occurring during upstroke.

Several aspects of the pelvic girdle suggest that pterosaurs were specialized for pelvic aspiration during flight. As in birds, the three pelvic bones of pterosaurs were solidly fused into a single unit (Fig. 9), and an increased number of dorsal vertebrae were incorporated into the sacrum (3 to 5 in *Rhamphorhynchus* and as many as 10 in *Pteranodon*) (Wellnhofer, 1978, 1987). The preacetabular process of the ilium was very long and in pterodactyloids it was fused with additional dorsal vertebrae to form a synsacrum-like structure (Eaton, 1910). The distal ends of the pubic bones did not meet on the ventral midline, but the ischiadic portion of the puboischiadic plate was fused at the midline (Padian, 1983); making the pelvis partially open ventrally. In *Pteranodon* and other large pterodactyloids, as many as 8 dorsal vertebrae of the thorax were fused into a notarium. Between the notarium and synsacrum were several dorsal vertebrae that may have provided some level of dorsoventral mobility. These characters would have facilitated volume changes of the coelomic cavity due to dorso-ventral rotation of the "synsacrum" on the dorsal vertebrae.

### The evolution of locomotor stamina

The lateral bending and sprawling posture of early tetrapods, such as *Diadectes,* may have limited their ventilation during locomotion (Carrier, 1987*a*). This suggestion is based on the observation that locomotion was the primitive function of the hypaxial muscles that are responsible for costal ventilation in modern amniotes (Carrier, 1996). Locomotion also appears to be the predominate function of most of the hypaxial muscles during locomotion in running lizards (Carrier, 1989, 1990, 1991; Rit-

ter, 1995, 1996), many walking and running birds (Nassar, 1994; Boggs *et al.,* 1999), and trotting dogs (Carrier, 1996). Given these observations, one should not be surprised to learn that the costal ventilation of lizards is constrained by running (Carrier, 1987*b*). Both lung ventilation and oxygen consumption decline as locomotor speed increases above a slow walk in *Iguana iguana* (Wang *et al.,* 1997); and although varanid lizards can supplement aspiration breathing with gular pumping during locomotion, when gular pumping is eliminated experimentally, both ventilation and oxygen consumption decline as locomotor speed increases (Owerkowicz *et al.,* 1999). Given the anatomical similarities between basal tetrapods and recent lizards, we believe it is reasonable to suggest that a mechanical constraint on simultaneous running and breathing may have limited the locomotor stamina of the first terrestrial vertebrates.

Cuirassal breathing may have helped to separate ventilatory and locomotor function, allowing early archosaurs to breathe more effectively during locomotion. The proposed basal mechanism of cuirassal breathing is based on a ventral expansion and contraction of the abdomen due to the active shortening of muscles that were located along the ventral midline: the ischiotruncus, caudotruncus, and rectus abdominis muscles. Because of their location, these muscles would have played little or no role in the production of lateral bending of the trunk or in the torsional stabilization of the trunk during locomotion. Hence, a ventilatory mechanism that made use of ventral musculature may have increased the independence of locomotion and ventilation. This appears to be the case in walking alligators, in which ventilation is not constrained by the locomotor movements (Farmer and Carrier, 2000*a*) and activity of

the ischiotruncus, ischiopubis, and rectus abdominis muscles is correlated with ventilation rather than locomotion (Farmer and Carrier, 2000*b*). Thus, selection for improved locomotor stamina may have played a role in the evolution of cuirassal breathing.

## REFERENCES

Baumel, J. J. 1988. Functional morphology of the tail apparatus of the pigeon *(Columba livia)*. Adv. Anat. Embry. Cell Biol. 110:1–115.

Baumel, J. J., J. A. Wilson, and D. R. Bergren. 1990. The ventilatory movements of the avian pelvis and tail: Function of the muscles of the tail region of the pigeon *(Columba livia)*. J. Exp. Biol. 151: 263–277.

Berger, M., O. Z. Roy, and J. S. Hart. 1970. The coordination between respiration and wing beats in birds. Z. Verl. Physiol. 66:190–200.

Boggs, D. F. 1997. Coordinated control of respiratory pattern during locomotion in birds. Amer. Zool. 37:41–53.

Boggs, D. F., P. J. Butler, R. V. Baudinetter, and P. B. Frappell. 1999. Relationships amongst air sac pressures, steps and abdominal muscle activity in waddling and running birds. FASEB Journal 13: A495.

Boggs, D. F., F. A. Jenkins, and K. P. Dial. 1997. The effects of the wing-beat cycle on respiration in Black-Billed Magpies *(Pica pica)*. J. Exp. Biol. 200:1403–1412.

Brackenbury, J. H. and P. Avery. 1980. Energy consumption and ventilatory mechanics in the exercising fowl. Comp. Biochem. Physiol. 66A:439–445.

Bramble, D. M. and F. A. Jenkins. 1994. Mammalian locomotor-respiratory integration: Implications for diaphragmatic and pulmonary design. Science 262:235–240.

Carpenter, R. E. 1986. Flight physiology of intermediate-sized fruit bats (Pteropodidae). J. Exp. Biol. 120:79–103.

Carrier, D. R. 1987*a*. The evolution of locomotor stamina in tetrapods: Circumventing a mechanical constraint. Paleobiology **13**, 326–341.

Carrier, D. R. 1987*b*. Lung ventilation during walking and running in four species of lizards. Exp. Biol. 47:33–42.

Carrier, D. R. 1989. Ventilatory action of the hypaxial muscles of *Iguana iguana:* a function of slow muscle. J. Exp. Biol. 143:435–457.

Carrier, D. R. 1990. Activity of the hypaxial muscles during walking in the lizard *Iguana iguana.* J. Exp. Biol. 152:453–470.

Carrier, D. R. 1991. Conflict in the hypaxial musculoskeletal system: Documenting an evolutionary constraint. Amer. Zool. 31:644–656.

Carrier, D. R. 1996. Function of the intercostal muscles in trotting dogs: Ventilation or locomotion? J. Exp. Biol. 199:1455–1465.

Carrier, D. R. and C. G. Farmer. 2000. The evolution of pelvic aspiration in archosaurs. Paleobiology (submitted).

Claessens, L. 1996. Dinosaur gastralia and their function in respiration. J Vert. Paleo. 16:28A.

Claessens, L. 1997. Gastralia. *In* P. J. Currie and K. Padian, (eds), *Encyclopedia of Dinosaurs,* pp. 269–270. Academic Press, San Diego.

Colbert, E. H. and C. C. Mook. 1951. The ancestral crocodilian *Protosuchus.* Bull. Amer. Mus. Nat. Hist. 97:146–182.

Crush, P. J. 1984. A late Upper Triassic Sphenosuchid crocodilian from Wales. Palaeontology 27:131–157.

Eaton, C. F. 1910. Osteology of *Pteranodon.* Mem. Conn. Acad. Arts Sci. 2:1–38.

Ewer, R. F. 1965. The anatomy of the thecodont reptile *Euparkeria capensis* Broom. Phil. Trans. Roy. Soc. Lond., B 248:379–435.

Farmer, C. G. and D. R. Carrier. 2000*a*. Ventilation and gas exchange during walking in the American Alligator *(Alligator mississippiensis).* J. Exp. Biol. (In press).

Farmer, C. G. and D. R. Carrier. 2000*b*. Pelvic aspiration in the American alligator *(Alligator mississippiensis).* J. Exp. Biol. (In press)

Fedde, M. R., P. D. DeWet, and R. L. Kitchell. 1969. Motor unit recruitment pattern and tonic activity in respiratory muscles of Gallus domesticus. J. Neurophysiol. 32:995–1004.

Gatesy, S. M. and K. P. Dial. 1993. Tail muscle activity patterns in walking and flying pigeons *(Columba livia).* J. Exp. Biol. 176:55–76.

Gauthier, J. 1986. Saurischian monophyly and the origin of birds. *In* K. Padian (ed.), *The origin of birds and the evolution of flight,* pp. 1–55. Memriors of the California Academy of Sciences 8.

Gauthier, J. and K. Padian. 1985. Phylogenetic, functional and aerodynamic analysis of the origin of birds. *In* M. K. Hecht, J. H. Ostrom, G. Viohl, and

P Wellnhofer (eds.), *The Beginnings of Birds,* pp. 185–198. Freunde des Jura-Museums, Eichstätt.

Jenkins, F. A., K. P. Dial and G. E. Goslow. 1988. A cineradiographic analysis of bird flight: The wishbone in starlings is a spring. Science 241:1495–1498.

Kadano, H., T. Okada, and K. Ono. 1963. Electromyographic studies on the respiratory muscles of the chicken. Poul. Sci. 42:121–128.

Lambe, L. M. 1917. The Cretaceous carnivorous dinosaur Gorgosaurus. Geol. Sur. Canada Mem. 100:1–84.

Lee, H. and R. B. Banzett. 1997. Mechanical links between locomotion and breathing: Can you breathe with your legs? News Physiol. Sci. 12: 273–278.

Nassar, P. N. 1994. A dual role for the abdominal musculature of running birds. Amer. Zool. 34:15A.

Nassar, P N., D. R. Carrier, A. Jackson. 1995. Oscillatory mechanics of the avian respiratory sytem: Tuning of respiratory and locomotor frequencies. Amer. Zool. 35:572A.

Owerkowics, T., C. G. Farmer, J. W. Hicks, and E. L. Brainerd. 1999. Contribution of gular pumping to lung ventilation in monitor lizards. Science 284: 1661–1663.

Padian, K. 1983. A functional analysis of flying and walking in pterosaurs. Paleobiology 9:218–239.

Padian, K. and J. M. V. Rayner. 1993. The wings of pterosaurs. Amer. J. Sci. 293:91–166.

Pennycuick, C. J. 1972. *Animal flight.* Studies in Biology, no. 33. Edward Arnold, London.

Perry, S. F. 1983. Reptilian lungs, functional anatomy and evolution. Adv. Anat. Embry. Cell Biol. 79: 1–81.

Ritter, D. 1995. Epaxial muscle function during locomotion in a lizard (*Varanus salvator*) and the proposal of a key innovation in the vertebrate axial

musculoskeletal system. J. Exp. Biol. 198:2477–2490.

Ritter, D. 1996. Axial muscle function during lizard locomotion. J. Exp. Biol. 199:2499–2510.

Romer, A. S. 1923. Crocodilian pelvic muscles and their avian and reptilian homologues. Bull. Amer. Mus. Nat. Hist. 48:533–552.

Romer, A. S. 1956. *The osteology of the Reptilia.* The University of Chicago Press, Chicago.

Simmons, A. D., D. R. Carrier, C. G. Farmer, and C. S. Gregersen. 1997. Lack of locomotor-cardiac coupling in trotting dogs. Am. J. Physiol. 273: R1352–R1360.

Suthers, R. A., S. P Thomas, and B. J. Suthers. 1972. Respiration, wing-beat and ultrasonic pulse emission in an echo-locating bat. J. Exp. Biol. 56:37–48.

Thomas, S. P. 1981. Ventilation and oxygen extraction in the bat *Pteropus gouldii* during rest and steady flight. J. Exp. Biol. 94:231–250.

Unwin, D. M. 1999. Pterosaurs: Back to the traditional model? TREE 14:263–268.

Unwin, D. M. and N. N. Bakhurina. 1994. *Sordes pilosus* and the nature of the pterosaur flight apparatus. Nature 371:62–64.

Wang, T., Carrier, D. R. and Hicks, J. W. 1997. Ventilation and gas exchange during treadmill exercise in lizards. J. Exp. Biol. 200, 2629–2639.

Wellnhofer, P. 1978. Pterosauria. Handbuch der Paläoherpetologie, Teil 19. Gustav Fischer Verlag, Stuttgart.

Wellnhofer, P. 1987. Die Flughaut von Pterodactylus (Reptilia, Pterosauria) am Beispiel des Weiner Examplares von Pterodactylus kochi (Wagner). Annal. Naturhist. Mus. Wien 38:149–162.

Young, I. S., R. D. Warren, J. D. Altringham. 1992. Some properties of the mammalian locomotory and respiratory systems in relation to body mass. J. Exp. Biol. 164:283–294.